DISSERTATION

MATERNAL BEHAVIOR BEFORE AND AFTER PARTURITION OF RED ANGUS BEEF COWS AND THE INVESTIGATION OF WOLF PREDATION ON LIVESTOCK POPULATIONS IN THE NORTHERN ROCKY MOUNTAINS

Submitted by

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ABSTRACT

MATERNAL BEHAVIOR BEFORE AND AFTER PARTURITION OF RED ANGUS BEEF COWS AND THE INVESTIGATION OF WOLF PREDATION ON LIVESTOCK POPULATIONS IN THE NORTHERN ROCKY MOUNTAINS

The objective of this dissertation was twofold: 1) define maternal behaviors such as protectiveness and defense towards the offspring after parturition, and 2) examine depredation losses in cattle in areas with high predation pressure. All experiments incorporated the temperament of the animal, measured by the facial hair whorl pattern (HW) on the forehead of the animal.

To define maternal behaviors, we conducted three experiments. 1) Evaluating differences in individual calf defense behavior patterns and maternal protective behavior of beef cows 24 h after calving. 2) Measuring separation distance from the herd for parturition and the relationship between age and temperament on the separation. 3) Analyzing calf birth weights, average daily gain, weaning weight and time until weaning to investigate a possible connection between maternal traits and the physiological body conditions of the calf. The 'Bradbury Land and Cattle' cow-calf ranch near Byers, Colorado, USA collaborated with us for all data collection. Ninety-five percent of cows were commercial Red Angus and the remaining 5% were Red Angus x Hereford commercial crossbreds. Free-ranging multiparous cows (total herd: N = 836; 3-6 years old), kept in an open pasture were used. The single pasture was 320 ha with undulating hills, small bushes (height: 40 - 60 cm) and sandy soil but no trees.

In experiment one, each cow-calf pair was approached with an unfamiliar utility vehicle that circled the pair and gradually decreased the distance to cow and calf (N = 341). Four distance measurements were taken with a digital range finder to evaluate maternal protectiveness: 1)

Approach: the first time the cow raised her head and oriented towards the vehicle; 2) Protection: when the cow placed herself between her calf and the vehicle or lowered her head; 3) Vocalization: when the cow vocalized towards the calf to call it to come closer; and 4) Closest distance: before the cow-calf pair retreated. Calf defense behavior patterns were recorded as yes/no-classifications and were: protection: the cow positioned herself between the vehicle and her calf; aggression: the cow lowered her head; and vocalization. This study showed that 99% of the cows moved between the vehicle and their calf to protect it, 13.2% lowered their heads as a sign of aggression and 78% vocalized. Cows with high HW or multiple HW oriented towards the vehicle at a further distance, compared with cows in other HW groups ($P < 0.05$). Cows with a high HW vocalized at a further distance than cows in other groups. Younger cows (3 years) could be approached more closely with no behavioral changes than older (5 years) cows ($P < 0.05$). The results suggest different levels of vigilance towards the surroundings depending on the HW pattern of the cow.

Experiment two investigated the separation distance from the herd for parturition and the relationship between age and temperament on the separation. By measuring the distance (m) between the birth place of each individual cow and the main herd with a GPS device we could determine the separation distance at parturition (N = 333). The age of a cow influenced the separation distance for parturition ($P < 0.001$). Four year old cows separated on average about 150 m further than other aged cows when calving. Hair whorl position had no influence on the separation distance ($P = 0.405$). In conclusion, separation for parturition is likely affected by the social dominance of cows within the individual herd. Our study shows that more dominant and older cows calve closer to the herd and younger, more inexperienced cows calve further away at random places. About 88% of cows separated over 100 m from the herd. Separation for parturition is an innate behavior of cows and depending on the age, individual differences in separation distance were found.

Experiment three analyzed a possible connection between the temperament, measured by the facial HW, age and body conditions of the cow on physiological traits of the calf. Physiological measurements of the calf were: calf birth weight, gender, ADG, weaning weight and days until weaning. Complete records of 507 cows and calves were analyzed. Calf birth weight and weaning weight were influenced by the gender of the calf ($P < 0.001$; steers were heavier than heifers) and by the cow weight ($P < 0.001$; heavier cows give birth to and wean heavier calves). There was a tendency of HW to affect the birth weight ($P = 0.093$; cows with middle HW gave birth to the heaviest calves) and an effect on weaning weight ($P = 0.043$, cows with abnormal non-spiral HW weaned heavier calves compared with normal round spiral HWs). The age of cows had no effect on calf birth weight ($P = 0.593$) but affected the weaning weight ($P < 0.001$). Older cows wean heavier calves. Further, the body conditions of calves depend on the physiological constitution of the cow. Selection towards cows with abnormal HW should however be prevented because earlier findings reported sperm abnormalities in bulls with abnormal HW.

The second emphasis of this dissertation was to examine depredation losses of cattle in areas with high predation pressure. Depredations are not occurring in Colorado so far but neighboring States of Yellowstone National Park (YNP), such as Montana, Idaho, and Wyoming face great losses since the reintroduction of Canadian gray wolves in 1995. We analyzed depredation of calves near Council, ID in 2011. A herd of 588 Black Angus x Charolais crossbreds (age range: 5-17 years old) was used for observations. We identified a connection between the HW, the age of a cow and the depredation loss ($P < 0.001$). The HW of a cow significantly influenced the probability of losing the calf to predation ($P < 0.001$). Cows without the facial HW faced the highest number of losses (probability of 19.6% of losing the calf) compared to other HWs (probability between 0 – 6.1%). We also found an age effect on the probability of losing the calf ($P = 0.023$). Cows over the age of 10 years have an increased probability of losing their calf to predation. Our findings suggest that behavioral differences between cows with different HWs exist. Differences in protectiveness or vigilance towards the surroundings in cows without a facial HW may lead to an increased probability of losing the calf to predation.

The results of this dissertation indicate that cows vary in maternal protectiveness and calf defense. Individual differences can be attributed to differences in temperament measured by the facial HW on the forehead of cows. When giving birth, younger cows separate further from the herd whereas older cows stay closer to the herd and the feeding ground. This finding likely represents the dominance structure within the herd. The HW did not affect the calving location. After parturition, cows with high and multiple HWs paid the most attention to their surroundings compared with other HW which may give these individuals more time to react in case of a predator approach. Even though there are so far no wolves in Colorado, cattle herds near YNP face great losses. Our results showed that cows without a HW are more likely of losing the calf to predation than cows with other HWs. We can only speculate about the reasons for the highly increased probability of losing the calf because no research in this area is available. The embryonic development or especially any deviation from a normal development may give insights into answering this question. Ongoing research in the areas of predator-prey/livestock interactions, human-wildlife conflict and animal behavior will be needed to support carnivore conservation and maintain ranch practices.

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Science is Life,
but there is more in Life than Science!

DEDICATION

I dedicate this dissertation to my grandpa, Karl Flörcke, who passed his love for animals on to me.

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CHAPTER 1

REVIEW OF LITERATURE

1. Introduction to the History of Domestication and Selection

Proximity to humans, rearing environment and number of offspring of modern livestock species changed during the course of evolution. Most reproductive behaviors, however, remained constant throughout this period (Diamond, 2002). To successfully reproduce, copulation and fertilization, healthy pregnancy, delivery, protection and upbringing of the offspring need to take place. Over the millennia, animals adapted to environmental challenges and changes by natural selection. Domestication required adaptation to faster changing conditions. This put additional new demands on the animals by artificial selection (Price and King, 1968; Price, 2002). Successful domestication required individual and genetic adaptation to captive environments. Better adapted animals reproduce more successfully which caused long-term genetic alterations. Only, six percent of ungulates and elephants are domesticated (Tennessen and Hudson, 1981) which shows the difficulties of domestication. Failure of domestication occurs due to the following reasons. They are: hard to supply diets, slow growth rates, poor reproduction, dangerous behaviors, unwillingness to breed in confinement, lack of a dominance hierarchy or following behavior and the tendency to panic in enclosures (Diamond, 2002).

Human societies tamed certain animals for food, leather, social and symbolic purposes (Vigne, 2011). After a few generations, various behavioral and physiological changes occurred, such as reduced aggressiveness (Carlborg et al., 2006). Domesticated silver foxes showed changes in fur color, tail position, ear shape, stress, sexual physiology as well as behavior

(Belyeav, 1979; Belyeav et al., 1981). The domesticated silver foxes showed less aggressiveness towards humans and could even be petted. Many production improvements resulted from domestication of livestock; such as higher milk yield in dairy cows (Rendel and Robertson, 1950), improved breeding (Goddard and Hayes, 2009) and increased weight gain of calmer cattle (Voisinet et al., 1997). However, further studies involving modern genomics and behavior are required to understand the connection between genotype and phenotype. This may assure the sustainability of breeding programs by reducing negative side effects (Jensen and Andersson, 2005; Goddard and Hayes, 2009).

An emerging problem is the loss of genetic variability due to directed selection towards production traits without preservation of the overall genetic diversity (Dobney and Larson, 2006). Various negative effects evolved in non-livestock species due to inbreeding. Selection and inbreeding altered courtship behavior of *Drosophila melanogaster* (Sharp, 1984) and guppies (Mariette et al., 2006), as well as parental behaviors of mice (Margulis, 1998). Livestock producers focused on increased productivity of their animals and selection programs were designed to reach this goal (Price, 1999). Undesirable side effects were clinical lameness in cows (Boettcher et al., 1998), piglet crushing in sows (Fraser, 1990), neonatal mortality in sheep (Lindsay, 1996) and leg weakness in chicken with abnormally large breasts (Kestin et al., 1992). In recent years, farmers reported increasing mothering problems with overly calm beef cows and cases of calf starvation and neglect. Selection programs ignored maternal behaviors when selecting for specific reproduction traits. Today, Holstein cows are less fertile and difficult to breed. Occurring hereditary diseases in the increasingly narrow gene pool raise the question of cattle, goats and sheep become the next endangered species (Taberlet et al., 2008). The underlying cause for the above listed problems is the connectedness of traits (Macneil et al., 1984) and the nescience of people selecting for certain characteristics, while ignoring the consequences. Increasing mortality rates related to overly intensive selection continue to compromise animal welfare as well as economic profitability.

An improvement in production traits through selection programs is immediately visible. The consequences of these programs on maternal behaviors of livestock species are however largely unknown. Measuring maternal behavior of cattle requires long labor intensive observational periods, thereby discouraging new research. The following sections will provide an overview of the maternal behaviors pre- and post-parturition of cattle and other domestic animals. It will discuss maternal influences on production traits of the calf, incorporate the relationship of the hair whorl pattern on temperament and behavior and highlight the recently occurring problems with increased wolf predation losses of cattle (depredation).

2. Maternal behavior

Maternal behaviors describe the maternal care directed towards the offspring occurring before and after parturition. With those behaviors we associate the delivery, responsiveness, attentiveness and concomitant care to guarantee greatest possible survival of the young (Buddenberg et al., 1986). In cattle, important maternal behaviors before, during and after the birth of the young include separation from the herd to guarantee isolated parturition, cleaning, stimulation of the newborn to motivate suckling and establishing the maternal-offspring bond (Leuthold, 1977). Imprinting between cow-and calf is particularly important because Lent (1974) found that parturition often attracts other conspecifics and even males which may lead to less well developed mother-young bonds (Edwards, 1983; Illmann and Spinka, 1993; Owens et al., 1985). Licking by conspecifics can even lead to desertion of the newborn calf (Edwards, 1983). However, allowing a cow and calf a minimum contact period of five minutes after parturition will enable the formation of a strong maternal bond (Hudson and Mullord, 1977). This bond even persists if the calf is removed for 12 h and then returned (Hudson and Mullord, 1977), but most cows cannot recognize their calf after 24 h. Expressing adequate maternal behaviors is important for both, the survival of the young and efficient and profitable production for the livestock industry.

In extensive pasture conditions, the expression of strong maternal behaviors is essential (Simm et al., 1996). Attempts to increase fecundity and profitability in unnatural environments put increased stress on maternal behaviors, leading to failures (mismothering) and inefficiency (Mellor and Stafford, 2004). For example, high stocking intensities in sheep lead to lowered lamb survival because of starvation and mismothering compared to lower stocking intensities (Robertson et al., 2012). Modern swine productions often keep sows in farrowing crates for parturition which limit maternal behaviors due to space confinements and lack of straw or other substrates for nest building. Providing straw and branches in a semi-natural environment enables sows to engage in nest building behavior before parturition (1-7 h). This increases time spend in lateral recumbency (Damm et al., 2000). Genetic selection for maternal behaviors at farrowing may reduce piglet losses and stillbirths without negatively affecting the total number of piglets born (Leenhouwers et al., 2003). The pre-lying behaviors of sows are important for piglet survival. Sows that perform ‘sniffing’, ‘looking around’ and ‘nosing’ before lying down are less likely to crush piglets compared to sows that don’t perform these maternal behaviors (Wischner et al., 2010). Additionally, sows that did not crush piglets were more restless pre partum and more frequently engaged in nest building behaviors than calmer sows (Wischner et al., 2009). Fortunately, industry standards are changing and progressive producers are remodelling their facilities and move away from crates to open housing which improves animal welfare (Tonsor et al., 2009).

Dairy operations usually separate calves from their mothers within the first 24 h after parturition. This raises the question: do these calves experience maternal deprivation? (Latham and Mason, 2008). Separation of the cow and calves allows grouping lactating cows together for milking while keeping calves in individual pens. Possible negative effects of the isolation on the calf are agonistic social behaviors when encountering other calves later in life (Le Neindre and Sourd, 1984) and reduced maternal behaviors when these calves become parturient themselves (Donaldson et al., 1972; Le Neindre, 1989). The reason farmers separate the cow and calf at this early stage is to reduce diseases in calves (Nielsen, 2009) and to increase production efficiency of the cows. Animal welfare concerns about the early separation of cow and calf are growing. Under natural conditions, cows isolate themselves from the herd for parturition and hide their calves in proximity after birth. A cow-calf bond forms immediately after parturition and the cow and calf engage in frequent licking, sniffing and social contact (Jensen, 2011). However new research shows that allowing cow and calf to stay together for the first two weeks after parturition has positive effects (Flower and Weary, 2001). Calves that had prolonged maternal contact gain more weight, develop better social behaviors and are less fearful. A second study about the effects of early separation on the dairy cow and calf by Flower and Weary (2003) additionally showed that the cow's health and productivity can be positively affected by the presence of the calf.

In ungulates, Walther (1965) described the relationship between a dam and her newborn, and he made the clear distinction between "follower"- and "hider"-species. Follower-type young are able to follow the dam shortly after birth, whereas hider-type young stay in between bushes when the dam forages nearby. Saiga antelope (*Saiga tatarica*; Singh et at., 2010) and wildebeests (*Connochates taurinus*; Estes, 1976) are both follower species, which have aggregation behavior and breeding synchrony. Aggregation of many females allows for greater offspring survival because the females actively engage in group defense. Caribou (*Rangifer tarandus*; Rettie and Messier, 2001) and moose (*Alces alces gigas*; Bowyer *et al*., 1999) are a hider species. They separate from the herd for parturition and give birth unaccompanied which reduces predation and intraspecific aggression (Lent, 1974).

Cattle are a hider species, typically leaving calves between shrubbery for cover (Langbein and Raasch, 2000). Research by Torriani et al., (2006) suggests that in followers, such as domestic sheep and reindeer, acoustic mother-offspring recognition is mutual. On the other hand, it is unidirectional in hider species such as fallow deer, where fawns can recognize the mothers' voice but the dam cannot recognize the fawn. Similar results have been found in dairy cattle. After separation from the cow, calves can distinguish calls from the birth mother but the cows have difficulty recognizing their own calf (Marchant-Forde et al., 2002). Nonetheless, the follower-hider relationship needs to be seen as a continuum (Ralls et al., 1986) with varying occurrence of the behavior in different species. For example cattle may make use of either follower or hider behavior depending on environmental cues and management.

