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Correlates of rank in female groups of Bighorn Sheep, Ovis canadensis

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Correlates of rank in female groups of Bighorn Sheep, *Ovis canadensis*

by

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Abstract

In many animal groups it is common to find a social structure. This social structure can come in the form of a dominance hierarchy in which high ranking individuals possess control over resources. Common correlates of dominance are body mass, age, and weapon or ornament size. Bighorn sheep (*Ovis candensis*) have been shown to establish linear dominance hierarchies in their sexually segregated groups. The type of hierarchy, correlates of dominance, and advantages and disadvantages of dominance for female groups were explored. Data analysed did not support the idea that ewes establish linear dominance hierarchies but did support that rank is correlated with age, and mass but not horn length. High ranked individuals had the advantage of leadership but the disadvantage of peripheral positions. No fitness consequences were associated with rank.

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CHAPTER ONE – CORRELATES OF BIGHORN RANK

Introduction

The most noticeable sexually dimorphic characteristic of bighorn sheep, the species of interest for my thesis, is their body size. In a study of bighorns from Ram Mountain in Alberta, rams were 75% heavier than ewes (Pelletier and Festa-Bianchet, 2006). It is differences such as these that lead to their sexual segregation (Ruckstuhl and Neuhaus, 2005). Among bighorn sheep groups there are sometimes one or a few individuals of the opposite sex within a primarily single sex group and they don't seem to be excluded from group activities (Ruckstuhl, 1998). Bighorn sheep establish linear dominance hierarchies in their social groups (Geist, 1971). Bighorn rams compete against each other during the breeding season for access to ewes in oestrous (Hogg and Forbes, 1997). During this time they establish a linear dominance hierarchy and their rank in the hierarchy directly impacts their reproductive success (Hogg and Forbes, 1997). The idea that dominance in males would affect reproductive success is not surprising; for dominance to evolve there should be some advantage for dominant individuals such as siring a greater proportion of offspring than their subordinates. For rams, dominance is a major determinant of reproductive success, and 10-15% of the rams acquire 50-60% of the paternities (Pelletier and Festa-Bianchet, 2006). Male dominance structures which provide mating opportunities exist in a diverse array of animal species, including bighorn sheep (Pelletier and Festa-Bianchet, 2006), green swordtail fish, *Xiphophorus helleri* (Earley and Dugatkin, 2006), gorillas, *Gorilla gorilla beringei* (Robbins, 1999), dung beetles, *Onthophagus acuminatus* (Emlen, 1997).

Since previous studies (Festa-Bianchet, 1991; Eccles and Shackleton, 1986) showed that bighorn females do form dominance hierarchies but that rank was not correlated with resource acquisition or measures of reproduction in ewes, I designed a study to examine a female bighorn dominance hierarchy and its possible advantages or disadvantages.

Several factors such as age, mass and horn size may affect the dominance structure of the ewes in the study. Also, there are a number of benefits that a ewe might receive by being dominant. For instance, she may benefit by being a group leader and thus being able to dictate the group movements and activity budget. This would allow her to lead the group in her preferred direction to acquire food, water, and rest when it is optimal for her. The dominant female may also benefit by getting superior positions within the groups while bedded and grazing (McFarland, 1999). A dominant female may frequently acquire position in the middle of groups and be more secure from predators there than individuals on the periphery of groups (Krebs and Davies, 1993).

Knowledge of female social structure and benefits of dominance will contribute to a better understanding of sexual differences in life history evolution, reproductive success, population dynamics, and the overall ecology of bighorn sheep. Bighorn sheep make a good study species to address my hypotheses because they are easy to observe, group-living, sexually dimorphic, sexually segregated, and both females (ewes), and males (rams) are known to form dominance hierarchies (Favre et al., 2008; Pelletier and Festa-Bianchet, 2006; Festa-Bianchet, 1991).

Hypotheses, Research Questions and Predictions

I explored the following hypotheses, research questions and made the accompanying predictions:

1. Physical characteristics influence dominance rank in bighorn sheep. Are there any physical characteristics of the sheep that could be used to predict rank in an established population? My prediction is that age, mass and horn size will be positively correlated with rank in the hierarchy because age has been shown to be correlated with rank previously (Archie, 2006; Cote, 2000) and mass and horn length are known to increase with age. Age may be a strong correlate of rank because with age comes experience.

2. Dominance rank influences behaviour of bighorn sheep. Can some observable behaviours be explained by rank in the established hierarchy? I predict that high ranked females will be the leaders of groups, will take positions with a greater number of immediate neighbours in laying groups, and will more frequently initiate agonistic interactions because these behaviours produce fitness benefits.
3. Dominance rank influences the fitness of bighorn sheep. Are there any ultimate advantages to being a high ranked ewe? My prediction is that rank will be positively correlated with reproductive success and survival because these advantages could help explain the evolution of the establishment of rank in bighorn sheep.

Methods of Data Collection

The field research for this study took place in Sheep River Provincial Park. The park is located in Alberta, Canada in the foothills of the Rocky Mountains, 100km southwest of Calgary. The park is known to be the over-wintering grounds for a well studied, ear-tagged population of bighorn sheep (and some non-residents) (Ruckstuhl, 1998). All measurements and observations were made between September 30th 2007 and May 15th 2009. Approximately 1360 hours of observations were made of the sheep in the park. Observations were taken between the hours of 8:30am and 4:30pm. Daylight hours were the best times to observe because the ear-tags become difficult to distinguish in dim light. Observations could still be made in overcast weather but during periods of heavy snowfall I was unable to see the sheep well enough to identify individuals. During observations, I positioned myself from 10 to 100m away and used the naked eye or a spotting scope to view the sheep. A total of 155 instances of agonistic interactions were recorded between female sheep in the study population (Appendix A). The interactions were recorded for use in determining the females' dominance hierarchy. All agonistic interactions observed were recorded ad libitum including the ID's of the sheep, a winner and loser of the interaction and the type of interaction. The winner of an interaction was the individual that cause another to concede, by moving away, and was the initiator in all but 4 interactions. The types of interactions observed included mainly 'threats' in which one sheep was observed lowering its horns towards another, 'displacements', in which one sheep caused another to move from their standing or bedded position without contact, 'horn butts' in which one sheep contacts another's body with her horns, and 'horn clashes' in which the pairs horns contacted each other. The outcome of these interactions were then placed into a dominance matrix (Figure 1) and analysed using the computer program ‘MatMan’ (Noldus Information Technology, 1998). MatMan calculated Landau’s Linearity Index (corrected for unknown relationships), the Directional Consistency Index, and the individual rank of each sheep within the hierarchy. This program has been used for similar calculations in previous studies (Pelletier and Festa-Bianchet, 2006; Hirsch, 2007; Ceacero et al, 2007; Andersen and Boe, 2007) and its use as a tool for analyzing dominance is discussed in further papers (deVries, 1993); deVries,1995; deVries, 1998).

The exact age of all the resident bighorn sheep is known as all animals were caught and tagged as lambs. Individual information on mass and horn size was recorded, and data were collected regarding sheep leadership, decision making, and bedded position relative to other sheep in their group (see detailed methods below). Individual rank in the dominance hierarchy was compared with age, mass and horn size to test whether these factors were correlated with rank. Sheep mass was recorded ad libitum on any day that observations were being made. Proximity of the sheep to a suitable location for the scale primarily determined when mass measurements were taken. The measurements were taken using a free-standing platform scale baited with a salt block. Natural saltlicks are important for the sheep and in short supply so they are attracted to the salt block (Ayotte et al., 2006). The electronic scale was placed on a flat section of the paved park road and tarred to zero kilograms. Certain sections of the road are clear of snow in the winter due to melting from direct sunlight. Barriers were placed, and secured with heavy stones, on either side of the scale allowing only one sheep to stand on the scale at a time (Figure 2). The scale had been used for a number of years in the population and the sheep were accustomed to it. The digital remote readout was observed from 50 metres away within viewing distance of the scale to allow witness of all 4 of the sheep's hooves on the scale.

Horn size was measured remotely so that the sheep did not need to be captured; live captures are costly and there is always a risk to the animal. The device used to measure the horns was a bracket on which 2 lasers and a digital single-lens reflex camera, with an 18-200mm zoom lens, were mounted and then secured to a tripod (Figure 3). This setup was used in a previous study on ibex (*Capra ibex*) in which the device was found to have a high degree of accuracy when compared to manual measures (Bergeron, 2007). The laser beams were shone parallel to one another onto a horn. With the attached camera the observer took a photo of the horn with laser points visible. The distance between the two laser points was a known fixed distance of 4cm so the size of the horn was extrapolated from the photograph (Figure 4). The computer program 'Image J' (National

Institutes of Health) was utilized to extrapolate horn size from the photographs. Using this software, a line was drawn from the centre of one laser point to the other and the known length of 4cm was assigned to that line. Another line, or curve in this case, was drawn to follow the curve of the sheep horn from base to tip similar to where a measurement would be taken on a live sheep. The length of the second line was calculated by the software from the length of the first line. Since the angle at which the horn was photographed would affect the apparent length of the horn, multiple photographs of each horn were taken and the longest measurement was used for the horn length value. Of the 27 sheep in this study I gathered horn length measurements for 18 of them, using between 2 and 31 photographs for each sheep.

To assess possible advantages and disadvantages of being a dominant female, some measures of leadership, position within groups, first access to a limited resource (salt block and hay), survival and reproductive success were recorded. To assess whether dominant females were the group leaders, the individual that initiated group movements and appeared to be leading a moving group through its front position, and those that followed, was recorded when a change in behaviour took place. A clear, easily observable change in position such as standing from a bedded position or a change in the direction of movement by 90 degrees or more was considered a change in behaviour. For example, a sheep that the others walked behind while actively grazing or the sheep which incited others to stand up and move after a period of resting were considered to be leading the group.

Bedded positions were recorded whenever possible to determine sheep with positions within the group with presumably the greatest protection from predation. To achieve this, a laying position drawing was made by the observer noting position and distance between all sheep relative to one another (Figure 5). The protection afforded by a bedded position was determined from the drawings of bedded groups. A sheep with a higher number of immediate neighbours was considered to have a position of greater protection and advantage. An immediate neighbour was defined as an adjacent sheep in the bedded group that was less than or equal to 3 'sheep lengths' away (approximately 3m).

During times when weighing sheep a salt lick and a small amount of alfalfa hay was available to the sheep. The first sheep to reach the salt lick or hay was recorded at that time, as well as subsequent displacements.

Another assessment of advantage or disadvantage considered was the relative number of agonistic interactions dominants and subordinates engaged in. The number of agonistic interactions was tallied for each ewe and analyzed against the rank of the ewes. The number of interactions was square root transformed for normality.

Using data available from other research done on my study population during other seasons in the same time period as my study I was able to analyze for any relationships between rank and ewe survival, and rank and reproductive success. Ewes were classified as alive during a study year if they were alive at the end of the year. If a ewe died during a study year she was classified as deceased. Lamb survival was used as a measure of reproductive success. A ewe that birthed a lamb which survived to one year of age was considered to have a surviving lamb for the year in which the lamb was born.

Winner

	ID	282	316	580	602	640	724
L	282		3	2	1	4	3
o	316	1		1	3	2	2
s	580				2	3	4
e	602					2	3
r	640				1		5
	724						

Figure 1. A simplified example of a dominance matrix. ID numbers of all individuals are across the top and repeated again down the side. At the intersection of 2 ID's the number of interactions won or lost by individuals are displayed.

Figure 2. A photograph of sheep gathering around the freestanding platform scale. One sheep is standing between the barriers, with all four feet on the scale.

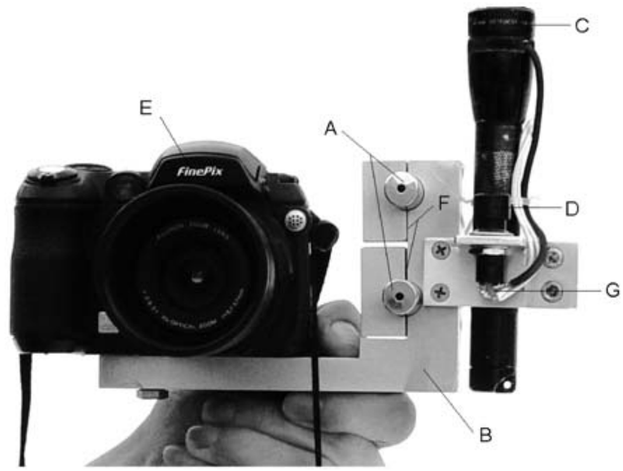

Figure 3. A photograph of the laser bracket with camera attached. a) laser pointers, b) frame, c) battery casing, d) on/off switch, e) camera, f) laser mounting blocks.

Figure 4. A photograph of the laser points, from the laser and camera bracket device, shone on a sheep horn. Horn lengths were determined from these photographs using ImageJ software.

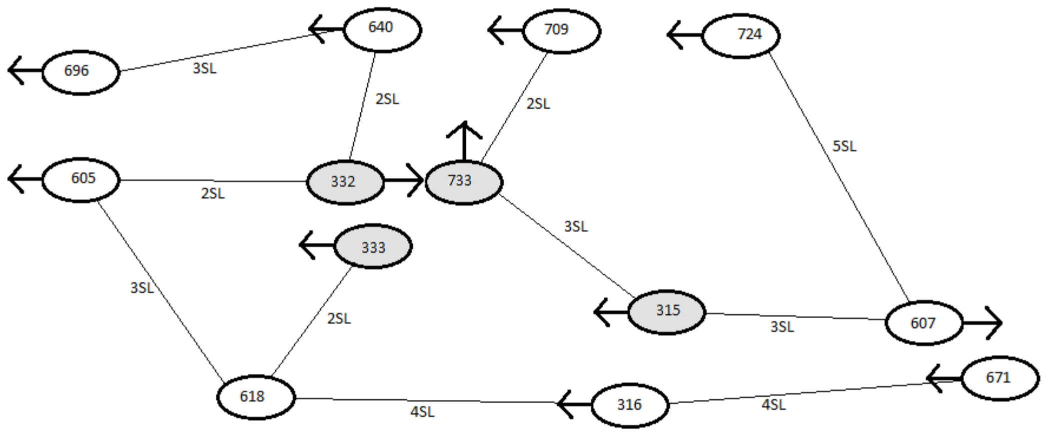

Figure 5. An example of a drawing of bedded positions of sheep (ovals) displaying anterior ends (arrows) and approximate position of and distance between sheep. Distance between sheep is expressed in 'sheep lengths' where 1SL is approximately equal to 1m. Shaded ovals indicate a sheep with a high number of immediate neighbours and therefore a more protected position.