2.1. Pre partum behaviors

Cows, sheep and goats that are not parturient congregate and graze in social groups. The onset of parturition is often accompanied with a change in congregation behavior and pregnant female will separate from the herd to give birth in isolation (Lickliter, 1985; Keyserlingk and Weary, 2007). The study of Lidfors et al., (1994) examined behavior at calving, choice of calving place and the influence of different environments on dairy cattle in a grass pasture (35 ha). In their study, cows increased the nearest neighbor distance and younger cows separated further from the herd than older cows. Cows prefer shelters over open areas during parturition (Arthur, 1961; Lidfors et al., 1994). Following social isolation, some cows perform nest-building-like behaviors. Wehrend et al., (2006) observed nest-building behaviors pre partum, even though in the study cows were housed inside and transferred into individual calving boxes for parturition. In the calving boxes, 93% of cows performed an intensive olfactory check of the ground which turned into nest-building behaviors in 48% of all animals. Cows perform nest-building by moving straw in the box with their head and front limbs and varying degrees of restlessness accompany this behavior. During the pre partum period, dairy cows frequently change their posture between standing and semilateral recumbency, with reduced drinking and ruminating (Houwing et al., 1990).

Similar behaviors such as pawing the ground, restlessness and social isolation before parturition are also frequently seen in goats (Lickliter, 1985) and sheep (Arthur, 1961; Arnold and Morgan, 1975). Parturient females often become intolerant of conspecifics, especially other females. This explains the urge to actively separate from the herd. With approaching parturition, restlessness usually increases and lying and walking occurs interchangeably (Arnold and Morgan, 1975). The normal duration for parturition, defined as the time when heavy contraction starts until delivery, in cattle is 30 min to 4 h (Neary and Hepworth, 2005). Sheep have a slightly shorter parturition time (1min to 3 h; Arnold and Morgan, 1975) with frequent twin pregnancies and swine deliver piglets every 10 to 20 min (Neary and Hepworth, 2005).

In extensive pasture systems, cows prefer dry soft bedding as a parturition site (Lidfors et al., 1994). Other ungulates, such as water buffalo (*Bubalus bubalis*; Tulloch, 1979) search for cover by woody vegetation. American Bison (*Bison bison*; Lott and Galland, 1985) prefer cover by oak trees. The environment a cow chooses for parturition is the most important criteria for offspring survival. Inherent genetic variation between individual cows lead to different choices in birth sites with some being superior with higher availability of cover and resources than others. Therefore, maternal care starts prior to parturition and is not restricted to post partum behaviors.

In general, cows show a considerable degree of plasticity in pre parturient behaviors. External influences such as nutrition, climate, landscape ecology and predation pressure affect the choice of parturition site and the expressed behaviors (Poindron and Le Neindre, 1980). Despite the former influences on selection of the parturition site, endocrine and neuronal changes occurring before delivery are similar between individuals. In sheep, changes in the plasma concentrations of progesterone, oestradiol and the release of oxytocin in the brain trigger maternal behaviors (Nowak et al., 2000). Together, these changes in hormone levels induce maternal responsiveness towards signals from the offspring, and nursing behaviors (Grandinson, 2005). Females express endogenous opioids, such as endorphins, from the central nervous system during birth, starting up to 12 h before parturition (von Borell et al., 2007). These opioids modulate pain reception by raising the nociception threshold (Blood and Studdert, 1988) and are potent analgesics. Before birth, the endogenous opioid concentration rises in several mammalian species, such as: humans (Cogan and Spinnato, 1986), cattle (Aurich et al., 1990), sows (Jarvis et al., 1997), goats (El-Anwar, 1993) and rats (Wardlaw and Frantz, 1983). Increased opioid levels are probably an endogenous defense against the pain of parturition. In cows, the pulse, respiratory rate and body temperature rise immediately before parturition. The pulse reaches 70 to 90 beats per minute, respiratory rates result in values of 100 to 120 per minute and the temperature can reach up to 103/104℉ (39.5/40℃; Arthur, 1961).

2.2. Post partum behavior

In extensive systems, pregnant cows separate from the herd for undisturbed parturition which helps to guarantee imprinting between mother and newborn (Edwards and Broom, 1982; Lindsay, 1996). Different studies examined the time of day when calving occurred but results were ambiguous and not concise. The study by Edwards (1979) found no bias towards day or night calving whereas Keyserlingk and Weary (2007) reported increased calving rates in the late afternoon and evening. Both of these findings may be due to different management practices. Parturition involves increased restlessness and cows frequently lie down and stand up. Interestingly, the delivery position directly affects calf survival. Approximately 4.% of *Bos indicus* calves delivered in a recumbent position die, and this number increases to 16.1% if delivered while standing (Paranhos da Costa et al., 2006). The delivery position can be affected by: 1) the lack of calving experience and 2) the presence of predators near the parturition site (Toledo, 2005; Paranhos da Costa, 2008a). Naturally, cows get nervous when predators are in the surroundings.

Following a normal birth (eutocia), typical post partum behaviors include licking the neonate, absorbing fetal fluids and consuming birth membranes (Arthur, 1961). The olfactory bulb largely controls the development of maternal behaviors (Fleming and Rosenblatt, 1974). Birth fluids and membranes are usually repulsive to females (Lévy et al., 1983; Lévy et al., 2004), but become temporarily attractive during the sensitive period after parturition (Gonyou and Stookey, 1987; Machado et al., 1997a; Lévy and Keller, 2009). This highlights the importance of cleaning. After birth, cows often engage in placentophagia (Edwards and Broom, 1982). The increased attraction to birth fluids and membranes starts about 12 h before parturition (von Borell et al., 2007) and lasts up to 24 h after birth (Machado et al., 1997b). By consuming the amniotic birth fluids, but not the placenta, cows raise their nociception response (Machado et al., 1997a). Nociception, in general, is the perception of potentially damaging stimuli or pain by sensory receptors. Consuming birth fluids helps relieve pain which may assist the cow in caring for her newborn immediately after parturition (Machado et al., 1997a).

In sheep, producers associate intensive licking, grooming and close proximity between lambs and mother throughout lactation with superior maternal abilities (Dwyer, 2008). Mutual vocal communication and suckling by the calf within the first hours after parturition are the most important behaviors. These behaviors increase survival of the neonate by establishing a close bond between the ewe and her lamb (Nowak, 1996). Weaker expression of the previous behaviors often leads to starvation or neonatal mortality of the lamb(s) (Dwyer, 2008). Hormonal changes in the post partum period support maternal behaviors (Nowak et al., 2000). By absorbing the fluids and membranes the dam “learns” the individual smell of her newborn and this facilitates imprinting. The dam usually starts licking the head of the newborn to remove fetal membranes which sometimes cover the nose and could lead to suffocation. Additionally, licking dries off the newborn, improves blood circulation, stimulates teat-seeking and helps bonding (Le Neindre et al., 2002).

In cattle, different individuals express maternal behaviors to varying degrees depending on the breed. Hoppe et al., (2008) compared the maternal protective behavior score (MBS) of German Angus and Simmental cattle 24 h after parturition during routine handling procedures, such as ear-tagging and weighing. Cows scoring a 1 behaved indifferently during the procedures performed by the stockman and stood quietly, whereas cows scoring a 5 were dangerous and attempted to push the handler away from the calf. These results indicated that German Angus cows paid more attention to their calves and had a higher tendency to interfere with the handling procedures than Simmental cows. Further, the lactation number of Simmental cattle significantly influenced MBS, with younger cows being more docile than older cows (Hoppe et al., 2008). Originally, Simmental cattle were reared as a dual-purpose breed for milk and beef production which may explain the lower MBS scores. Selection of Simmental cattle has likely influenced their temperament and reduced maternal protective behaviors after parturition.

In dairy breeds, calves are usually separated from the cow shortly after birth. The study of Le Neindre (1989) compared Friesian dairy cows with a beef breed (Salers) and their study showed differences in the expression of maternal behaviors exhibited by both breeds. The beef breed showed more maternal behaviors than the dairy breed (Selman et al., 1970; Le Neindre, 1989). Beef cows also left the herd more readily for parturition than dairy cows (Lidfors et al., 1994), suggesting reduced maternal abilities in dairy cows due to selection and management practices. In the study discussed above by Hoppe et al., (2008), Simmental cattle were more docile after parturition than German Angus. In summary, dairy breeds express lower maternal abilities. Beef calves also stand up and suckle much sooner than dairy calves (Selman et al., 1970; Arave and Albright, 1981). Further, when comparing mothering ability and milk yield, older cows outperform younger cows which can partly be attributed to maternal experience (Drewry et al., 1959).

One of the primary factors of maternal ability is the willingness and motivation of the cow to protect the calf after birth. Buddenberg et al., (1986) measured maternal behaviors on a scale from 1 to 11 while catching, weighing and tattooing the calf, with one being the most aggressive and 11 being the least attentive. The different breeds in their study were: Angus, Hereford, Charolais and Red Poll cows. Mean maternal behavior scores were: Angus: 5.3, Hereford: 6.2, Charolais: 6.0 and Red Poll cows: 5.7. Buddenberg et al., (1986) interpreted Angus cows as being more attentive towards their calves and more aggressive towards caretakers compared to the other breeds. Le Neindre et al., (2002) reported a weak positive genetic relationship between reactivity to humans and maternal behaviors in Limousin cattle tested in a docility test. Cows that licked their calf longer showed less reactivity during human handling (Le Neindre et al., 2002). Handling the calf immediately after birth is necessary for most routine ranch procedures (Turner and Lawrence, 2007) such as ear-tagging, weighing or applying castration bands. Skilled handling is required to perform these procedures without creating fear and aggression in the dam (Boivin et al., 2003; Boissy et al., 2005). Depending on previous experiences with husbandry and the suddenness, proximity, duration or intensity of the handling, the dam may create a negative memory in relation to these events (Boissy, et al., 1998; Désiré et al., 2002). Once learned, fear-related responses can be stable over time with a high degree of consistency across situations (Burrow, 1997; Ball et al., 2002). Long or painful procedures, such as bull castration in the squeeze chute, can lead to life long avoidance behaviors and fear when run through the squeeze chute for routine handling. Therefore, it is important to avoid creating fearful negative memories during routine handling procedures.

Further, the genetic background and epigenetic factors, such as early experiences and influences, can interact and create fearfulness (Boissy, et al., 2005).

However, attentiveness and aggression are not a continuum of behavioral traits, as introduced in the study by Buddenberg et al., (1986). Rather, they are two separate behaviors processed in separate brain regions. The basal ganglia and the ventral striatum process aggressive behaviors. Attention incorporates two pathways in the brain (Ungerleider and Mishkin, 1982). A ventral pathway ('what'-pathway) processed in the temporal lobe and a dorsal pathway ('where'-pathway) involving the parietal lobe. The brain automatically analyzes the nature, location and potential danger of each stimulus. Attention and aggression are highly connected behaviors, but comparing them on a single continuous scale is not recommended. A cow that is attentive towards her surroundings after parturition (Flörcke et al., 2012) may not necessarily be aggressive towards caretakers.

High maternal motivation to protect and care for the newborn improves calf survival. However, in neonates, adapting to the extra-uterine environment and getting up to suckle shortly after birth is just as important. Failure to suckle quickly after birth can cause insufficient colostrum intake, causing the calf to be more susceptible to infections, dehydration or starvation (Nowak, 1996). Weak teat seeking behavior may also cause delayed bonding with the mother and possible separation from her (Nowak et al., 2000). Failure to bond increases neonatal mortality and causes large economic losses (Paranhos da Costa et al., 2008b). Good cow-calf interactions during the first hours after calving are crucial for calf survival. Younger, inexperienced cows may show aggression towards their calf and cow aggression can lead to avoidance by the young. Schmidek et al., (2006) found that calf directed aggression was more frequent in primiparous (55.7%) than in multiparous cows (22.0%). This resulted in a failure to suckle within the first 3 hours in 15.7% of primiparous and 5.7% of multiparous cows. Other causes of failure to suckle within the first 3 hours are big udders, enlarged teats or calf birth weights lower than 25kg as shown in newborn Guzerat cattle by Schmidek et al., (2008). These findings reinforce the importance of proper maternal behaviors after parturition to achieve the highest reproductive performance. Further, the individual temperament of a cow can influence calf survival which will be discussed in the next section.

3. Influences of temperament traits on cattle production

Increased selection for favorable production traits causes a change in behavior (Brouček et al., 2008). Selection for cattle with a calm temperament has increased during the last 15 years. In 1991, Limousin breeders indentified reducing dangerous dispositions as the number one priority in cattle breeding. By using docility tests, they put strong emphasis on selection towards calmer cattle and the temperament of Limousin cattle improved drastically (Hyde, 2010). Cattle with a calm temperament have higher average daily gain (ADG) compared to animals that become highly agitated during restraint in the squeeze chute (Voisinet et al., 1997). Gauly et al., (2001) estimated genetic variability in temperament traits in German Angus and Simmental cattle and confirmed that very excitable cattle have reduced ADG compared to calmer cattle. In their study, Simmental cattle had slightly higher temperament scores than German Angus cattle, suggesting a more easily excitable temperament.

Cattle show a considerable amount of behavioral variability during handling and in different management practices. These behavioral variations reflect individual differences in temperament and reactivity to stimuli. Temperament is consistent over time and within different environments with predictable behaviors (Grandin, 1993; Morris et al., 1994; Gosling, 2001; Sih et al., 2004) and a moderate heritability (German Angus 0.61 ± 0.17, Simmental 0.59 ± 0.41; Gauly et al., 2001). Possible methods to measure temperament of cattle are (1) agitation score (2) flight speed score (3) exit score from a squeeze chute as well as (4) the spiral hair whorl pattern (HW) on the forehead of the animal. The agitation score (1) is recorded while the animal is restrained in the squeeze chute and it can range from 1 to 5 (Grandin, 1993). Animals that receive a score of 1 were calm and stood still and animals ranked as 5 were rearing, twisting their body and struggling violently. However nowadays, most large ranches use hydraulic squeeze chutes which restrain the animal more tightly, making assessment of animal movement difficult. An alternative measure for temperament while the animal is in the squeeze chute is to locate the position of the spiral hair whorl pattern (4). Animals with high HWs, located above the upper eye-line, are more easily agitated during restraint whereas cattle with lower HWs below the lower eye-line are calmer (Grandin et al., 1995; Randle, 1998). Another method is to measure the exit score of an animal when leaving the squeeze chute (3). Four categories of exit scores exist: walk, trot, canter and run (Vetters et al., 2012). Usually, the exit score is determined by one observer and therefore, represents a more subjective method. Vetters et al., (2012) found a day effect and an observer effect when comparing exit score values over several days. Different observers may interpret the exit score differently and the day effect may have been related to different people handling the cattle in different ways. A more reliable method is to measure the flight speed (2) when the animal leaves the squeeze chute. Infrared sensors determine the time that an animals needs to traverse a fixed distance after exiting the squeeze chute and calculate the flight speed. Müller and von Keyserlingk (2006) found that individuals with faster flight speeds have reduced weight gain compared to individuals that leave the squeeze chute with slower flight speeds. Flightier individuals are more easily agitated whereas slower animals are calmer. Also, flight speed is consistent over time and may be used to indicate animal temperament. The research by Vetters et al., (2012) agreed with the findings of Müller and Keyserlingk (2006). Flight speed is a more robust measure because human errors are avoided with this technology but the Vetters et al., (2012) study indicates that exit score is a reasonable alternative for use on ranches where electric technology is not available. Livestock producers frequently use several methods to measure an animals' temperament. In summary, the above mentioned techniques for temperament assessment are reliable over time and serve to predict differences in ADG and behavior.

Selecting animals according to their temperament has huge economic implications. The industry prefers calmer animals which reduce the number of injuries caused by overly agitated cattle and makes handling easier. Human-cattle interactions, safety, welfare, herd productivity and meat quality all profited from selection programs incorporating temperament (Fordyce et al., 1988; Grandin, 1993; Brouček et al., 2008). More easily agitated animals have tougher meat and a higher incidence of borderline 'dark cutters' (Voisenet et al., 1997). The term 'dark cutters' refers to a dark red or almost black meat color. Stressed animals have a depletion of glycogen in the muscle and increased muscle pH. These metabolic changes reduce shelf life and consumers associate poor quality, toughness and bad flavor with darker meat.