Statistical Methods

The key value generated in the determination of the dominance hierarchy by the MatMan software is Landau's Linearity Index (h'). This value indicates the degree of linearity in the hierarchy based on the analysis of the agonistic interaction data. The Directional Consistency value is also useful in determining what effect circular relationships, instances of a lower ranked sheep winning an interaction over a predominantly higher ranked sheep, have on the hierarchy.

Statistical analysis was performed using JMP 8 and JMP 9 statistical software packages. Where possible, some analysis of correlations was performed using ranks relative to the other individuals within the group rather than the absolute ranks based on the whole population. The relative rank was used for the leadership and laying association data.

The data for the independent variables, horn length, age and mass, were used to formulate a model, using standard least squares, which best predicts rank, the dependent variable. The year the data were collected was also included in the models to look for any interactions. Upon examining the data collected, small sample size (n=4) required the 2009 data to be left out of the model analysis. Horn length data were also excluded from the model because there was no horn length data for 2007 and the data from 2008 alone were not significant. A model containing age, mass, year and their interactions was pared down to find the simplest model. The variance inflation factor, or VIF, was calculated for each effect in the model.

A bivariate fit was used to analyze the data for laying associations; relative rank in a group and the mean number of immediate neighbours for an individual of that rank were used. Leadership was analyzed in the same manner as laying associations; a bivariate fit using relative rank in a group and the mean position of an individual of that rank in a group. Position was quantified as 1=leader, and 0=follower. A bivariate fit was used to analyze the relationship between rank and the number of initiated interactions; the values for initiated interactions were square root transformed for normality. The relationship between rank and reproductive success (lamb survival to one year of age) was analyzed using a logistic fit. For the analysis of ewe survival I also used a logistic regression. In the first two years all ewes survived so I performed no analysis for 2007 or 2008. In 2009, six ewes from my study population were deceased. Since the six ewes had no rank in 2009 I used the 2008 ranks to analyze the relationship between rank and ewe survival for 2009. For all of the statistical analysis there is no need to include random effects because sheep aren't used more than once in each analysis of their correlation to rank, in the population or relative group.

Results

The percentage spread of the various types of agonistic interactions was approximately: threats (12%), displacements (42%), horn butts (25%), horn clashes (13%), other (7%). In only 3% of the interactions the initiator ID was unknown. In 94% of interactions the initiator was also the winner of the respective interaction. The results of the MATMAN analysis of the recorded interactions are presented below. For 2007, Landau's Linearity Index (corrected) was not significant (h' = 0.291667, p = 0.56) and the Directional Consistency was equal to 1. The dominant ewe of the hierarchy was sheep #733 (Table 1). For 2008, Landau's Linearity Index (corrected) was not significant (h' = 0.18, p = 0.10) and the Directional Consistency was equal to 1. The dominant ewe of the hierarchy was sheep #725 (Table 1). For 2009, Landau's Linearity Index (corrected) was not significant (h' = 0.202941, p = 0.39) and the Directional Consistency was equal to 1. The dominant ewe of the hierarchy was sheep #640 (Table 1). The insignificant values of h' indicate that the hierarchies in all three years are not detectably linear. However, the directional consistency values of all three years indicate the absence of any circular relationships.

The standard least squares model containing age, mass, year and their interactions was pared down to find a simpler model (R^2=0.49). Age nearly significantly explained rank in 2007 (P=0.064, VIF=1.47) and mass significantly explained rank in both 2007 and 2008; a mass*year interaction (P=0.0250, VIF=1.26). A model for each year was created because of the mass*year interaction found in the previous model. The two models included the variables age, mass, and an age*mass interaction. The age*mass interactions were not significant in either year. Age was significant in 2007 (R^2=0.41, P=0.0333, VIF=1.13) (Figure 6), and mass was significant in 2008 (R^2=0.52, P=0.0227, VIF=1.39) (Figure 7). Horn length data were left out of the model because of non-significance; a separate correlation analysis of 2008 rank and horn length was completed (R^2=0.043, P=0.50) (Figure 8).

Analysis of the data pertaining to leadership was completed for years 2008 and 2009; no data were available for the year 2007. In 2008, the relationship between leadership and rank was significant, with dominants leading foraging groups (R^2 = 0.266928, p = <0.0337) (Figure 9). In 2009, the relationship between leadership and rank showed the same trend, of high ranked individuals leading groups, but was not significant (R^2 = 0.376125, p = 0.11) (Figure 10).

Analysis of the data of laying associations was completed for years 2008 and 2009; no data were available for the year 2007. In 2008 a significant relationship was found between the number of immediate neighbours a sheep had and their relative rank in that group (R^2 = 0.355061, p=0.0091) (Figure 11). Higher ranked individuals had fewer immediate neighbours. For the year 2009, the results did not show a significant relationship between number of neighbours and relative rank (R^2 = 0.000406, p = 0.96) (Figure 12).

The number of initiated interactions with relation to rank was analyzed for 2007, 2008 and 2009. In 2007 the results were not significant (R^2 = 0.085843, p = 0.14) (Figure 13). The results in 2008 and 2009 showed a significant relationship between rank and the number of interactions initiated (R^2 = 0.343197, p = 0.0013) (Figure 14) and (R^2 = 0.669284, p = 0.0001) (Figure 15) respectively. The trend in all three years showed that high ranked individuals initiated more interactions than lower ranked individuals.

The relationship between rank and lamb survival, as an estimate of reproductive success, for all three years was also analyzed. None of the three years' results were significant; 2007 (R^2 = 0.0172, p = 0.56) (Figure 16), 2008 (R^2 = 0.0557, p = 0.25) (Figure 17), 2009 (R^2 = 0.0085, p = 0.68) (Figure 18).

An analysis of the relationship between rank and ewe survival revealed no significant result despite a trend toward greater survival in lower ranked individuals ($R^2 = 0.0805$, $p = 0.13$) (Figure 19).

Table 1. Table of sheep ranks in the linear hierarchies of 2007, 2008 and 2009. The ID column contains the identification numbers of all sheep used to calculate the hierarchies. Deceased sheep where not included in calculating the hierarchies in the year they died. A rank of 1 corresponds to the highest ranked ewe of that year.

	Rank		
ID	2007	2008	2009
259	27	12	Deceased
282	7	22	3
314	12	11	2
315	18	14	7
316	8	15	Deceased
319	5	16	9
328	21	21	18
332	23	20	21
333	24	17	Deceased
334	14	27	20
596	2	10	10
605	17	26	19
610	15	7	15
612	9	13	16
618	25	5	11
624	20	18	Deceased
630	11	19	12
640	3	9	1
671	19	3	8
685	22	6	13
686	4	25	17
709	26	4	4
724	10	23	Deceased
725	16	1	6
733	1	8	5
734	13	2	14
791	6	24	Deceased

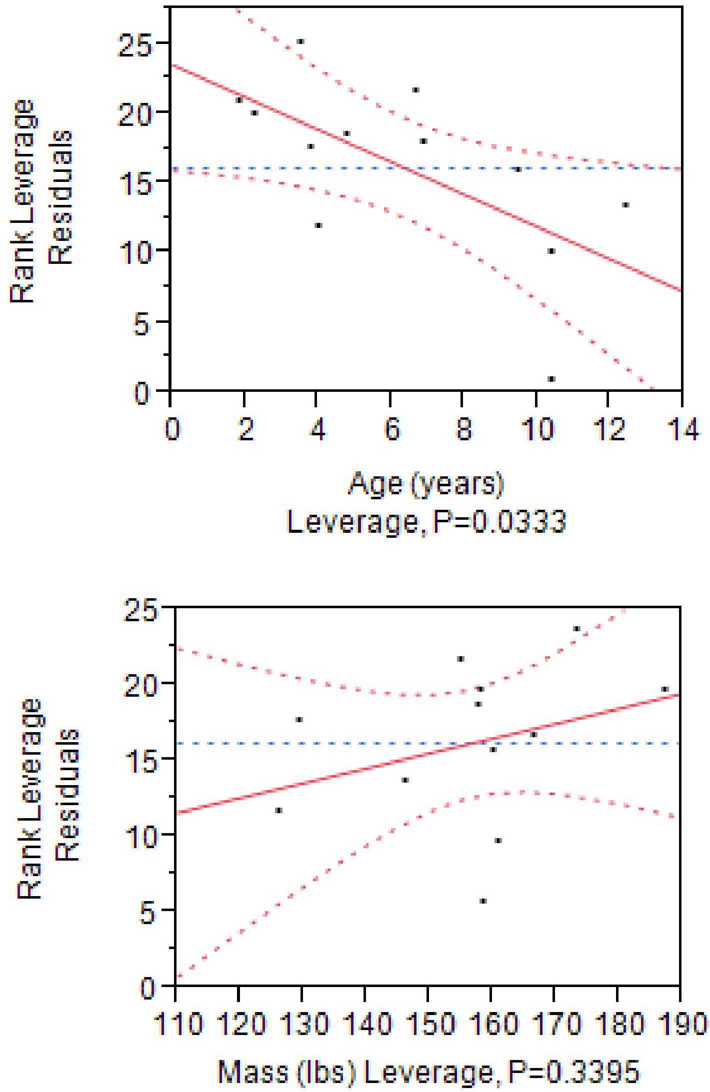

Figure 6. Leverage plots of the relationship between rank and age (top) and rank and mass (bottom) for the standard least squares model of 2007 data. Age and mass are increasing from left to right on the respective x-axis. The y-axis displays rank: high rank is 1 and rank decreases along the axis.

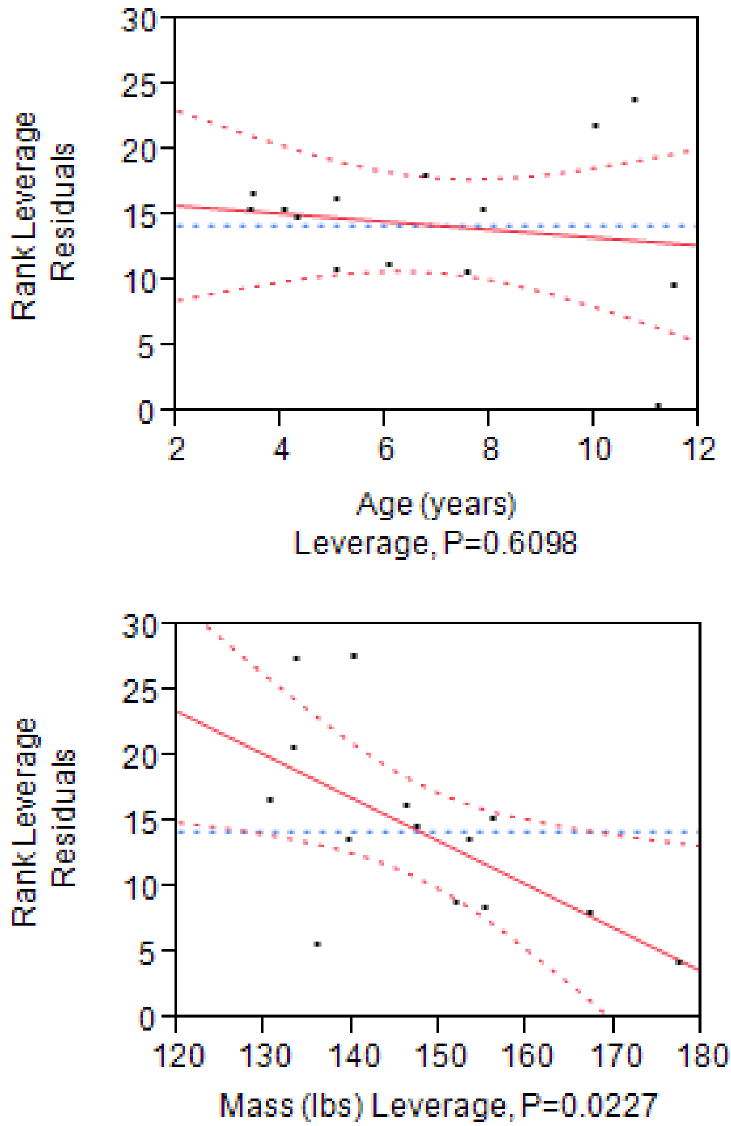

Figure 7. Leverage plots of the relationship between rank and age (top) and rank and mass (bottom) for the standard least squares model of 2008 data. Age and mass are increasing from left to right on the respective x-axis. The y-axis displays rank: high rank is 1 and rank decreases along the axis.

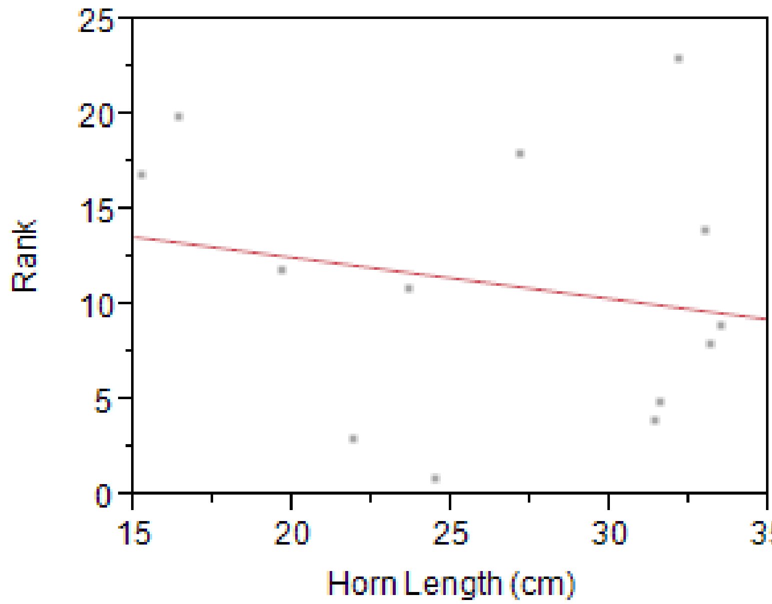

Figure 8. The relationship between horn length and rank for 2008. Horn length is on the x-axis, to visualize the effect it has on rank, and increases across the axis from left to right. Rank is on the y-axis; high rank is 1 and rank decreases along the axis.