Genetic correlations between temperament and the height of Japanese Black cows suggested that shorter and fatter cows have a more desirable temperament than taller cows (Oikawa et al., 1989). However, selecting animals solely based on their behavioral characteristics or a desired phenotype can be problematic as discussed in the example of the silver foxes by Belyeav (1979). A better approach is to identify individual genes or markers for certain traits, such as fearfulness to humans. Studies with laboratory mice identified quantitative trait loci (QTL) which are directly linked to fear states (Plomin et al., 1991; Wehner et al., 1997). QTL analyses helped to detect fear related responses in other animal species, such as cattle (Davis and Denise, 1998; Haley and Visscher, 1998). Fischer et al., (2001) discovered several genetic markers which are linked to behavioral and physiological responses towards humans in Limousin-Jersey crossbred cattle. Fischer et al., (2001) linked flight speed, plasma cortisol levels and urine cortisol concentrations to several specific QTL. In addition, Schmutz et al., (2001) linked the reactions of calves towards humans to seven QTL. Direct selection for cattle with reduced fearfulness to humans may be possible with the advances in marker-assisted selection (MAS; Davis and Denise, 1998). This could have great promise in ruminant livestock selection. Cattle would cope better with stressful situations on farms and during transport and fear-based self-injury rates should decline. Ultimately, the welfare of these genetically selected animals would be improved. The effects of MAS would be more substantial on extensive ranches were animals do not have daily human contact. In intensive systems, MAS is less important because animals establish a positive cattle-human connection by daily exposure (Boivin et al., 1992; Estep and Hetts, 1992; Krohn et al., 2001; Hemsworth, 2003; Boivin et al., 2009). By handling and stroking calves every day during an early period of life they were never aggressive to humans later in life (Boivin et al., 2003; Boivin et al., 2009). On the other hand, fearful associations with handling early in life can persist throughout the lifetime of an animal causing problems during future handling events. However, caution is recommended in selection programs. Reduced fearfulness to humans may also reduce fearfulness to predators which will be discussed in section 5. Before incorporating certain traits in selection programs the relationship between experience and genetics needs to be further investigated since they can limit the effectiveness of the selection (Torres-Hernandez and Hohenboken, 1979). Cattle with Brahman genetics are usually more reactive to humans than British breeds, such as Hereford and Angus. However, handling Brahman cattle early in life resulted in docile individuals (Torres-Hernandez and Hohenboken, 1979), indicating that experience can shape the reactivity to a stimulus.

4. Maternal influences on physiological traits of the calf

Before identifying quantitative trait loci (QTL) and temperament selection, the industry focused on increasing reproductive performance by selecting for preferred phenotypes and increased meat yield per animal, as discussed in section 3. Early research from the 1950s refers to maternal ability by stating the birth- and weaning weights of calves (Dawson et al., 1947; Gregory et al., 1950). Even in the 1970s maternal effects were referred to as milk yield of the cow (Koch, 1972). Physiological traits and body condition score (BCS) of a cow directly affect calf traits such as birth weight, ADG and weaning- and yearling weight (e.g. Gregory et al., 1950; Koch, 1972; Bourdon and Brinks, 1982; Holland and Odde, 1992). Moreover, the nutrition of the dam during and after pregnancy influences the calf’s health and productivity (Nowak et al., 2012).

Research in the past focused on post partum nutritional requirements, milk production of a cow and the impacts on daily gain of the calf. Newer research is starting to look at the nutritional needs of cows during pregnancy and especially the long-term effects of malnutrition during certain critical periods of gestation on the fetus (Funston et al., 2010). During early pregnancy, the fetus undergoes differentiation and organogenesis. During this phase, the size, morphology and nutrient transfer capacity of the placenta have major influences on development (Belkacemi et al., 2010). The term ‘fetal programming’ refers to the general idea that environmental effects on a developing fetus can change certain physiological parameters. Such changes may even persist into adulthood, resulting in trans-generational effects. Negative effects due to undernutrition of the dam on the fetus have been shown in humans (Belkacemi et al., 2010), sheep (Swanson et al., 2008; Field, 2012) and cattle (Hyttel et al., 2000; Summers and Funston, 2011). Even in birds, early nutritional stress affects adult exploratory behavior which is a representative measure for temperament, resulting in trans-generational effects on the next generation (Krause et al., 2009). The general theory predicts that the fetus can adapt to poor nutrition during gestation by altering its gene expression (Breier, 2006). This compensatory effect allows survival of the fetus in harsh early environments. Further, the alteration of gene expression maximizes the uptake and utilization of nutrients which often leads to compensatory growth.

Recently research shows a connection between fetal programming and skeletal muscle development in ruminants (Du et al., 2010). Undernutrition during fetal development reduces skeletal muscles fiber numbers, leading to altered muscle fiber composition, increased fatness and a reduced growth performance of the progeny (Du et al., 2010). Nutritional supplementation, on the other hand, improves fetal skeletal muscle development and adipogenesis. This may improve marbling in progeny and it would further directly improve the eating quality of meat.

In humans, fetal programming in combination with maternal undernutrition and perinatal infections can even influence reactivity to stress, behavior and increase the vulnerability to cognitive disorders (Hornig et al., 1999; Bilbo and Schwarz, 2009; Shi et al., 2009). A study in sows showed that stress experienced during gestation had long-lasting effects on offspring daughters, including their altered maternal behavior (Jarvis et al., 2006). Evidence for a behavioral transmission of post partum behavior from mother to female offspring exists. Stress during pregnancy in humans (Meaney, 2001) and mammals (Champagne, 2008) can influence developing neural pathways which control the expression of fearfulness (Caldji et al., 1998). Early post partum behaviors in rats and mice include licking and grooming (LG) of the offspring which helps form the maternal bond. However, depending on the amount of LG, the offspring has altered levels of hypothalamic oxytocin receptor binding (Champagne et al., 2001). The result is that low-LG offspring show reduced oxytocin receptor binding during their post partum period. Usually, estrogen and oxytocin work together during parturition by promoting a response to the physiological and behavioral demands of the offspring (Champagne, 2008). Consequently, low-LG females show less maternal care and this characteristic transfers to the next generation. These findings suggest that the behavior of mothers can directly shape the neuroendocrine and behavioral responses of the offspring at parturition and when exposed to stress (Meaney, 2001).

Trans-generational effects of maternal care in domestic livestock have not been documented. However, over the years, ranchers have reported increasing mothering problems with extremely calm cattle and even calf starvation and neglect. In sheep, proper maternal care often fails in twin pregnancies and this can compromise the survival of the newborn. The odor of monozygotic twins is more similar than that of dizygotic twins, thereby complicating discrimination between monozygotic twins for ewes (Lévy and Keller, 2009; Romeyer et al., 1993). New Zealand Merino and Romney sheep display poor maternal abilities (Whately et al., 1974) and twin-bearing Dorset Hom and Border Leicester ewes show low levels of maternal care (Alexander et al., 1983), compared to crossbred sheep with better maternal abilities. Romanov ewes on the other hand are known for their shy behavior measured by weak exploration and superior maternal abilities (Boissy et al., 2005). A recent multibreed sheep study in Brazil found a polymorphism (genotype AA or AB) in the aromatase gene (*Cyp 19*) affecting growth, reproduction and maternal ability. Genotype frequencies are 0.64 AB and 0.36 BB. Ewes with genotype AB have higher maternal abilities, defined by lamb birth weight, weight gain and weaning weight (Lôbo et al., 2009). Different breeds show differences in expressing maternal behavior at parturition and throughout lactation. Blackface sheep are more vigilant and Suffolk sheep allow more sucking bouts (Pickup and Dwyer, 2011). Age and parity of the dam (Koch and Clark, 1955), experience (Mangurkar et al., 1984) and the environment (Azzam et al., 1993) further affect survival and body condition of the offspring.

During the last decade, livestock populations in extensive areas in the Northern Rocky Mountains and Canada had to face a new challenge of reintroduction of a top-order predator, the wolf (*Canis lupus*; Bangs and Fritts, 1996). Expressing good maternal behaviors suddenly became a major importance. In the following section, I discuss ecosystem advantageous as well as disadvantages on local populations of livestock.

5. The ramifications of wolf reintroduction on livestock behavior and well-being

In the 1960s, wolves were essentially extinct after Theodore Roosevelt called them ‘the beasts of waste and destruction’ and allowed their persecution and extinction throughout the United States (White, 2011). Even though other predators such as bears and cougars were still present, calf losses were low. Back then, the scientific literature defined maternal ability as milk yield and birth weight, but expression of protectiveness towards the offspring was neglected.

Official reintroduction of Canadian wolves in the Yellowstone National Park (YNP) and central Idaho occurred in 1995/96 (Bangs and Fritts, 1996). In Idaho, a ‘quick-release’ method was used. This meant capture, transport and release with a minimum amount of handling and expense. Wolves transferred with this method traveled long distances from the releasing sites, and most of them survived and pair-bonded, afterwards. In YNP, a ‘slow-release’ method was chosen. Wolves were checked for health issues and stayed in large pens for several months for acclimatization. These wolves maintained the cohesiveness of their packs, settled close to the releasing sites and reproduced sooner (Bangs and Fritts, 1996). The wolf recovery plan estimated a minimum number of 122 wolves in Idaho and 116 wolves in YNP by the end of 1998 (Bangs et al., 1998). However, wolf numbers at both releasing sites progressed faster than expected (about 17% annual growth; Smith and Bangs, 2009) and populations became established after only two years instead of the predicted 3-5 years. A few years after the release, wolves were preying mainly on elk (90%), but kill rates on livestock were slightly higher than expected (12-15 ungulates/wolf/year instead of 12; Bangs, et al., 1998). Even though the wolf predation behavior was expected to stay constant over time, the almost exponential increase in wolf numbers resulted in greatly increased livestock losses. When preying on domestic livestock in the Northern Rocky Mountains, sheep were mainly killed (68%), whereas in Canada, the most predated livestock species was cattle (95%; Musiani et al., 2003). Musiani et al., (2005) found a seanonal pattern of predation on livestock (depredation). In the United

States, losses were higher from March until October, peaking in August, and depredation was lower from November to February. Typically, the cattle's grazing period is from May to October (Oakleaf, et al., 2003) and calving season starts in early March. It is likely that depredation on cattle starts during calving season, when calves are young, inexperienced and easy prey, and lasts until the end of the grazing season. During the winter months, wolves mainly prey on wild ungulates and their offspring.

Despite occurring depredation of cattle during recent years, the wolf recovery plan greatly improved the ecosystem in the Northern Rocky Mountains (Hebblewhite and Smith, 2010). The prior removal of a top predator disturbed terrestrial ecosystems by disrupting vegetative communities which are often dynamic (Terborgh et al., 1999). Large groups of elk and deer were browsing riparian sites, reducing growth of riparian species and decreasing biodiversity (Ripple et al., 2001; Ripple and Beschta, 2003) before wolf reintroduction. Cottonwoods (*Populus spp.*), aspen (*Populus tremuloides*) and willows (*Salix spp.*) have not been able to successfully recover over extended periods of time due to climate, long-term fire suppression and overgrazing by ungulates (White et al., 1998). Wolves were extinct in YNP and surrounding areas for 70 years and this had a tremendous effect on cottonwood recruitment and overall growth. In 1937, slopes in the Gallatin Valley, MT, were almost bare of forage and under risk of erosion. Willows and aspen were over-browsed by elk, and conifer trees were stripped of their needles as high as elk could reach (BDC, 1937; Ripple and Beschta, 2004).

In 1998, White et al., (1998) proposed a multi-level 'trophic cascade model' involving humans, elk, wolves and aspen relations in the Rocky Mountain National Parks and the potential effects of wolves on elk densities. The model predicts that reintroducing a top-order predator, such as the wolf, into the ecosystem alters the abundance or behavior of the next lower trophic level species (elk), which releases the next level species (cottonwoods, aspen and willows) from predation and suppression (Ripple and Beschta, 2004). Slowly, riparian vegetations are recovering and the biodiversity is improving. After being suppressed for decades, willows are increasing in size only 3 years after the reintroduction (Beyer et al., 2007), and aspen growth is occurring in the periphery areas of elk winter range. Beavers returned in several areas (Baker et al., 2005) and the numbers of songbirds multiplied. As predicted by the trophic cascade model, the movement patterns of wild ungulates changed after wolves returned (Fortin et al., 2005). In low-risk areas, elk prefer aspen stands > open areas > conifer stands. In high-risk areas, elk favor conifer stands over aspen stands. Aspen trees are slowly recovering with reduced elk and deer browsing. During summer, elk avoid wolf areas by selecting higher elevations and less open habitat. In winter, elk and wolf areas often overlap and elk stay in open areas but aggregate for group defense (Mao et al., 2005).

If we now compare the 2-season pattern of depredation described by Musiani et al., (2005) with the findings of Mao et al., (2005), the following diagram as shown in Figure 1-1 can be compiled.

6. Cattle losses

When elk move to higher and steeper slopes, wolves start to prey on livestock. Depredation has significant monetary costs, and livestock producers have warrantable concerns about their economic future (Naughton-Treves et al., 2003). Muhly and Musiani (2009) compared livestock prices with land prices and depredation. Between 1987 and 2003 livestock prices had a negative trend with high year-to-year variations, whereas land prices are steadily increasing. The best way for livestock producers to profit seemed to sell their land. Selling, however, often leads to fragmentation of rangelands into smaller parcels. This causes habitat losses (Hobbs et al., 2008) and significantly changes ecosystems as well as wildlife communities (Mitchell et al., 2002).

Even though financial losses appear minimal on the entire livestock industry scale, the ramifications for individual livestock producers are significant since depredations are not distributed evenly (Muhly and Musiani, 2009). Rarely, wolves engage in ‘surplus killings’ of livestock. In these cases, wolves kill more animals during one attack than needed to satisfy hunger and they consume only small amounts of the carcasses (Short et al., 2002). In Idaho, Wyoming and Montana, the estimated costs of livestock depredation increased drastically between 1987 and 2003, especially after reintroducing wolves in 1995/96. Livestock populations have been artificially selected to be easy to handle with a reduced fear response to humans, compared to their wild ancestors (Lankin, 1997). Poor anti-predator behaviors of livestock reduce their potential to survive in nature by self-defense. Diamond (2002) found that the sense organs are less well developed due to a smaller brain size. Selection towards profitable economic traits, such as weight gain, wool production and improved handling let to poor anti-predator behaviors and altered morphological traits (Mignon-Grasteau et al., 2005).

7. Conclusions

The role of maternal protectiveness and defensive behaviors to protect the offspring from predation after parturition has been overlooked in the past. The major concern of the industry was an improvement of production traits through artificial selection. In cattle, selection towards calmer temperament animals seemed to have advantages, such as higher ADG, reduced agitation and easier handling for ranchers. Wool production in sheep increased, as well as fertility rates in sows. Selection programs should, however consider that many circumstances have changed. Maternal behaviors of sows kept in crates are poor and piglet crushing occurs often. Twin pregnancies in sheep lead to high lamb mortalities because females care for only one lamb. Wolf reintroduction in the Northern Rocky Mountains and livestock depredation are a sector of increasing importance not only financially but also emotionally. Expressing adequate maternal behaviors towards the offspring in extensive systems has never been so important. Concerns regarding animal management, welfare and the environment will continue to grow, forcing the industry to change practices and rethink standards.

The objective of this dissertation was twofold: 1) define maternal behaviors such as protectiveness and defense towards the offspring after parturition, and 2) examine depredation losses in cattle in areas with high predation pressure.

FIGURE

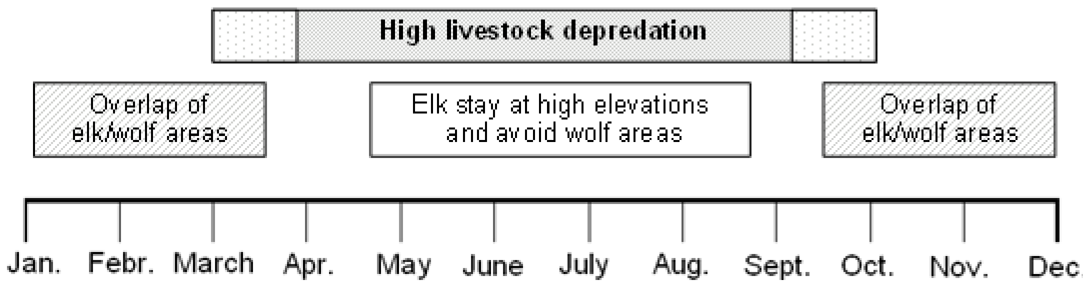

Figure 1-1: Two season pattern of depredation. Mao et al., (2005) described increased livestock depredation during the months March – October (upper bar with reduced predation in the beginning and end and higher depredation during the core months; especially August). The three lower bars (striped) indicate times when wolf and elk join the same areas (winter months) and when elk move to higher elevations to avoid wolf territories (summer months; Musiani et al. 2005).