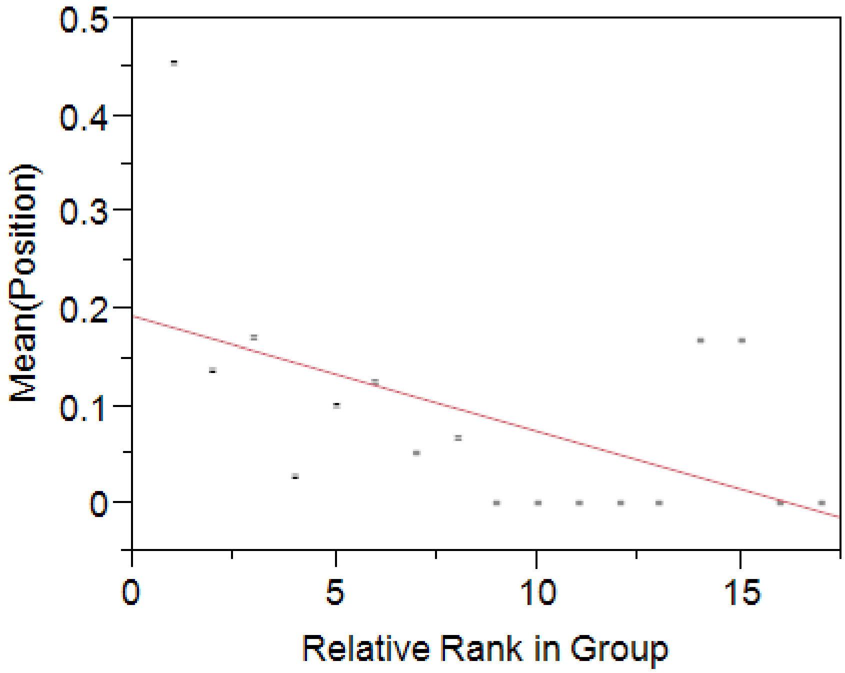

Figure 9. The relationship between relative rank within group and mean position in group for 2008. On the y-axis, the mean position range is from 0 to 1; 1 indicating leadership behaviour was always observed in groups and 0 indicating following behaviour was always observed in groups. High rank is 1; rank is decreasing from left to right on the x-axis.

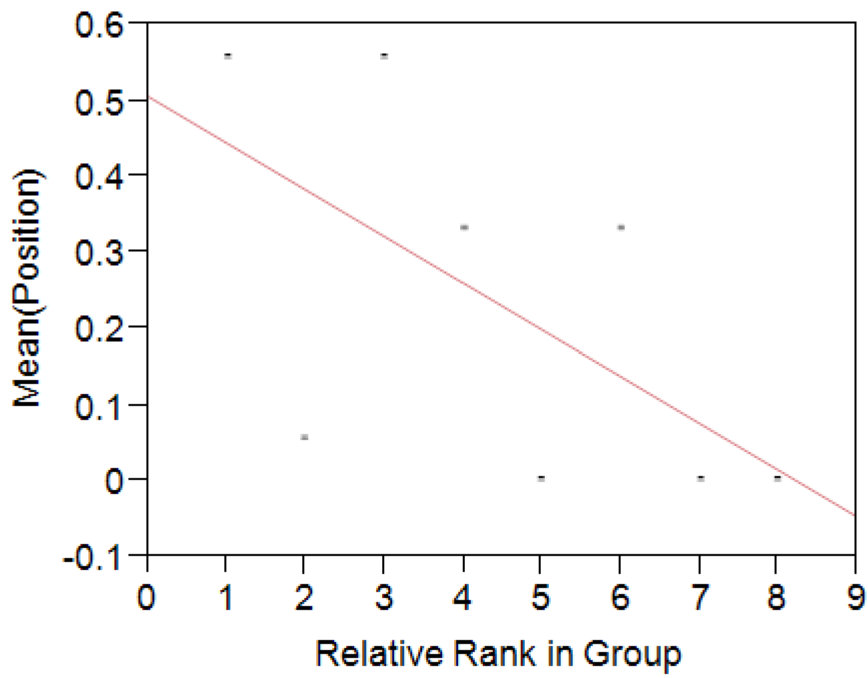

Figure 10. The relationship between relative rank within group and mean position in group for 2009. On the y-axis, the mean position range is from 0 to 1; 1 indicating leadership behaviour was always observed in groups and 0 indicating following behaviour was always observed in groups. High rank is 1; rank is decreasing from left to right on the x-axis.

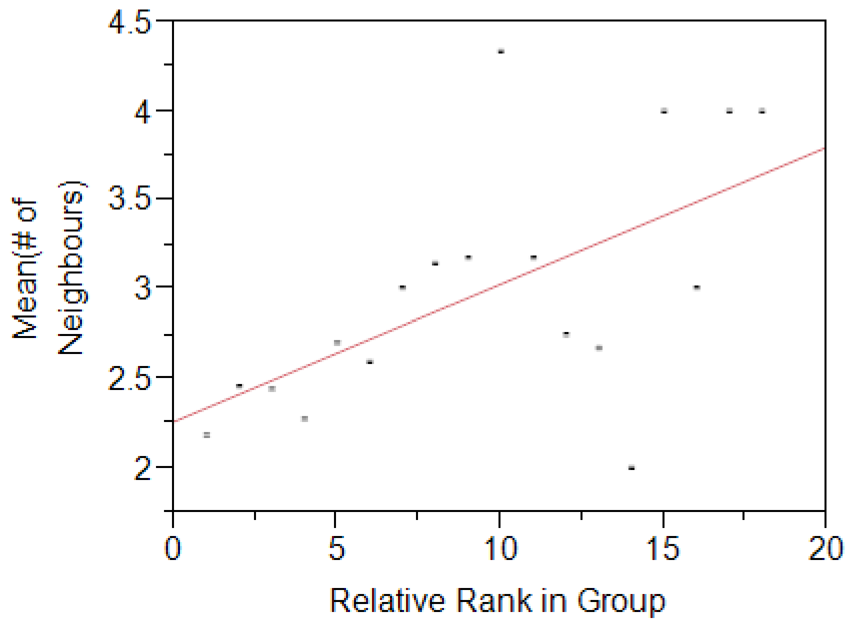

Figure 11. The relationship between relative rank within group and the mean number of neighbours in bedded groups for 2008. On the y-axis, a higher number of neighbours indicate a more protected position in a group. The highest relative rank is 1; rank is decreasing from left to right on the x-axis.

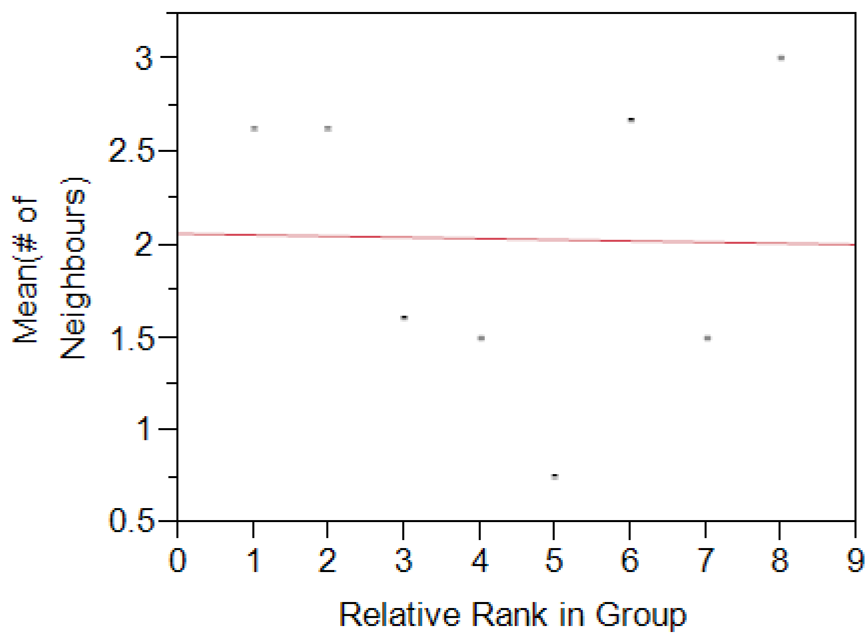

Figure 12. The relationship between relative rank within group and the mean number of neighbours in bedded groups for 2009. On the y-axis, a higher number of neighbours indicate a more protected position in a group. The highest relative rank is 1; rank is decreasing from left to right on the x-axis.