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CHAPTER 2

INDIVIDUAL DIFFERENCES IN CALF DEFENSE PATTERNS IN RED ANGUS BEEF COWS[1]

SUMMARY

The objective of this study was to evaluate differences in individual calf defense behavior patterns and maternal protective behavior of beef cows 24 h after calving. A single herd was observed on an extensive ranch in Colorado, USA. A total of 341 cow-calf pairs (95% Red Angus and 5% Angus x Hereford commercial crossbreds) were used. Each cow-calf pair was approached with an unfamiliar utility vehicle that circled the pair and gradually decreased the distance between the vehicle and the pair. The following four distance measurements were taken with a digital range finder to evaluate maternal protectiveness: 1) the first time the cow raised her head and oriented towards the vehicle; 2) when the cow placed herself between her calf and the vehicle or lowered her head; 3) when the cow vocalized; and 4) closest distance the vehicle approached the cow-calf pair. Calf defense behavior patterns were recorded as yes/no-classifications and were: 1) protection: the cow positioned herself between the vehicle and her calf; 2) aggression: the cow lowered her head; and 3) the cow vocalized. Hair whorl patterns on the forehead of each cow were used as a measure of individual differences in temperament. HW and age were collected when the cows were in a squeeze chute during routine handling. HW was classified into the following groups: high, middle, low, abnormal, multiple HWs or no

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HW. Ninety-nine percent of the cows moved between the vehicle and their calf to protect it, 13.2% lowered their heads as a sign of aggression and 78% vocalized. Cows with high HW or multiple HW oriented towards the vehicle at a further distance, compared to cows in other HW groups ($P < 0.05$). Cows with a high HW vocalized at a further distance than cows in other groups. Younger cows (3 years) were approached more closely with no behavioral changes than older (5 years) cows ($P < 0.05$). The results suggest that cows with a high HW and older cows may be more vigilant of their surroundings.

INTRODUCTION

Since the reintroduction of gray wolves in the Northern Rocky Mountains in 1995 (Bangs and Fritts, 1996), wolf populations have increased exponentially and so have livestock losses due to predation (Clark and Johnson, 2009). During the last 10 years, ranchers have reported mothering problems (weak calves, maternal neglect, and calf starvation) in very calm cows. Some ranchers speculate that a loss of calf protective behavior in beef cows may further increase predation losses. Predation has already reduced profitability for ranchers substantially (Sime and Bangs, 2010; U.S. Fish and Wildlife Service, 1994a, b).

Maternal behavior represents the responsiveness and concomitant care that an animal provides before and after parturition for the young to protect and care for it (Buddenberg et al., 1986). A possible reduction in maternal calf protective behavior may be due to selection during the last 15 years for calmer cattle temperament (Hyde, 2010). Temperament is consistent over time and within different environments with predictable behaviors (Gosling, 2001; Morris et al., 1994; Sih et al. 2004) and moderate heritability (Gauly et al., 2001). Cattle with a calmer, less excitable temperament have higher average daily gain (ADG), whereas easily excitable cattle tend to gain less weight per day (Voisinet et al., 1997). More recently, Müller and von

Keyserlingk (2006) found that the flight speed from a squeeze chute can also be used as a measure of temperament. In their study, individuals with faster flight speeds had reduced weight gain. Spiral HWs on the forehead are also related to the animals' temperament (Grandin et al., 1995; Randle, 1998). Animals with higher HW positions are more excitable and more easily agitated during restraint.

The question arises as to whether selection for calm temperament has reduced calf protective behaviors in cows. The purpose of this study was to examine individual calf defense behavior patterns and maternal protective behavior in cows within the first 24 h after parturition in free-range beef cows in an extensive pasture system. A second goal was to determine if individual differences in cow behavior were related to the HW position since HW is related to temperament (Lanier et al., 2001; Grandin et al., 1995).

MATERIALS AND METHODS

Observations were in compliance with Colorado State University Animal Care and Use Committee Protocol IACUC # 10-2267A.

1. Animals and Environment

The study was conducted on a commercial cow-calf ranch near Byers, Colorado, USA, in 2011. Ninety-five percent of cows were commercial Red Angus and the remaining 5% were Red Angus x Hereford commercial crossbreds. For this study, free-ranging multiparous cows (N=341; total herd N=836), 3-6 years of age, were used which were maintained in an open pasture. The single pasture was approximately 320 ha with undulating hills, small bushes and sandy soil but no trees. Cows were fed corn stalks each morning between 8:00 – 10:00 h and had unlimited access to water from water troughs. Each day, cows that were pregnant, or had recently given birth, or had a calf that was able to walk on its own would all aggregate in the morning at the feeding area. This facilitated identification of pregnant cows that would give birth on each observation day. Cows that were chosen as subjects for observations were separate from other cows in the herd (minimum distance of 25 m), were not grazing and had their calf in close proximity. Interference from other cows while performing the observations did not occur due to the large size of the pasture and the natural separation behavior of the cows.

2. Behavioral observations and hair whorl data collection

Prior to pasture behavioral observations, the HW positions on the forehead of all cows as well as the age were recorded in October 2010. This was done while the cows were in a squeeze chute for routine pregnancy diagnosis. HWs were classified as being high, middle or low position (Grandin et al. 1995) with the eye-line used as a reference point. They were further classified as being abnormal (without a clear centre), multiple (more than one) or none (no hair whorl on forehead). Classifications were mutually exclusive and cows were classified into one of these six groups.

Behavioral observations were conducted from February 16th - April 6th 2011 during the main calving season. During this period, the observations were conducted each morning starting at 8:00 h to ensure that cows could be easily observed when the main herd aggregated at the feeding area. All cow-calf pairs were observed within 24 h of parturition. Within this time period the calf has the highest need for protection by the cow and is most vulnerable. The main predators on this ranch were coyotes which were sighted on multiple occasions consuming afterbirth. They did not kill any livestock during the observed calving season. However, in several previous calving seasons, predation losses were recorded. Therefore, most of the cows had experienced the presence of predators.

To obtain data on maternal protectiveness, each cow was approached as follows: the cow and her newborn calf were spotted with binoculars on the pasture at a distance greater than 200 m. Before the start of the observation, the cow-calf pair was observed to assure that the calf was able to get up and walk on its own. Each cow-calf pair was approached in a spiral pattern with a utility vehicle gradually decreasing the distance between the cow-calf pair (Figure 2-1) with the range of speed during the observation being 8-16km/h. Observations started at 150 m from the cow-calf pair and ended when the cow-calf pair retreated. The car represented an unknown object for the cow and by circling around the cow the movement resembled the approach of a predator getting closer to the cow (MacNulty et al., 2007; Murie, 1944). The car was a gray GMC utility vehicle that was different from all the white trucks on the ranch. This unfamiliar vehicle was never used by the ranchers for routine checking or other ranch work. Cows that calved later in the season might have seen the vehicle before, but during the approach within the 24 h post calving interval, the cows showed increased nervousness and vigilance. Each cow was only approached once and therefore habituation to the vehicle was unlikely.

Data on maternal protectiveness was collected by taking four distance measurements (m) during the approach with the car (Figure 2-1) using a range finder (Archer's Choice Rangefinder 8366, Nikon Inc., Melville, NY, USA):

- Approach distance (Figure 2-1, distance a): when the cow first perceived the presence of the car and stopped performing previous behavior. The cow followed the movement of the vehicle by raising her head and looking directly at it.
- Protective distance (Figure 2-1, distance b): when the cow walked between the calf and car, or lowered her head as an aggressive movement (Klemm et al., 1983) which indicated that the she perceived the car as a potential threat.

- Vocalization distance (Figure 2-1, distance c): when the cow vocalized towards her calf. Calves were able to distinguish the cows' individual call (Marchant-Forde et al., 2002) and reacted to it by getting closer to the cow.

- Closest approach (Figure 2-1, distance d): the closest distance between car and cow before the cow-calf pair moved away.

In addition, the flight behavior of the cow-calf pair after the approach was categorized in one of three categories: 1) no flight (cow and calf did not move); 2) the pair walked away; or 3) trotted away. If the cow-calf pair did not retreat the closest approach was set to 4 m. In addition to the distance measurements for maternal protectiveness, different calf defense behavior patterns were recorded. These were yes/no-classifications for 1) protection (the cow positioned herself in between the car and calf); 2) aggression (the cow lowered her head) and 3) vocalization (the cow vocalized).

3. Statistical analyses

Statistical analyses were conducted using the program SPSS 17.0 (SPSS inc.) by performing analysis of variance with the different observational measurements for maternal protectiveness as dependent variables and the HW as a factor. Fisher's LSD was used as a post-hoc test to indicate differences between the groups. Data variances were not normally distributed and log10-transformations were performed. Data on observed differences in calf defense patterns are presented numerically with percentage values. We further analyzed the influence of the age of the cow, in years, on maternal protectiveness using age as a factor in the analysis of variance. After initial evaluation of data regression analysis was performed on age of cows and closest approach. Chi-square analyses were used to evaluate flight behavior and aggressiveness of the cows.

Grandin et al. (1995) found that cows with higher HWs were more easily agitated and Randle (1998) supported the finding that there was a relationship between temperament and the facial HW position, insofar that individuals with higher HWs had greater flight distances. In our study, high, middle and low spiral HWs represented the majority of the HWs in this herd. We analyzed these three HWs separately in chi-square-tests from abnormal, multiple and no HWs. Chi-square analyses were also used to evaluate a relationship between HW and the flight behavior. The significance level was set to 0.05 and graphs show mean values with error bars ± ½ LSDs.

RESULTS

A total of 341 cows were approached with the procedure described in the section 2 in the materials and methods. Observations on different calf defense patterns (Table 2-1) during the approach showed that 99.1% of cows protected the calf from the vehicle by positioning themselves between it and the calf. Only 13.2% reacted aggressively (lowering the head) during the vehicular approach. Seventy-eight percent vocalized and all calves reacted to this by moving closer to the cow. The most observed flight behavior was to walk away with the calf. Only three cows in the observed population left the calf behind and retreated without it, and interestingly all three of these cows did not perform protection and did not vocalize towards the calf.

The overall distribution of HWs was: 8.2% high HW, 36.7% middle HW, 25.8% low HW, 7% abnormal, 11.4% multiple HWs and 10.9 % no HW. Observations on maternal protectiveness indicated variations in distance between the different HWs (Table 2-2). There was a trend ($P = 0.057$) for the approach distance suggesting that the approach by an unknown object was perceived unequally among the six different HW groups. Post-hoc analysis between these groups for the approach distance showed that cows with high HW ($P < 0.05$) as well as cows with multiple HWs ($P < 0.05$) reacted at a further distance to the vehicle than cows with middle

HWs. Cows with a high HW also communicated much sooner (at a greater distance) towards their calf than most other HW groups. Neither the protective distance nor the closest approach distance differed with HW.

The closest approach between cow-calf pair and car was significantly influenced by age ($P = 0.041$, Figure 2-2). The older cows (5 years) kept a greater distance (n = 75, = 7.6 m) from the vehicle, whereas younger cows (3 years) allowed the vehicle to approach closer (n = 88, = 5.9 m) before retreating ($P < 0.05$). The closest approach for 4-year-old cows was = 6.5 m (n = 87) and for 6-year-old cows = 7.1 m (n = 91), respectively. Overall, the added regression line (Figure 2-2; $R^2 = 0.68$) indicated that there is a positive relationship between the cows' age and the closest approach. Given that the car was perceived as a strange object, most cows retreated with their calf once the car entered their flight zone (Grandin, 1980).

Analyses of flight behaviour and aggressiveness within cows with high, middle and low HW patterns showed that 50% of cows that trotted away also performed aggressive movements ($\chi2 = 18.3$, $P < 0.001$), but there was no relationship between aggressiveness and HW pattern ($\chi2 = 3.3$, $P = 0.51$). For cows with abnormal, multiple and no HW there was no relationship between flight behavior and aggressiveness ($\chi2 = 1.7$, $P = 0.43$). No relationship between HW and the flight behavior was found ($\chi2 = 8.4$, $P = 0.59$).

DISCUSSION

Our findings on individual calf defense patterns showed that almost all cows protected their calf when approached by a vehicle. During this approach, only a minority of cows displayed aggressive movements. This can be seen as a positive trait because with less aggressive cows, animal handling is safer for ranchers and attacks may be reduced. Vocalization towards the calf was another major pattern during calf defense which was performed by more than three-quarter of all animals. Kunowska-Slósarz and Różańska (2009) showed that there is increased vocalization during the post partum interval between cow and calf and this vocal behavior may give important information about the endogenous and exogenous factors of cow and calf (Watts and Stookey, 2000). By vocalizing towards the calf during the vehicle's approach, cows may have been indicating a concern about the unfamiliar object.

The most common form of flight behavior by the cow-calf pair was to walk away, but almost 40% of cows remained and defended the calf by not retreating. A possible explanation for this might be that the observations were performed within 24 h after parturition. Prior to the start of the observation we assured by binocular observation that calves were able to get up by themselves and walk, but impaired walking abilities of calves might have influenced the type of flight behavior made by cows. All forms of flight behaviors observed in this study can be seen as effective strategies for calf defense with the exception of the three cows that left their calves behind.

The relationship between HW and approach distance indicated that individual differences in temperament contributed to the protective patterns of cows. In our study, cows with a high HW as well as cows with multiple HWs were more vigilant and reacted earlier (at a greater distance) to an approaching car, indicating increased alertness to their surroundings. This can be seen as an advantageous type of calf defense pattern because the vigilance level of these cows makes them perceive a possible threat earlier and subsequently react sooner. Cows with a high HW also vocalized towards their calf sooner (at a greater distance), and calves reacted to this by getting closer to the cow. This kind of maternal protectiveness is clearly beneficial when predators are present.

Earlier studies (Grandin et al., 1995; Lanier et al., 2001; Randle, 1998) were able to identify a positive relationship between the height of the spiral hair whorl position on the animal's forehead and its temperament. In the study of Grandin et al., (1995), 14% of 1500 cattle in a feedlot in Colorado had high HW pattern and in our study population only 8.2% had high HWs. Animal selection by producers has favored animals with calmer temperaments which are easier to handle (Hyde, 2010). Anecdotal field observations by the third and fourth author also indicate that cattle have lower HWs than they had 15 years ago. Clear advantages of the selection for calmer temperament are a higher ADG in calmer cattle (Voisinet et al., 1997), reduced risks for the stockpersons (Boivin et al., 2003; Boivin et al., 2009) and less time-consuming handling procedures with calmer cattle.

However, traits are often connected, and selection for one trait (calm temperament) might not always lead to an improvement of other desirable traits. Even though almost all cows in this study performed protective movements towards the calf, we need to be aware of changes in behaviors due to direct selection. In extensive beef systems, increasing predation losses of calves by wolves (Bangs and Fritts, 1996; Clark and Johnson, 2009; Dorrance, 1982), black vultures and golden eagles (Avery and Cummings, 2004) have been observed, and the selection towards calmer temperament cattle might be part of the explanation for these losses.

In our study, three cows left their calf behind and retreated without it. Hudson and Mullord (1977) suggested that there is a sensitive period in which the mother-young bond is established, with the amniotic fluid (Lévy and Keller, 2009) and hormonal changes in the brain (rats: Fleming and Rosenblatt, 1974; rabbits, sows, and ewes: Nowak et al., 2000; Poindron, 2005; ewes: Dwyer, 2008) being major triggers for the onset of maternal protectiveness and bonding. Interestingly, the cows that retreated without their calf had middle HWs. None of the cows that left the calf behind protected it or vocalized and a less well developed mother-young bond might be the reason for the neglect in these individuals. In areas where predators are present, this maternal behavior would most likely cause the death of the calf.

The age of a cow also influenced calf protective behavior and affected the closest distance the cow and calf could be approached, with our data indicating that younger, and maybe less experienced cows, could be approached more closely than older cows. This might be effected by former calving experiences of individual cows (Naazie et al., 1991) but also by the existing conditions at the ranch, because both experience and environment shape the behavior of animals (Lorenz, 1935). To younger cows (second time of calving), calving may be a relatively new experience and they may pay less attention to their surroundings and more attention to the process of calving, whereas older cows are more experienced (Le Neindre et al., 2002) and may be more vigilant towards their surrounding and possible predators.

Treves et al., (2002) identified overall losses due to predation and even though only a small number of calves and cows get killed each year, financial losses reach into millions of dollars. There is zero profit from cows that lose their calf but maintenance costs stay the same (feed, vaccinations and veterinarian appointments). Also, up to 10% decreased pregnancy rates are observed in cows that lost a calf due to predation (C. Anderson; pers. comm.) If fewer calves are weaned then fewer cattle are ultimately available for slaughter.

CONCLUSIONS

Our research suggests that in extensive rangeland ranchers should be cautious about selecting the calmest cattle in the herd as breeders. Instead, they should select for animals that protect their calves and wean a live healthy calf every year. For safety, cows that are aggressive towards people should be culled. This recommendation applies only to beef systems where predation occurs. If temperament selection is implemented by using the HW, this can be easily performed when cows are in the squeeze chute. Cattle with a slightly higher HWs than a middle HW, that do not become highly agitated in the squeeze chute (Grandin et al., 1993) and leave it with a moderate velocity (Curley et al., 2006) should be selected.

TABLES

Table 2-1: Yes/No-classification of different calf defense patterns by cows (N = 341) in response to vehicular approach.

		n	%
Protection	Yes	338	99.1
	No	3	0.9
Aggression	Yes	45	13.2
	No	296	86.8
Vocalization	Yes	266	78
	No	75	22
Flight behavior	no flight	136	39.9
	walk	193	56.6
	trot	12	3.5

Table 2-2: Distances when cows showed behavioral responses to vehicular approach classified by hair whorl pattern. Data are log_{10}-transformed and show mean distances ± SE with back-transformed means (m) in parentheses.

Hair whorl pattern		Distances			
	n	Approach [1]	Protective [2]	Vocalization [3]	Closest [4]
high	28	1.99 ± 0.05 (98.5) **b**	1.57 ± 0.07 (37.4)	1.27 ± 0.07 (18.7)	0.92 ± 0.07 (8.4)
middle	125	1.89 ± 0.02 (77.1) **a**	1.53 ± 0.04 (34.1)	1.09 ± 0.03 (12.3)	0.81 ± 0.03 (6.5)
low	88	1.91 ± 0.02 (82.2) ab	1.56 ± 0.04 (36.2)	1.09 ± 0.04 (12.2)	0.86 ± 0.04 (7.2)
abnormal	24	1.97 ± 0.04 (93.9) ab	1.60 ± 0.05 (39.6)	1.18 ± 0.07 (15.1)	0.77 ± 0.05 (5.8)
multiple	39	1.99 ± 0.04 (97.0) **b**	1.62 ± 0.06 (41.9)	1.07 ± 0.05 (11.8)	0.82 ± 0.05 (6.6)
none	37	1.97 ± 0.03 (92.8) ab	1.62 ± 0.07 (41.6)	1.06 ± 0.06 (11.5)	0.80 ± 0.05 (6.3)
ANOVA	df	5	5	5	5
	F	2.175	0.531	1.406	0.906
	P =	0.057	0.753	0.222	0.477

Post hoc Fisher's LSD: means in the same column with different letters differ ($P < 0.05$).

[1] Approach distance: when the cow first perceived the presence of the car and stopped previous behavior.

[2] Protective distance: when the cow got between car and calf, or lowered the head as an aggressive movement.

[3] Vocalization distance: when the cow vocalized towards the calf.

[4] Closest approach: before the cow-calf pair retreated.

FIGURES

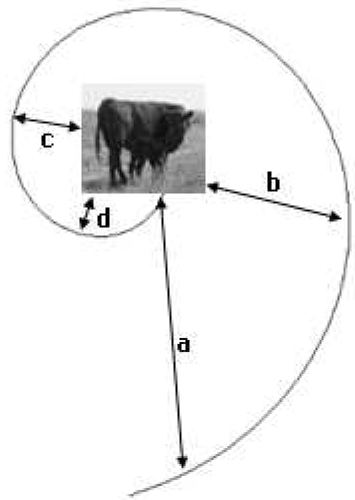

Figure 2-1: Illustration of the observers' route when approaching the cow. Distances were collected while the car performed spiraling movement around the cow-calf pair, thereby gradually coming closer. Distance measurements were: a (approach = cow first perceived the presence of the car and stopped previous behavior), b (protective distance = cow got between the car and calf, or lowered the head as an aggressive movement), c (vocalization = cow vocalized towards the calf) and d (closest = closest approach between cow-calf pair and the car before retreat).

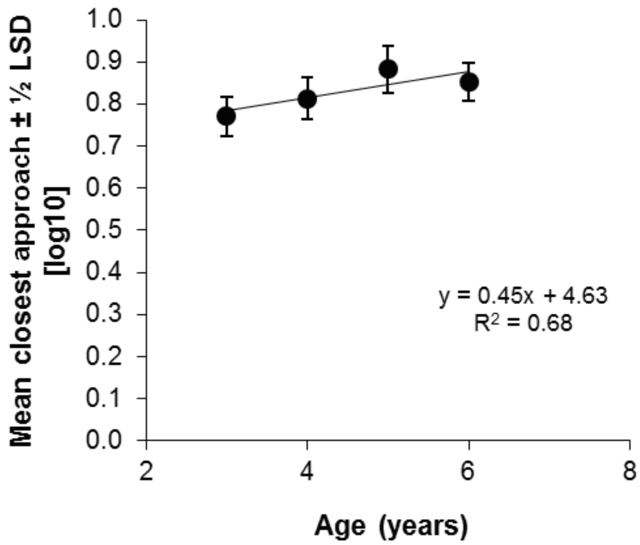

Figure 2-2: Closest distance between the cow-calf pair and the car during the observational approach for maternal protectiveness before retreat. Shown are mean values ± ½ LSD (log_{10}-transformed data) for the different cow ages. Regression line added.

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CHAPTER 3

SEPARATION BEHAVIOR FOR PARTURITION OF RED ANGUS BEEF COWS

SUMMARY

Increased predation losses in beef cattle in the Northern Rocky Mountains raise the importance of research concerning maternal behavior around the time of parturition. Separation behavior of multiparous cows at parturition was studied by measuring the distance (m) between the birth place and the main herd with a GPS device. Age of cows and forehead hair whorl pattern (HW) were analyzed as possible factors affecting separation distance. A total of 333 cows (95% Red Angus and 5% Angus x Hereford commercial crossbreds; age range: 3-6 yrs) were studied. Separation distance was determined by approaching the cow-calf pair with a utility vehicle that gradually decreased the distance to the pair. The geographic coordinates per pair were recorded and the separation distance was calculated as a straight line between each pair and the place were the main herd was fed every day. The HW on the forehead of each animal was used as a measure of individual differences in temperament. Age and HW were collected when the animals were held in a squeeze chute. HW was classified into one of six groups: high, middle, low, abnormal, multiple HWs and no HW. The age of a cow influenced the separation distance for parturition ($P < 0.001$). Four year old cows were on average about 150 m further away than other aged cows when calving. Hair whorl position had no influence on the separation distance ($P = 0.405$). In conclusion, separation for parturition is likely affected by the social dominance of cows within the individual herd. It is an innate behavior of cows to separate from the herd for calving though there are individual differences in separation distance.

IMPLICATIONS

Keeping cows alive and healthy in an environment where grey wolves have been reintroduced has become an increasing challenge for ranchers. Therefore, good maternal protective behavior at parturition is very important. Our study shows that more dominant and older cows tend to calve closer to the herd and younger, more inexperienced cows calve further away at random places. About 88% of cows separated more than 100 m from the herd. In areas with predation pressure, it is recommended to keep parturient cows closer to the barn to reduce losses and to frequently monitor cows.

INTRODUCTION

In ungulates, when a cow approaches parturition, there are two distinctively different behaviors that are observed. One is aggregation behavior, which is observed in saiga antelope (*Saiga tatarica*; Singh et al., 2010) and wildebeests (*Connochates taurinus*; Estes, 1976) which is often influenced by resource availability and predator presence. The other is separation behavior which is observed in caribou (*Rangifer tarandus*; Rettie and Messier, 2001) and moose (*Alces alces gigas*; Bowyer et al., 1999) in which females move away from the herd to give birth unaccompanied. Aggregation behavior is effective because other females will cooperate with defending the group against the predator. Separation behavior is also effective because predators have greater difficulty locating the parturient dam. Leuthold (1977) suggested that maternal isolation at calving reduces the risk of predation and facilitates imprinting between the cow and her newborn calf.

The investigation of maternal protectiveness towards the calf after parturition has become of increasing importance since the reintroduction of grey wolves in the Northern Rocky Mountains (Bangs and Fritts, 1996). A study by Flörcke et al., (2012) investigated maternal protectiveness and calf defense patterns of cows 24 h after parturition and found that cows vary in their level of vigilance towards their surroundings. Vigilance is associated with the temperament of the cow. The separation for parturition represents a potential risky situation for cow and calf as well as for producers. Steadily increasing losses due to predation have been observed by Clark and Johnson (2009). Learning more about parturition behavior in cows may assist ranchers in reducing predation.

In cattle, Lidfors et al., (1994) reported large individual differences in separation behavior between parturient cows and those cows also appeared to be able to cope with different environments. In forest areas, cows exhibit shelter seeking behavior similar to wild relatives. In open areas without trees, soft dry bedding seemed to be the most important factor and calving occurred at random places. Individual differences, also referred to as temperament or personality, can be used to predict behaviors in unfamiliar environments and these differences are also heritable and consistent over time (Morris et al., 1994; Gauly et al., 2001; Dingemanse et al., 2002). The spiral HW on the forehead of a cow can be used as a predictor of the individual temperament of the animal (Grandin et al., 1995; Randle, 1998). Cows with higher HW positions were more excitable and more easily agitated during restraint (Grandin et al., 1995). Maternal vigilance of animals with a high HW is greater than vigilance behavior in animals with a lower HW position. These cows pay more attention to their surroundings and they perceive threats earlier (Flörcke et al., 2012). In horses, there is an association between the facial HW position and motor behaviors (Murphy and Arkins, 2008). Horses with a spiral HW that turns counter-clockwise tend to be left-lateralized and horses with clockwise HW are more likely to be right-lateralized. In addition, there is an association between visual laterality and emotions (De Boyer Des Roches et al., 2008). Laterality was shown when the mares were confronted with a familiar positive -, a novel - and a negative object. Mares preferred to use their right eye to look at the novel object and their left eye to investigate the negative object (De Boyer Des Roches et al., 2008).

In this study we examined the possible influence of HW position and age of the dam on the separation distance from the herd for parturition. We further investigated if the rotation of the spiral HW (clockwise/counter-clockwise/radiant) had an effect on separation distance. Within the first 24 h after parturition the separation distance of cows was recorded and analyzed. An understanding of maternal and separation behaviors around the time of parturition may help ranchers reduce predation losses.

MATERIAL AND METHODS

Observations were made in compliance with Colorado State University Animal Care and Use Committee Protocol IACUC # 10-2267A.

1. Animals and Environment

This study was conducted on a commercial Red Angus cow-calf ranch near Byers, Colorado, USA, in 2011. It was the same herd that was studied by Flörcke et al., (2012). Calving season started in early February and lasted until June, 2011. Ninety-five percent of cows were commercial Red Angus and the remaining 5% were Red Angus x Hereford commercial crossbreds. Free-ranging multiparous cows (total herd: N = 836; 3-6 years of age), maintained in an open pasture were used. Cows on this ranch calved for the first time as 2-year old heifers while housed in a small pen where they were observed closely at all times. Two-year old heifers were not included in the study due to differences in handling and pen size. The 3-year-old cows were turned out with the older cows on a big pasture and calved unobserved for the first time. The single pasture was approximately 320 ha with undulating hills, small bushes (height: 40 - 60 cm) and sandy soil but no trees. The pasture had a rectangular layout with one narrow corner on the north side (Figure 3-3). Cows were fed corn stalks each morning between 0800 – 1000 h and had unlimited access to water from water troughs. Each day, cows that were pregnant, or had a calf that was able to walk on its own would all aggregate in the mornings around the feeding ground. This facilitated identification of pregnant cows that would give birth on each observation day. Cows that were chosen as subjects for observations were separated from the herd (Minimum = 25 m), were not grazing and had their calf in close proximity. There may have been cows that calved within the herd but they were not observed in our study and therefore excluded from our data. The main predators on this ranch were coyotes. They were sighted on multiple occasions consuming afterbirth but they did not kill any livestock during the observed calving season. However, during several previous calving seasons, predation losses were recorded. Therefore, most of the cows had experienced the presence of predators.

2. Cow age and hair whorl pattern (HW) collection

Previously, the age and HW on the forehead of all cows had been recorded in 2010 (Flörcke et al., 2012). Hair whorl position had been recorded while the cows were in a squeeze chute for routine handling procedures. The experimenter stepped in front of the cow, identified the HW position and rotation, and drew it on a piece of paper as shown in the examples in Figure 3-1. Hair whorls were classified as being high, middle or low position (Grandin et al., 1995). The eye-line was used as a reference point. They were further classified as being abnormal (one of five possible patterns without a clear spiral centre, Figure 3-1), multiple (more than one, all with a clear centre) or none (no HW on forehead). Classifications were mutually exclusive and animals were classified into one of these six groups.

3. Global Positioning System (GPS) data collection

GPS data were collected from 16 February - 6 April, 2011 during the main calving season utilizing a Garmin GPS device to locate the position of cow and calf on the pasture (Manufacturer: Garmin etrex H Yellow, Garmin International Inc., Olathe, KS, USA). Data collection started at 0800 h every morning to ensure that all cows could be easily observed when the main herd aggregated around the feeding ground and lasted for up to four hours. The centre area of the feeding ground was used as a reference point for GPS calculations. All separation distances were calculated as a straight line to this centre point. All cow-calf pairs were approached within the first 24 h after parturition. The mobility of the cow-calf pair was lowest and cows usually stayed with the calf until the calf stood up and walked by itself. To obtain data on the distance between the feeding area and the parturition site, the cow and her newborn calf were spotted with binoculars on the pasture. Each cow-calf pair was approached with a utility vehicle (grey GMC Jimmy) which gradually decreased the distance to the cow-calf pair (range of speed during approach: 8-16 km/h; Flörcke et al., 2012). The position (degree of latitude and longitude) of cow and calf was recorded and subsequently calculated, and each pair was approached only once. Separation data was obtained for 333 cow-calf pairs after parturition. Collecting data on all of the cows was not possible because numerous cows either calved at night and returned to the herd in the morning or could not be found during the day. Interferences from other cows while performing the observations did not occur due to the large size of the pasture and the natural separation behavior of cows. The maximum distance a cow could separate from the herd before parturition was 1250 m.

4. Statistical analyses

Data were normally distributed and variance was homogeneous (Levene's test). Analysis of variance was conducted using SPSS 17.0 (SPSS, Inc.) with separation distance as the dependent variable and age, HW and HW rotation as factors. We discovered an effect of age on separation distance (*P* < 0.05) and thus conducted a post-hoc protected Fisher's LSD test to determine differences between each combination of age groups (3 vs. 4, 3 vs. 5, 3 vs. 6, 4 vs. 5, 4 vs. 6 and 5 vs. 6). The significance level was set to *P* < 0.05 for this study and graphs show mean values with standard error bars.

RESULTS

The separation distance for parturition ranged from 25 m to 1250 m. Hollows with sandy soil surrounded by small bushes were preferred for calving. The cows in our study spent approximately 12 to 24 hrs at the parturition site. A total of 95.2% (n = 317) of cows separated further than 50 m from the feeding area where the main herd was located, 88.3% (n = 294) separated further than 100 m for parturition. The age of a cow greatly influenced the separation distance for parturition (*P < 0.001*, Figure 3-2). When cows separated from the main herd and the feeding area, the 4-year-old cows were on average 714 m (± SE 38.3 m) away, and the other aged cows (3,5 and 6 years) were much closer to the herd (on average 508 m ± SE 23.5 m). To visualize the spatial distribution behavior of cows on the pasture when separating from the herd for parturition we plotted the geographic coordinates for each cow-calf pair, separated by age of the cow (Figure 3-3). Only one cow within the observed herd calved in a narrow corner (age 3, latitude: 39,893, longitude: 104,052). The HW of cows had no influence on the separation behavior (*P = 0.405*) and we did also not find an association between the HW rotation and separation distance (*P = 0.782*).