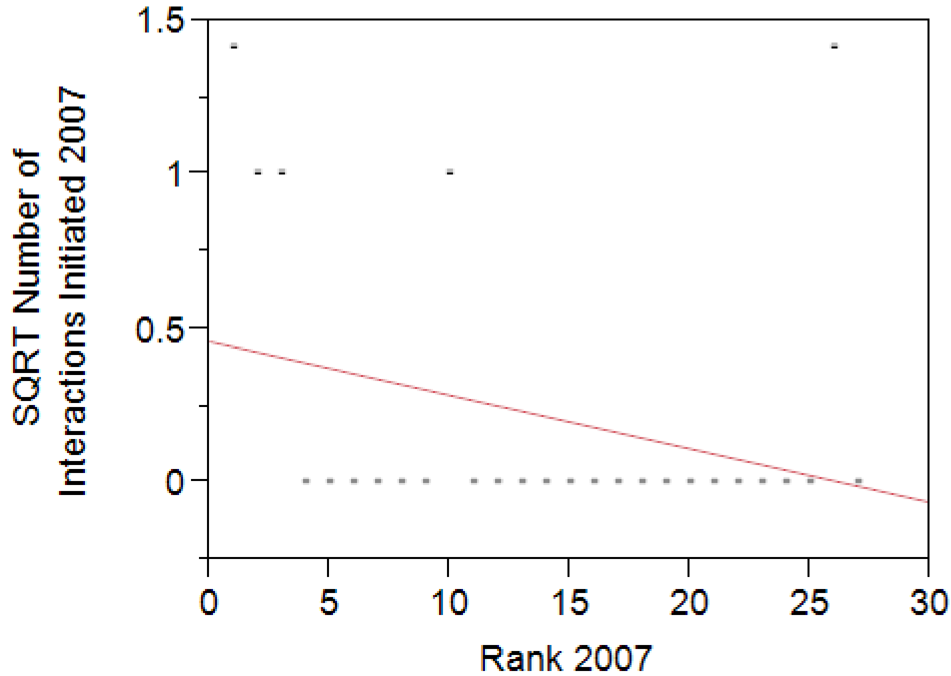

Figure 13. The relationship between dominance rank of each individual ewe and the number of interactions (square root transformed values) initiated by the individual for 2007, 2008, and 2009. On the y-axis, the number of initiated interactions is increasing from bottom to top (square root was used to normalize the values). The highest rank is 1; rank is decreasing from left to right on the x-axis.

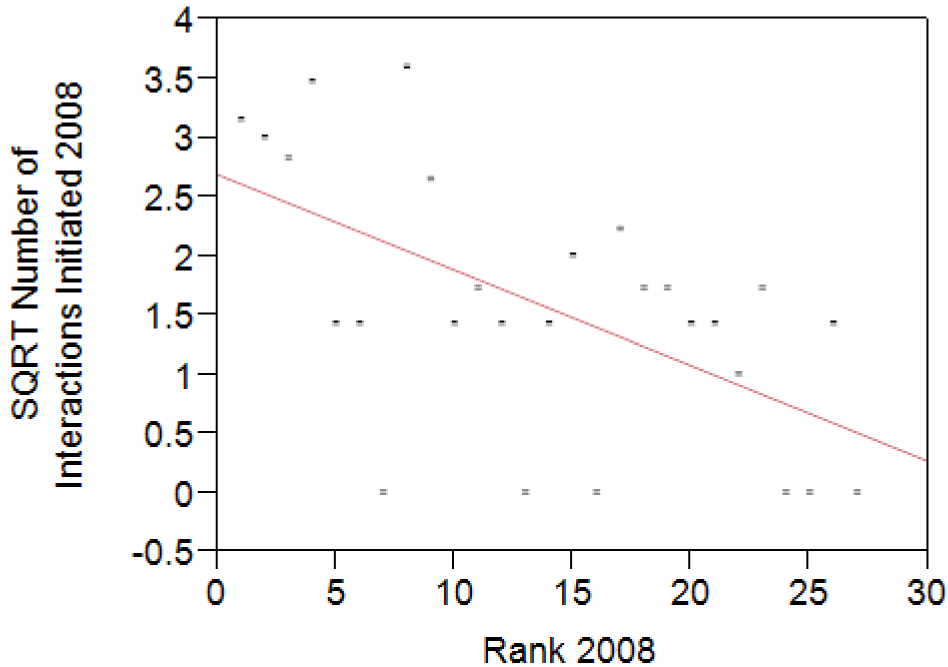

Figure 14. Relationship between dominance rank of each individual ewe and the number of interactions (square root transformed values) initiated by the individual for 2008. On the y-axis, the number of initiated interactions is increasing from bottom to top (square root was used to normalize the values). The highest rank is 1; rank is decreasing from left to right on the x-axis.

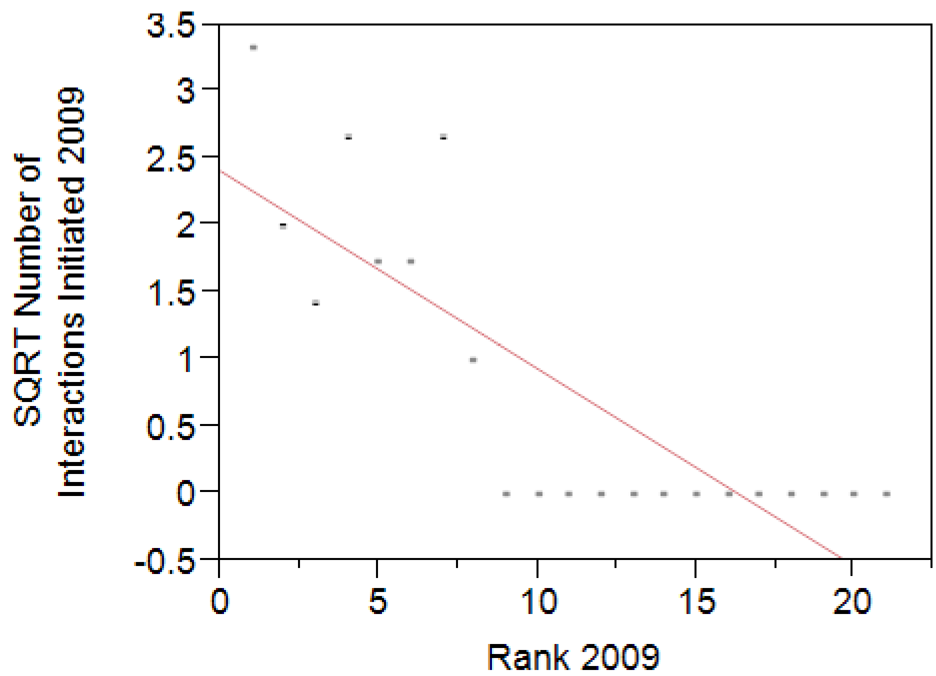

Figure 15. Relationship between dominance rank of each individual ewe and the number of interactions (square root transformed values) initiated by the individual for 2009. On the y-axis, the number of initiated interactions is increasing from bottom to top (square root was used to normalize the values). The highest rank is 1; rank is decreasing from left to right on the x-axis.

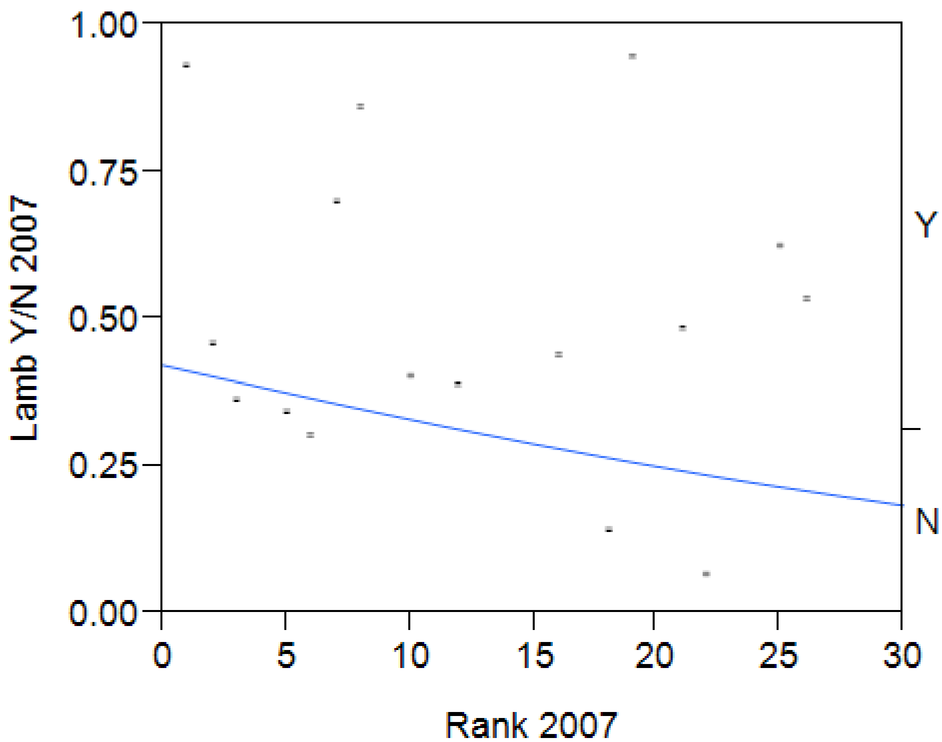

Figure 16. Relationship between ewe rank and reproductive success for 2007. On the y-axis is the probability that a ewes lamb survived to one year of age. The highest rank is 1; rank is decreasing from left to right on the x-axis.

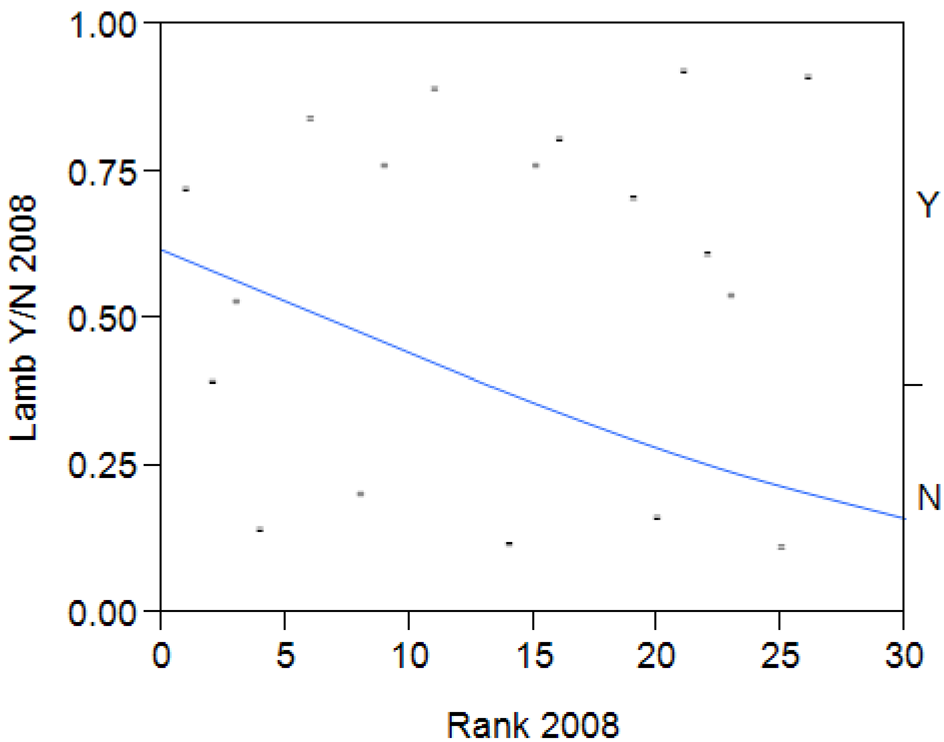

Figure 17. Relationship between ewe rank and reproductive success for 2008. On the y-axis is the probability that a ewes lamb survived to one year of age. The highest rank is 1; rank is decreasing from left to right on the x-axis.

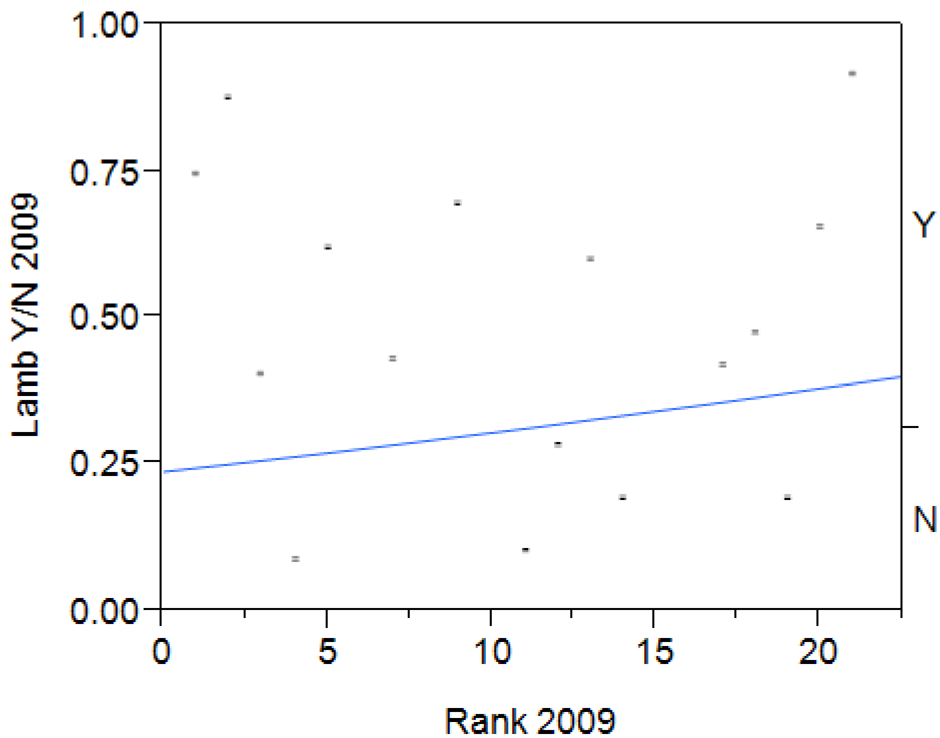

Figure 18. Relationship between ewe rank and reproductive success for 2009. On the y-axis is the probability that a ewes lamb survived to one year of age. The highest rank is 1; rank is decreasing from left to right on the x-axis.