DISCUSSION

Our observations showed that the separation distance for parturition is highly variable between cows, ranging from as little as 25 m to up to 1250 m. The maximum separation distance may be larger but the pasture fence limited the movement of the cows. Several researchers reported that separation behavior is influenced by the environment. In open environments with few trees, females of many wild ungulate species often tend to aggregate in large numbers to give birth. This may serve as a confusion strategy against predators (Estes, 1976; Milner-Gulland, 2001; Singh et al., 2010). In forest environments, ungulate females tend to seek isolation either in woody vegetation or tall grasses (Leuthold, 1977; Tulloch, 1979) and American Bison prefer cover by oak trees (Lott and Galland, 1985).

The difference between wild ungulates and our study is that the cows were fed every morning in the same location. This influenced their dispersal behaviors. Before parturition, 88% of cows actively separated more than 100 m from the main herd and the feeding area. Our findings are in agreement with the model of Barbknecht et al., (2011). Their model predicts that females should select parturition sites based on the features of the macro- and microhabitat. The macrohabitat represents topographical and vegetative cover for physical protection such as hill and groups of trees and the microhabitat provides visual cover within the macrohabitat such as hollows or bushes to hide within.

The time spent at the parturition site may alter the strength of the selection for cover (Barten et al., 2001). Cows in our study spent only a few hours (12 to 24 hrs) at the parturition site. This short period of time at the parturition site made GPS data collection difficult. The limited availability of bushes for cover may have reduced the time spent at the parturition site since cows were not as secluded as they would be in higher bushes or a forest. However, the short-time period of separation allowed for undisturbed parturition and potentially a greater cow-calf bond at the expense of reduced protection and increased predation risk. Leaving the birth site shortly after parturition may have corresponded with higher calf survival, as has been found in a similar study in woodland caribou (*Rangifer tarandus*) by Gustine et al., (2006).

The age of cows had a significant effect on separation distance. With an age range of 3-6 years, cows on this ranch were relatively young. The 2-year old heifers (first time calving; not included in the study) may have had a less well developed mother-young bond due to the limited space for parturition in the pen and separation behavior was impossible. Three-year old cows calved unobserved on the big pasture for the first time. Separation behavior may have been less likely in these cows because they had previously calved in a small pen. Aberrant maternal behaviors have been found in inexperienced mothers (Price et al., 1981). It is also interesting to look at the spatial distribution of all the cows (Figure 3-3). Only one 3-year-old individual chose to calve in a narrow corner which may represent a trap in case of predation presence. This may be due to inexperience. The 4-year-old cows that calved on the pasture for the second time had the greatest separation distance. Possibly seeing coyotes during the first year calving on the pasture influenced their separation behavior. Based on life history characteristics associated with parturition cows may be more vigilant towards their surroundings to assure protection of the calf (Flörcke et al., 2012) and the separation behavior may help imprinting between cow-and calf (Leuthold, 1977). Lent (1974) found that parturition frequently attracts other conspecifics and even males which may lead to less well developed mother-young bonds (Edwards, 1983; Owens et al., 1985; Illmann and Spinka, 1993) and licking by conspecifics can even lead to desertion of the newborn calf (Edwards, 1983). Therefore, the separation of 4-year-old cows may represent a learning process to guarantee a close mother-young bond and improved protection. However, in areas with high predation this behavior may be disadvantageous in terms of predation pressure and we would recommend keeping parturient cows in close proximity to the barn, if possible. Cows that are older than four years are likely more dominant because they are full grown and established their social rank in the herd. These cows can calve in closer proximity of the herd and chase away younger cows to prevent licking of the newborn calf (Illman and Spinka, 1993) and still develop a strong mother-young bond. Separation of younger cows may be a defensive strategy (Rubenstein, 1978) to guarantee the maternal bond without being interrupted during parturition. Further studies should be conducted in an area with wolf predation to assess possible differences in separation and maternal behavior of cows in different predation environments.

Surprisingly, the temperament of the cow, measured by the HW, appeared to have no influence on separation distance. Grandin et al., (1995) found that animals with higher HWs tend to be easily agitated and our suggestion was that these animals may also behave differently at parturition, but this was not found in our study. Furthermore, a possible effect of the rotation of the HW on separation behavior was analyzed but this also did not influence the separation behavior and distance in any way.

CONCLUSIONS

We observed distinct separation behavior before parturition from the feeding area and the main herd (Red Angus and Red Angus x Hereford commercial crossbreds). We suggest that the short-time period of separation for parturition probably allowed for a greater separation distance and additionally improved imprinting between cow and calf even though predation risk may be increased. Four-year old cows moved the furthest away from the herd and overall, 88% of cows separated more than 100 m from the feeding area. No effect of temperament, measured by the spiral HW on the forehead of cows, on separation distance for parturition was found. Maternal behaviors around the time of parturition have become of increasing importance and need to be included in selection programs to maintain sustainability for ranchers in areas with high predation.

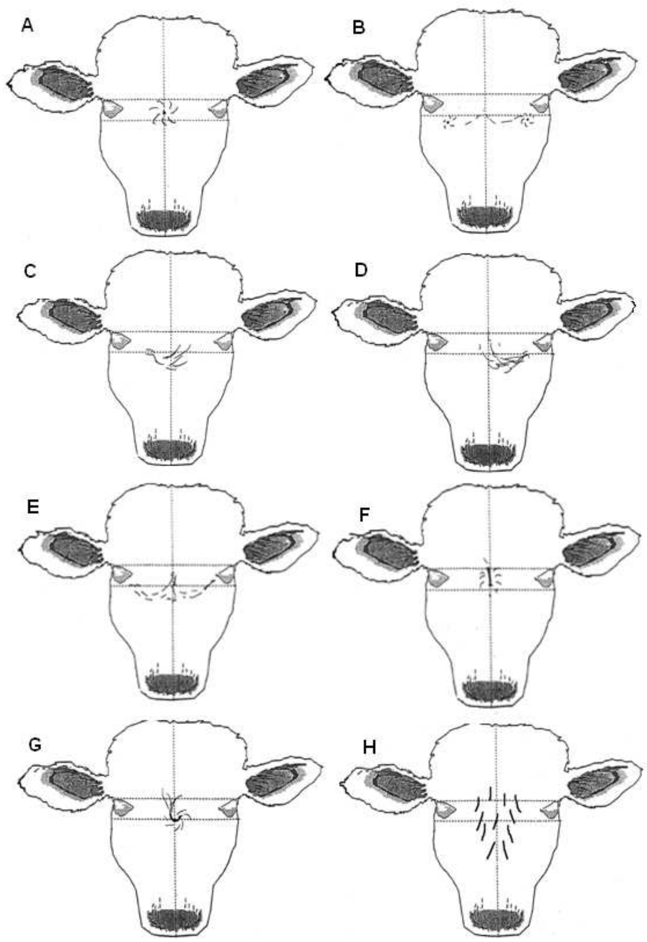

Figure 3-1: Description of the six hair whorl patterns (HW): **A:** a normal middle HW with a clear center and a spiral pattern. Low and high HW would look like this, too with the low HW being below the lower eye-line and the high HW being above the upper eye-line. **B:** an example of multiple, spiral HW of the forehead, each with a clear center. **C** to **G**: examples of abnormal HWs; **C:** one single flair starting under the right eye of the animal growing towards the middle. **D:** one single flair starting under the left eye of the animal growing towards the middle. **E:** a double flair starting under each eye. **F:** a long vertical line on the forehead with no spiral pattern. **G:** every other form like a sickle or curved vertical line. **H:** no HW and all the hair lays straight down.

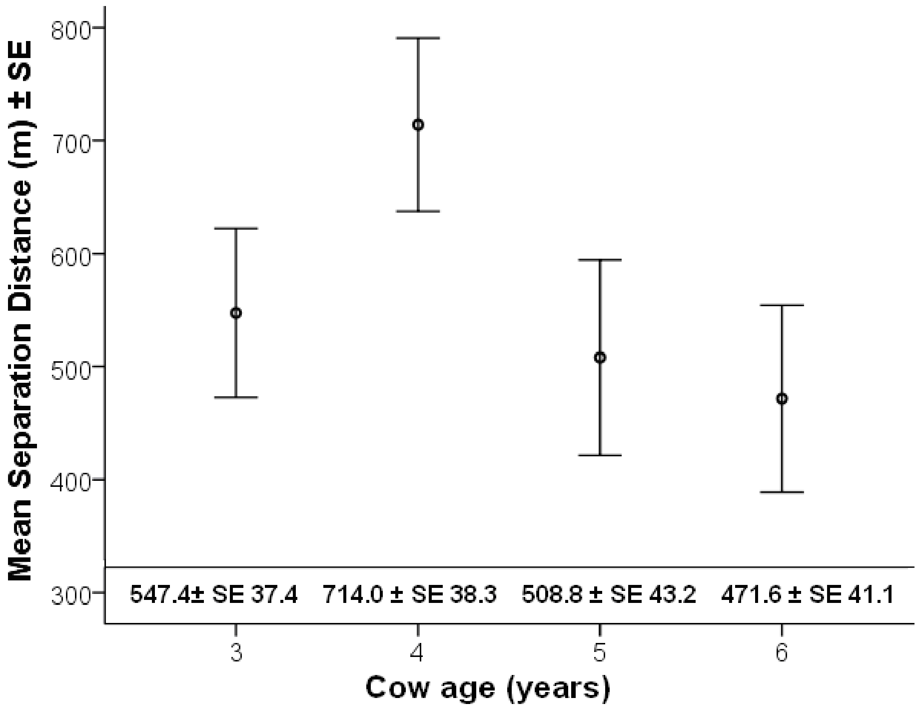

Figure 3-2: Mean separation distance (m) of cows after parturition from the main herd and the feeding area, classified by the age of cows. Included are mean values per age group ± SE (age 3, n = 85; age 4, n = 86; age 5, n = 73; age 6, n = 89).

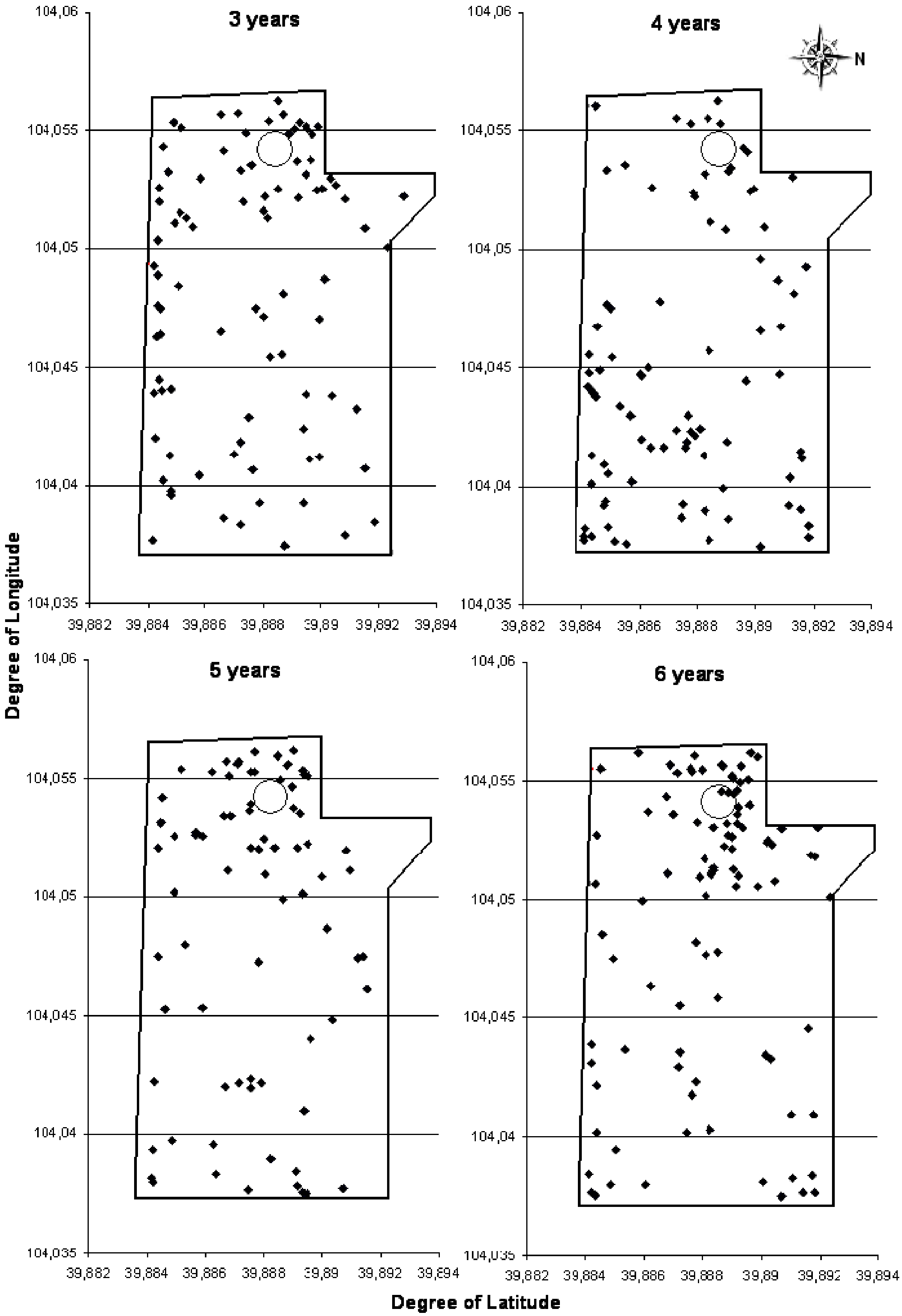
3 years
4 years
5 years
6 years
N
Degree of Longitude
Degree of Latitude
104,06
104,055
104,05
104,045
104,04
104,035
39,882
39,884
39,886
39,888
39,89
39,892
39,894

Figure 3-3: Geographic coordinates (degree of latitude and longitude) of each cow-calf pair on the pasture, separated by age. The black frame is the boundary fence of the pasture. The width is approximately 900 m at the widest point and the length is approximately 1200 m. Each diamond represents the parturition side of one cow-calf pair. Coordinates were collected from February 16th – April 6th, 2011 during the main calving season. The main feeding area is indicated by a black circle located in the upper right corner of the pasture.

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CHAPTER 4

THE INFLUENCE OF MATERNAL TEMPERAMENT ON PHYSIOLOGICAL CHARACTERISTICS OF THE CALF

SUMMARY

In this study we evaluate the possible influence of the hair whorl pattern (HW) of the mother on physiological traits of the calf. Physiological measurements such as calf birth weight, calf gender, ADG of calves, weaning weight and days until weaning were collected. Age of cows and forehead hair whorl pattern were analyzed as possible factors affecting calf measures. A total of 507 cows (95% Red Angus and 5% Angus x Hereford commercial crossbreds; age range: 3-6 years) were studied. The HW on the forehead of each animal was used as a measure of individual differences in temperament. Age and HW were collected when the animals were held in a squeeze chute. HW was classified into one of six groups: high, middle, low, abnormal, multiple HWs and no HW. Calf birth weight and weaning weight were influenced by the gender of the calf ($P < 0.001$; steers were heavier than heifers) and by the cow weight ($P < 0.001$; heavier cows give birth to/wean heavier calves). There was a tendency of HW affecting the birth weight ($P = 0.093$; cows with middle HW gave birth to the heaviest calves) and an effect on weaning weight ($P = 0.043$, cows with abnormal non-spiral HW weaned heavier calves compared to normal round spiral HWs). The age of cows had no effect on calf birth weight ($P = 0.593$) but affected the weaning weight ($P < 0.001$). Older cows wean heavier calves. Further, the body conditions of calves depend on the physiological constitution of the cow.

INTRODUCTION

Numerous earlier studies showed the relationship between cow and calf traits on birth weight, ADG, weaning weight and yearling weight (e.g. Gregory et al., 1950; Koch, 1972; Bourdon and Brinks, 1982; Holland and Odde, 1992). In addition, the nutrition of the dam during and after pregnancy directly influences the health and productivity of a calf (Nowak et al., 2012). However, the influences of maternal temperament on production traits of the calf are unidentified. Selection towards calmer temperament cattle occurred during the last 15 years, especially in Limousin cattle (Hyde, 2010) but also in other breeds such as Angus and Simmental (Gauly et al., 2001). The temperament of an animal is consistent over time and within different environments with predictable behaviors (Morris et al., 1994; Gosling, 2001; Sih et al., 2004) and a moderate heritability (German Angus 0.61 ± 0.17, Simmental 0.59 ± 0.41; Gauly et al., 2001). Calm temperament cattle have several advantageous. The animals have a higher average daily gain (ADG) compared to more easily excited cattle which gain less weight per day (Voisinet et al., 1997). Human-cattle interactions, safety, welfare, herd productivity and meat quality all profit from selection programs incorporating temperament (Fordyce et al., 1988; Grandin, 1993; Brouček et al., 2008). More easily agitated animals have tougher meat and a higher incidence of borderline 'dark cutters' (Voisenet et al., 1997). The term 'dark cutters' refers to a dark red or almost black meat color. Easily stressed animals have a depletion of glycogen in the muscle and increased muscle pH. The metabolic changes reduce shelf life and consumers associate poor quality, toughness and bad flavor with darker meat.

Selecting animals according to their temperament has huge economic implications. The industry prefers calmer animals which reduce the number of injuries due to overly agitated cattle and simplify handling. Even though the physiological advantageous of calmer cattle on production traits are well documented it is still unclear if the spiral HW of the cow can be correlated to production traits of the calf. In this study we investigate the influence of maternal temperament on physiological traits of the calf. The traits are calf birth weight, average daily gain (ADG) from birth to weaning, and weaning weight.

MATERIAL AND METHODS

Observations were made in compliance with Colorado State University Animal Care and Use Committee Protocol IACUC # 10-2267A.

1. Animals and Environment

This study was conducted in addition to the investigation of maternal protectiveness and separation behaviour of cows (Flörcke et al., 2012). The study was conducted on a commercial cow-calf ranch near Byers, Colorado, USA, in 2011 (the same herd as in chapters 2 and 3 was used). Ninety-five percent of cows were commercial Red Angus and the remaining 5% were Red Angus x Hereford commercial crossbreds. Free-ranging multiparous cows (total herd: N = 836), 3-6 years of age, which were maintained in an open pasture were used. The ranch used natural service with multiple-sire mating using 55 Red Angus bulls. Paternity of progeny was not analyzed. Calving season started in early February and lasted until June, 2011.

2. Cow weight, cow age and hair whorl pattern (HW) collection

The weight, age and HW on the forehead of all cows were recorded in 2010. This was done while the cows were in a squeeze chute for routine handling procedures. By stepping in front of the cow, the experimenter identified the HW of the individual cow and then drew it on a piece of paper. Afterwards, HWs were classified as being high, middle or low position (Grandin et al., 1995). The eye-line is used as a reference point. Hair whorls were further classified as being abnormal, multiple (more than one, all with a clear center) or none (no HW on forehead). Classifications are mutually exclusive and animals are classified into one of these six groups.

3. Calf weight and weaning weight

Within the first 24 h after birth, ranchers weigh and ear-tag calves. A hand-held scale (range 0-160 lbs; model: Hanson 8916, Taylor Precision Products, Oak Brook, IL, USA) was used to obtain calving weights. At this incidence, ranchers would also apply castration bands to male calves. Individual weaning weights of steers were obtained on average after 187 days after parturition and weights of heifers on average after 227 days. We corrected for the different lengths until weaning in all statistical models. All weights were collected in lbs and later converted into kg. Complete records (containing: calf birth weight, weaning weight, cow weight, and cow age) were obtained for 507 individuals which were used for analyses.

4. Statistical analyses

Data were normally distributed and variance was homogeneous (Levene's test). All analyses were conducted using SPSS 17.0 (SPSS, Inc.). GLMs were used to analyze the effect of calf gender (steer and heifer) and the six different HWs on the calf birth weight and weaning weight. We analyzed the influence of the cow weight on birth- and weaning weight of calves and additionally corrected for age at weaning. The correction for age at weaning was done by adding the individual days from birth to weaning as a covariate in the model. Further, we used linear backward regression to analyze the calf birth weight, ADG until weaning and weaning weight. The significance level was set to $P < 0.05$, tendencies are recorded at $P < 0.10$ for this study and graphs show mean values with standard error bars.

RESULTS

Calf birth weight and weaning weight were influenced by the gender of the calf (GLM: birth weight by gender: $F_{1,505} = 25.096$, $P < 0.001$; Weaning weight by gender: $F_{1,505} = 47.201$, $P <$

0.001; steers were heavier than heifers) and by the cow weight (GLM: birth weight by cow weight: $F_{1,505} = 17.790$, $P < 0.001$; Weaning weight by cow weight: $F_{1,505} = 27.976$, $P < 0.001$; heavier cows gave birth to/weaned heavier calves). There is a tendency for HW to affect the calf's birth weight (GLM: birth weight by HW: $F_{5,505} = 1.904$, $P = 0.093$; cows with a middle HW gave birth to the heaviest calves) and a significant influence of HW on the weaning weight (GLM: weaning weight by HW: $F_{5,505} = 2.313$, $P = 0.043$, cows with abnormal non-spiral HWs were weaning heavier calves compared to normal round spiral HWs). Differences in weaning weight by HW are shown in Figure 4-1. Calves from cows with abnormal non-spiral HWs had greater weaning weights than calves from cows with normal round spiral HWs. Cow age did not have an effect on calf birth weight (Figure 4-2) but affected the ADG of calves as well as the weaning weight (Table 4-1). Older, more mature cows, produced calves with greater ADG and heavier weaning weights (Figure 4-2).

DISCUSSION

Environmental and gestational maternal influences impact developing physiological characteristics and production traits of calves. We were able to replicate the results of former researchers regarding calf birth weight, ADG until weaning and weaning weight (e.g.: Gregory et al., 1950; Koch, 1972; Bourdon and Brinks, 1982; Holland and Odde, 1992). The following results of this study are in agreement with former research: (1) Male calves are heavier at birth and at weaning than female calves, (2) heavier cows give birth to/wean heavier calves compared to skinner cows and (3) calves of older cows (cow age: 5 years and up) gain on average more weight per day and have higher weaning weights than calves of younger cows. Male calves are genetically predisposed for being bigger compared to female calves which explains the weight difference at birth and weaning. Heavier cows are often mature cows which are fully grown. These cows can invest more resources in reproduction and milk production than younger cows that are still growing. These findings also represent the energy investment of the cow during different stages of age (Ferrell and Jenkins, 1985). Younger cows are immature and they need resources for body growth which reduces calf birth weight (Ferrell et al., 1976) whereas older cows can invest more in their offspring.

Further, we investigated the influence of maternal temperament, measured by HW, on the production traits of calves. Analysis regarding the influence of maternal temperament on production traits, measured by the HW of cows, revealed that the weaning- but not the birth weight was affected by the HW. The paper by Arnold et al., (1990) partly explains this finding because Angus cattle have been selected for low birth weights and high yearling weights. Therefore, we would not expect a difference in birth weight. Mean weaning weights of calves from cows with an abnormal non-spiral HW exceeded all other HW groups. However, selection for an abnormal HW should be avoided since bulls with an abnormal HW tend to have greater semen abnormalities and an increased risk of not passing breeding soundness exams (Meola et al., 2002; Meola et al., 2004; Evans et al., 2005). Even though weaning weights of calves with abnormal HW were significantly higher than those of other groups this may reflect a random coincidence.

CONCLUSIONS

The temperament of a cow, measured by the spiral HW on the forehead of the animal, had an effect on the weaning weight of calves. Cows with abnormal, non-spiral HW weaned the heaviest calves. Other calf traits such as birth weight and ADG were not affected by the temperament of the cow. Selection towards cows with abnormal HW should however be prevented because earlier findings reported sperm abnormalities in bulls with abnormal HW.

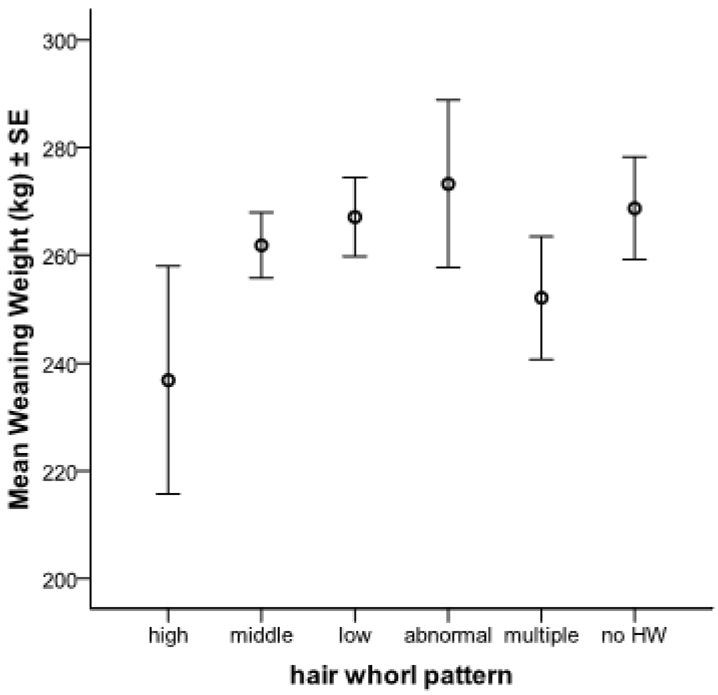
TABLE

Table 4-1: Linear backward regression results for the calf birth weight, average daily weight gain and weaning weights of calves. The initial model included the following independent variables: Cow weight, cow age and calf gender. Not significant variables were deleted stepwise.

Dep. Variable:					
calf birth weight (R^2 = 0.375)					
	B [a]	SE(B) [b]	β [c]	t	Sig. (*P*)
cow weight	0.009	0.002	0.216	5.211	< 0.001
calf gender	2.094	0.288	0.301	7.278	< 0.001
average daily weight gain (calf) (R^2 = 0.519)					
cow age	0.041	0.005	0.299	7.831	< 0.001
calf gender	0.128	0.012	0.415	10.870	< 0.001
weaning weight (R^2 = 0.374)					
cow age	11.188	1.576	0.294	7.101	< 0.001
calf gender	20.905	3.563	0.243	5.867	< 0.001

[a] = unstandardised Regression coefficient B
[b] = Standard error of B
[c] = standardised Regression coefficient β

FIGURES



HW	n	high	middle	low	abnormal	multiple	no HW
high	19	-	0.015	0.004	0.002	0.179	0.005
middle	204		-	0.277	0.123	0.128	0.274
low	127			-	0.428	0.028	0.810
abnormal	40				-	0.017	0.603
multiple	57					-	0.036
no HW	60						-

Figure 4-1: Mean weaning weight (kg) classified by hair whorl pattern (HW; GLM: HW: $F_{5,505} = 2.313$, $P = 0.043$) and protected Fisher's LSD Post-hoc statistical results. The table shows corresponding P-values for individual comparisons between the groups.

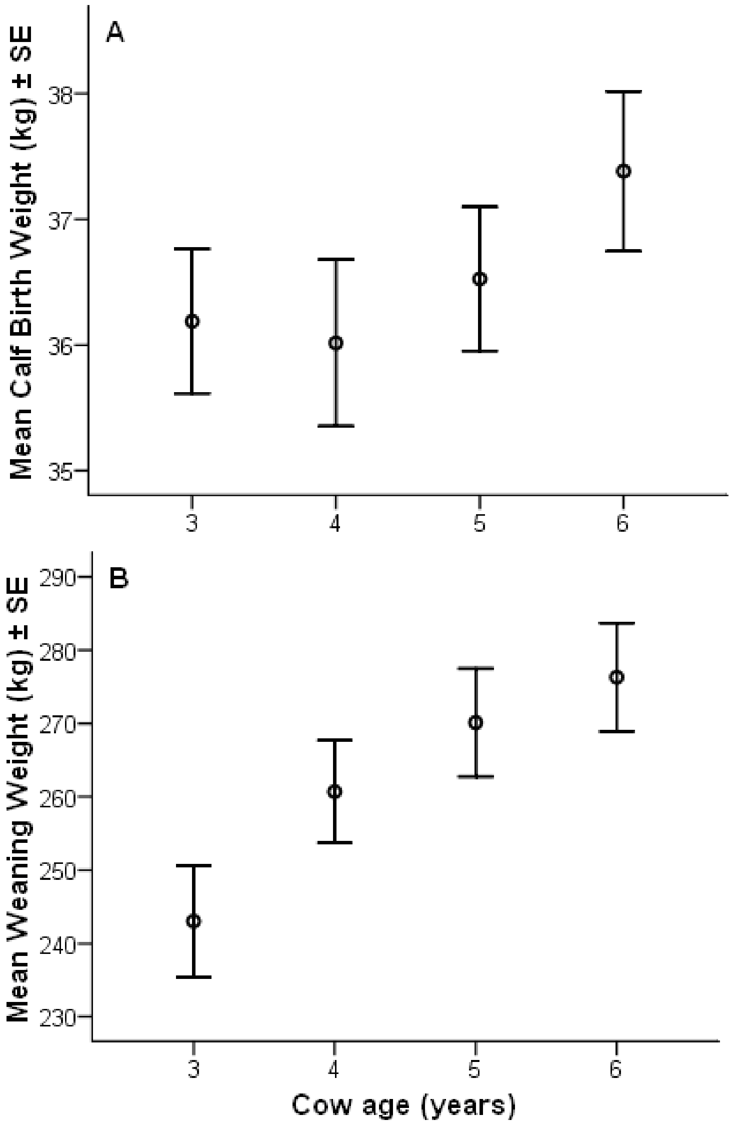


Figure 4-2: A) Mean calf birth weight (kg ± SE) by cows' age: $P = 0.593$ and **B**) mean weaning weight (kg ± SE) by cows' age: $P < 0.001$.

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CHAPTER 5

COWS WITH NO FACIAL HAIR WHORLS ARE MORE LIKELY TO LOSE THEIR CALF TO PREDATORS

SUMMARY

Managing livestock in areas with wolf (*canis lupus*) predation has become an increasing challenge. Conservation of wolves restricts ranchers from interfering since reintroducing wolves in Yellowstone National Park (YNP) greatly improved the ecosystem. However, rising predation incidences on livestock (depredations) create animosity in local farmers. Temperament selection of livestock, measured by the facial hair whorl (HW) pattern, occurred during the last 15 years and the industry prefers calmer temperament animals. Six HWs occur in cattle (high, middle, low, abnormal, multiple and none), which are mutually exclusive and can be identified by using the eye-line as a reference point. We analyzed depredation of calves near Council, ID in 2011. A herd of 588 Black Angus x Charolais crossbreds (age range: 5-17 years) was used for observations. By analyzing the HW and age of cows in relation to depredations, we could identify a connection between these three factors ($P < 0.001$). The HW of a cow significantly influenced the probability of losing the calf to predation ($P < 0.001$). Cows without the facial HW faced the highest number of losses (probability of 19.6% of losing the calf to predation) compared to other HWs (probability between 0 – 6.1%). An age effect on the probability of losing the calf was also found ($P = 0.023$). Cows over the age of 10 years have an increased probability of losing their calf to predation. Our findings suggest that behavioral differences between cows with different HW patterns exist. Differences in protectiveness or vigilance

towards the surroundings in cows without a facial HW may lead to an increased probability of losing the calf to predation.

INTRODUCTION

A natural conflict arises when the home ranges of predator and prey species overlap. By reintroducing Canadian gray wolves (*Canis lupus*) in Yellowstone National Park (YNP) and Central Idaho in 1995/96 (Bangs and Fritts, 1996) naïve prey species were suddenly exposed to predation. Wolves were extinct in YNP and surrounding areas for 70 years. Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) populations reproduced intensely during this period, thereby over-browsing riparian sites and various tree species (Ripple et al., 2001; Ripple and Beschta, 2003). A trophic cascade occurred by reintroducing wolves (White et al., 1998). Wolf populations decreased elk and deer numbers which, as a result, released the next lower trophic species of cottonwoods, aspen and willows from suppression (Ripple and Beschta, 2004; Beyer et al., 2007). A detailed map of the complexity of interactions in YNP can be found in Smith et al., (2003). The change in predator-prey species abundance was beneficial for the ecosystem (Creel and Christianson, 2009). In YNP and Idaho, wolves were mainly preying on elk (90%) and only occasionally killed livestock (Bangs, et al., 1998; Smith, et al., 2003). Overall, the reintroduction was seen as a great success because wolf populations became established after only two years (Smith and Bangs, 2009) instead of the predicted 3-5 years after reintroduction.

The almost exponential reproduction of wolves resulted in increased predation losses of livestock, called depredation. Stalking, harassment and depredation of wolves on domestic livestock is creating public concerns, causes financial problems for ranchers and animosity (Fritts et al., 2003). Overall, livestock depredations are minimal but the ramifications for an individual producer are significant because depredations are not distributed evenly. Certain producers experience higher losses than others (Muhly and Musiani, 2009) creating a challenge for wolf conservation and management in these areas (Fritts et al., 2003). In the presence of wolves, wild ungulates change their behavior (Creel and Christianson, 2008; Preisser and Bolnick, 2008) and movement patterns to avoid predation (Fortin et al., 2005). Anti-predator behaviors of elk during summer months include habitat changes by moving to higher elevations with steeper slopes (Creel et al., 2005; Mao et al., 2005) and increasing the group size (Hebblewhite and Pletscher, 2002; Creel and Winnie,2005; Jayakody et al., 2008). Due to increased fear, prey animals also increase their vigilance level (Berger et al., 2001; Laundré et al., 2001; Hamel and Coté, 2008; Li and Jiang, 2008). With elk being out of reach during summer months, wolves start to prey on livestock (Musiani et al., 2005).

Anti-predator behaviors of our domesticated livestock species, such as cattle and sheep, are however poorly developed because of artificial selection towards calmness over many generations (Price, 1984; Diamond, 2002). Most livestock species do not regularly face predators and show weak or no response to predator presence compared to wild ungulates (Price, 2002). Welp et al., (2004) reported vigilance levels of dairy cows as a potential measure of fear. Cows in their experiment differed in vigilance level based on the environment and novelty of the stimulus. In general, cattle vigilance is increased and foraging behaviors decreased when wolf stimuli are present; contrariwise, vigilance decreases when deer stimuli are presented (Kluever et al., 2009). The former study was able to shed light on the connectedness of ungulate-predator behaviors. Other research found that the vigilance level after parturition of beef cattle varies according to the facial HW of the cow (Flörcke et al., 2012). Cows with middle spiral HW and multiple HWs pay more attention to their surrounding and react earlier to an unknown approaching object (at a greater distance) than cows with other HWs (Flörcke et al., 2012). Increased vigilance in areas with high predation pressure could potentially make the difference between life and death for an animal. The facial HW is frequently used as a measure of temperament and can be identified easiest when the animal is in a squeeze chute (Grandin et al., 1995; Randle, 1998). Limousine breeders were using temperament selection during the last 15 years, thereby altering and improving the docility of cattle (Hyde, 2010).

Advantages of temperament selection are higher average daily gain of calmer cattle (Voisinet et al., 1997), improved human-cattle interactions (Boivin et al., 1992), easier transport (Grandin, 1997) and reduced fear (Brouček et al., 2008). However, recent increases in depredation raise the question if we out-selected protectiveness and fearfulness of our livestock species. The present study tries to identify a connection between the temperament of an animal, measured by the facial hair whorl pattern, and depredation losses of cattle in areas with increased predation.

MATERIAL AND METHODS

Observations were made in compliance with Colorado State University Animal Care and Use Committee Protocol IACUC # 10-2267A.

1. Animals and Environment

This study was conducted on a commercial cow-calf ranch near Council, Idaho, USA, in December 2011. The age range of cows was 5-17 years (average age: 7.4 years) and the total herd consisted of 588 cows (commercial Black Angus x Charolais crossbreds). During winter months, cows graze at lower elevations close to the barn (public land: ~15.000 acres, deeded land: ~ 5.000 acres) and are fed supplement and hay. During summer months cows graze at higher elevations on public and deeded land (public land: ~120.000 acres, deeded land: ~20.000 acres). Summer pastures consist of steep slopes and rough terrain which can only be accessed on horseback in most areas. Wolves represent the main predator during summer months and frequently injure and kill calves and even cows since grazing pastures and wolf territories overlap.

2. Cow age and hair whorl pattern (HW) collection

Age and HW on the forehead of all cows were recorded while cows were in a squeeze chute for pregnancy diagnoses. The experimenter identified the HW position and drew it on a piece of paper. Hair whorls were classified as being high, middle or low position (Grandin et al., 1995). Using the eye-line as a reference point, HW were further classified as being abnormal, multiple (more than one, all with a clear center) or none (no HW on forehead). A detailed description of the HW patterns is shown in chapter 3, Figure 3-1. Classifications are mutually exclusive and animals were classified into one of these six groups.

3. Statistical analyses

All data was analyzed using SPSS 20.0 (SPSS, Inc.). A binomial logistic regression was performed to analyze the probability of losing a calf. The dependent variable in the model is the 'loss of a calf' (0 = alive/1 = dead). Covariates are the hair whorl pattern (high, middle, low, abnormal, multiple and none) and the age of the cow (age range: 5-17 years). The logistic regression allows calculating the probability of losing a calf due to the hair whorl pattern and age of the cow. A Wald chi-square test is integrated in the model to indicate how well the logistic regression fits the data. The significance level was set to $P < 0.05$ for this study.

RESULTS

By analyzing the HW and age of cows in relation to depredations, we could identify a connection between these three factors ($P < 0.001$). The numbers and percentages of cows in each HW group are shown in Table 5-1. The average age of a cow in this herd was 7.4 years. The percentage of cows losing a calf to predation varied with the HW pattern ($P < 0.001$; Table 5-1). Even though cows with middle and low HW are numerically represented highest in the herd, the total number of losses within these two groups was relatively low. No cows with an abnormal HW lost a calf in 2011. The group of cows without a HW, on the other hand, lost 19.6% of calves. The age of the cow further influences the probability of losing the calf due to predation ($P = 0.023$). Figure 5-1 shows the probability of losing the calf in relationship to the age and HW of the cow. Cows in the age range of 5 to 10 years with high, middle, low, abnormal or multiple HWs have a probability between 2 - 8% of losing the calf to predation. Cows without a HW have a much higher probability of losing the calf starting at 15% and increasing up to 25%. The overall distribution of calf losses by the age of cows is shown in Table 5-2. Twenty young cows in the age of five and six years lost their calf, only a few middle aged cows were subject to predation and ten cows at age 14 lost their calf.

DISCUSSION

We identified a connection between the facial HW as well as the age of the cow and the probability of losing the calf to predation. The type of HW on the forehead of the cow can be associated with the probability of losing the calf. In our study, cows with high and abnormally shaped HW had the least number of losses in the herd. This may be explained by the increased vigilance of cows with high and abnormal HW as observed in the research of Flörcke et al., (2012). Cows in the former study paid more attention to their surroundings, thereby allowing themselves and their calf more time to react and retreat in case of a predator approach. Vigilance is an indicator for fearfulness as shown in dairy cows by Welp et al., (2004). By being less vigilant and fearful, cows in the present study may have lost their calf to predators.

Cows without a facial HW have a five-time higher probability of losing the calf to predation compared to cows with other HWs. In humans, the skin, neural tube and the nervous tissues develop during the third and fourth week of gestation (Drolet et al., 1995) and this is comparable to cattle. Hair follicles start to develop at week 10 and are extruded by week 18 of gestation in humans and cattle (Smith and Gong, 1973; Smith and Greely, 1978). The HW, or cowlick (in humans) can give information about the neuronal development. For simplicity purposes we will refer to cowlicks as HW as well. Failures of proper development during early gestation can lead to a ‘hair collar’ in humans (Drolet et al., 1995). Neuronal changes underlying a hair collar can be agenesis of the corpus callosum or a Dandy-Walker malfunction. In humans, abnormal scalp-hair patterning can indicate brain malfunctions (Smith and Gong, 1973). Without a parietal hair whorl, infants show severe brain deficits and most stillborns do not have a parietal HW (Higginbottom et al., 1979; Faye-Petersen et al., 2006). Cows without a facial HW lost more calves than any other group of cows in the present study. The absence of a facial HW may imply that cows without a HW have neuronal aberrations compared to other cows.

While collecting observational data on maternal protectiveness, the first author noted abnormal behaviors of young calves without a HW. The temperament of an animal, measured by the facial HW, has a moderate heritability (German Angus 0.61 ± 0.17, Simmental 0.59 ± 0.41; Gauly et al., 2001). Without paternity testing, we are however unable to determine the HW pattern of the calf, since both, the maternal and paternal HW pattern can shape the calf’s HW. It is unlikely that paternal behavioral influences occur during the calf's development. Bulls are kept separately from the cow herd and the behavior of calves is most likely shaped by the mothers influence. Cows are hider species and calves stay hidden between bushes during the first days while cows are foraging nearby (Langbein and Raasch, 2000). The normal reaction of a calf to an approaching unknown object/person is to jump up, call loudly for the mother and to run away. Calves without a HW, on the other hand, kept lying between bushes and allowed the first author to pet them all over the body. In case of an approaching predator this calf would probably die. The high number of calf losses of cows without a facial HW might be a combination of the reduced fear of the calf and possibly lower levels of protection of the cow. Cattle research in Canada identified alterations of the movement pattern and nearest neighbor distance in response to predator presence (Laporte et al., 2012). Anti-predator behaviors of cattle in the former study seemed, however, erratic and inconsistent. Since most cattle do not experience predation during their lifetime the question arises if the industry is selecting against anti-predator behaviors (Price, 1999)?

The age of a cow further influenced the probability of losing the calf to predation. The age range of cows observed in this study was 5-17 years, with an average of 7.4 years which represents a typical beef herd in the U.S. (http://www.agtoursusa.com/BeefCattleUSA.htm). Several young cows (5 and 6 years of age) lost their calves to predation. Younger cows may have less experience when encountering predators (Laporte et al., 2010) and react unadept. Social animals, such as cattle, are able to learn and alter their behavior based on their own or a conspecifics experience (Griffin, 2004). Usually, wolf depredations increase in later summer (August and September) as shown by Dorrance (1982), whereas bears and coyotes attack younger calves in early summer. Other studies also confirmed that calves younger than 9 months are the most frequent killed animals within the herd (Palmeira et al., 2008). To our knowledge, this is the first study showing an age effect of the mother on the probability of losing the calf to predation. While immature younger cows are at risk during calving (chapter 3), it appears that older cows over the age of 10 years have an increased probability of losing their calf. Anti-predator behaviors are most likely to occur when the predator and prey species naturally occur within the same area. This was found by Parsons et al., (2007), who showed that a familiar predator species (dingo (*Canis dingo*)) can elicit an anti-predator behavior in gray kangaroos (*Macropus giganteus*) whereas an unfamiliar predator species (coyote (*Canis* *latrans*)) elicits a much weaker response. Here, the inexperience of younger cows (5 and 6 years of age) may have contributed to depredation losses since slightly older cattle show a reduced amount of losses. Ongoing research in the areas of predator-prey/livestock interactions, human-wildlife conflict and animal behavior will be needed to support carnivore conservation and maintain ranch practices.

CONCLUSION

Temperament selection of livestock species and especially cattle during the last 15 years has led to calm and easy to handle cattle. With the reintroduction of Canadian gray wolves in the Northern Rocky Mountains, ranchers face a new challenge. Without defined protective abilities, losses in cattle have increased since cows perform only minor protective behaviors in response to a predator approach. Our study showed an age and temperament effect on the probability of a cow to lose the calf to predation. The HW on the forehead of cows was used as a measure of temperament. While cows with high, middle, low abnormal and multiple HWs have an average probability of 0 – 6.1% of losing the calf, cows without the facial HW have a greatly increased probability of 19.6%. Further, with increasing age the predation probability increases, too. To our knowledge, this is the first study showing a connection between animal temperament and predation losses in cattle. Further research around livestock-predator interaction needs to be conducted to continue wolf conservation in areas with high predation pressure.

TABLES

Table 5-1: Distribution of hair whorl pattern in the observed herd and distribution of calves alive/dead in 2011.

Hair Whorl Pattern	n	Alive	Alive in %	Dead	Dead in %
High	35	34	97.1%	1	2.9%
Middle	214	201	93.9%	13	6.1%
Low	179	171	95.5%	8	4.5%
Abnormal	53	53	100%	0	0%
Multiple	51	48	94.1%	3	5.9%
None	56	45	80.4%	11	19.6%
Overall	588	552	93.9%	36	6.1%

Table 5-2: Distribution of calf losses by hair whorl pattern and age of cow and the overall number of cows per age group. Age of cows ranged from 5-17 years.

		Hair Whorl Pattern						
Age	**n**	**High**	**Middle**	**Low**	**Abnormal**	**Multiple**	**None**	**Overall**
5	150	-	2	3	-	1	5	11
6	129	-	6	2	-	-	1	9
7	82	-	-	1	-	-	-	1
8	64	1	1	-	-	-	1	3
9	47	-	-	-	-	-	1	1
10	45	-	-	-	-	-	-	0
11	24	-	-	-	-	-	-	0
12	18	-	-	1	-	-	-	1
13	7	-	-	-	-	-	-	0
14	14	-	4	1	-	2	3	10
15	4	-	-	-	-	-	-	0
16	2	-	-	-	-	-	-	0
17	2	-	-	-	-	-	-	0
Overall: 588		1	13	8	0	3	11	**36**

FIGURE

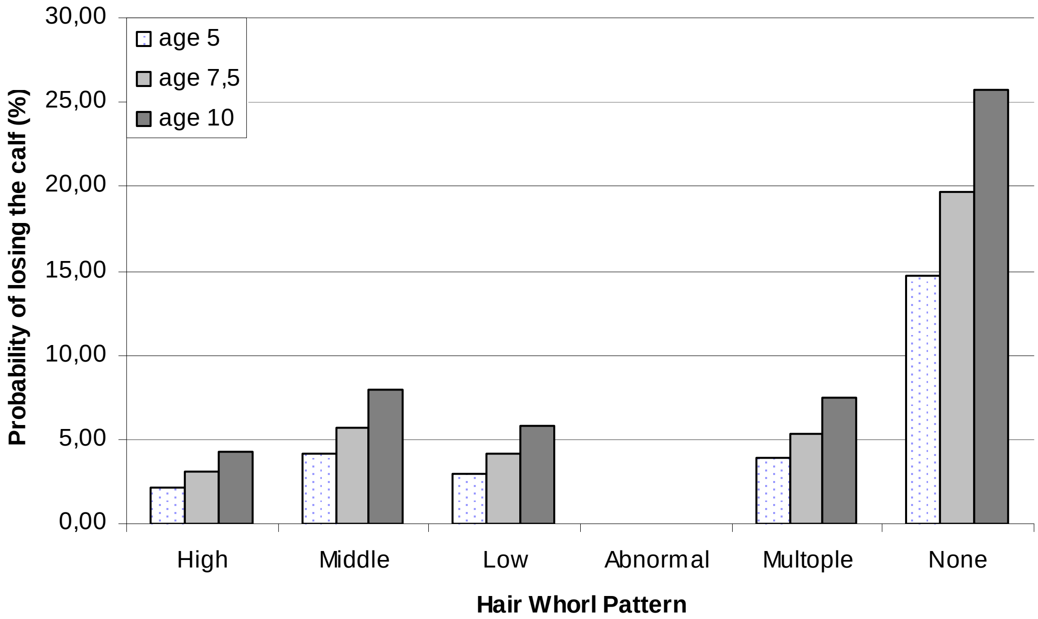

Figure 5-1: Probability of losing the calf to predation based on the age and the hair whorl position of the cow. Presented are probabilities for losing the calf for the age groups 5, 7.5 (average age of a cow in this herd) and 10 years. Probabilities for cows with an abnormal hair whorl are not shown since no depredation occurred in 2011.

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LIST OF ABBREVIATIONS

ADG	Average daily gain
BCS	Body condition score
CO	Colorado
HW	Hair whorl pattern
ID	Idaho
MAS	Marker assisted selection
MBS	Maternal protective behavior score
QTL	Quantitative trait loci
YNP	Yellowstone National Park