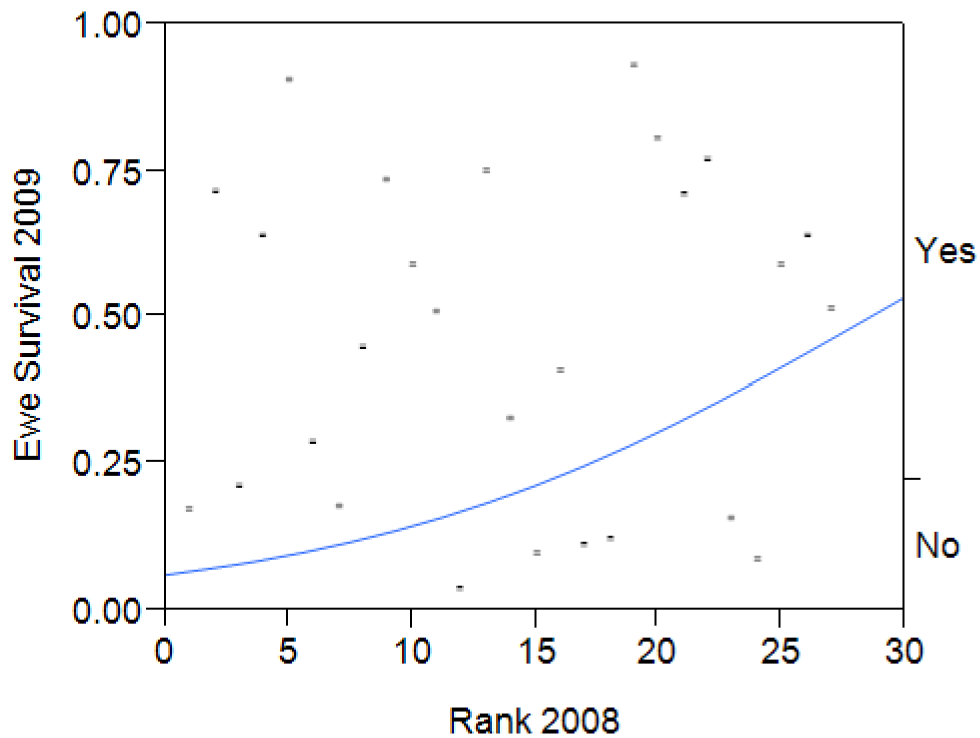

Figure 19. Relationship between rank and ewe survival for 2009. On the y-axis is the probability of a ewe surviving to the end of the calendar year 2009. The highest rank is 1; rank is decreasing from left to right on the x-axis.

Discussion

Analysis of the agonistic interactions between ewes yielded some interesting results. The range of possible values for Landau's Linearity Index is from 0 to 1. A value of zero would indicate a non-linear hierarchy, and a value of 1 would suggest a linear hierarchy. The highest value, of approximately 0.29, occurred in the 2007 study year. This value alone does not indicate that the study sheep formed a linear hierarchy. Many individuals had very few recorded interactions and some that had several interactions had been with only a few individuals rather than a large spread; this lead to a high percentage of unknown relationships. Landau's Linearity Index is affected by unknown relationships and a value correcting for unknown relationships was used. Although the corrected value was used, more numerous observations between all individuals would result in a higher value for Landau's linearity index. Another value to consider in the analysis of linearity of the hierarchy is the directional consistency. Contradictions of dominance between individuals reduce directional consistency. For example, multiple interactions between the same two individuals where the winner is not always the same individual, circular dominance, would reduce directional consistency. This value also ranges from 0 to 1, with zero indicating no directional consistency, and 1 full directional consistency. In all study years directional consistency was

1, which lends support for the establishment of a linear dominance hierarchy among the ewes in this population as has been shown for other populations in previous studies (Festa-Bianchet, 1991; Eccles and Shackleton, 1986).

The results of the standard least squares models indicate that the best model to predict rank would include the variables age and mass without any interaction. Age and body mass or body size have been shown to correlate in previous studies (Cote, 2001; Favre et al., 2008; Festa-Bianchet et al., 1996). Correlations between independent variables in the same model are not always a problem. Variance inflation factors, VIF's, indicate whether correlations between the independent variables are causing an increase in variance. Models should have VIF's less than 10; indicating no problem using these variables in the same model even though they may correlate with each other. The VIF's in the models presented were all very close to 1 which is very low.

In the 2007 model of age and mass where age significantly explained rank, the data only included sheep with a known age and mass. When a bivariate fit is run between rank and age, including all sheep with a known age, the age data no longer significantly explains rank (R^2=0.052, P=0.27) This finding may indicate that the model may not be robust if the model assumptions change. The separate horn length correlation analysis indicated that horn length had no significant effect on rank in 2008. I would be interested in seeing another study done focusing on remotely measured horn length data to see if the technique is a viable one for use with bighorn sheep as it was with Alpine ibex (Bergeron, 2007).

Previous studies suggest that dominance rank in bighorn females is correlated primarily with age (Festa-Bianchet, 1991). However, during my observations I have seen that it is not always the oldest sheep in the group which appears to be dominant. The highest ranking ewes in the study years, ID#'s 725, 733, and 640 are not the eldest sheep in their respective dominant year. There are several sheep of age equal to or greater than theirs in each year of the study. It is possible that age might be correlated with rank up to a certain point. After that, other correlates such as mass or horn size might outweigh age as a factor. Previous studies have shown that bighorn females reach an asymptotic mass around the age of 7 years (Favre et al., 2008; Festa-Bianchet et al., 1996). If after 7 years each sheep stops growing and has had an abundance of food during growth years, as there seems to be in the study location, the sheep may all reach a mass very similar to one another. Age 7 may be the age at which there is a change in correlation with rank from age and mass to horn length. A similar effect of asymptotic mass has been described for bighorn rams

(Pelletier and Festa-Bianchet, 2006) in which body mass began to explain a greater percent of variance in rank than age after the age of 6.

Other social species that form female dominance ranks correlated with age do so with an opposite correlation. An Australian ant species, *Pachycondyla sublaevis*, is one of them. In this species of ant a linear dominance hierarchy is established and it's the top-ranked worker who will be mated and produce female offspring. Again the correlate associated with this dominance is age; the top-ranked worker is usually a young individual and newly hatched worker ants take the ranks next to the top pushing those born earlier down in rank. The linear hierarchy resulted in the 2nd ranked individual taking over the top rank if the worker in top position were removed. No fighting occurs to establish dominance however displays are used to demonstrate dominance (Hagashi et al., 1994). This use of displaying may explain why although body size did differ between workers it was not significantly correlated with dominance rank.

In the general linear model of 2008 data, age and horn length were both included and a highly significant p-value resulted. In a 2007 study (Robinson and Kruuk, 2007) horns of soay sheep also had a correlation with dominance. Soay sheep have a polymorphism for horn development in which horns may be full, reduced, or absent. Ewes with horns initiated and won more agonistic interactions than sheep with no horns regardless of age or mass (Robinson and Kruuk, 2007). Since horn length can be measured and the age of a sheep estimated during a physical examination the linear hierarchy of an unstudied population of sheep could be determined from the capture of each individual once. The ranking may have some additional error due to the estimation of age, from horn annuli, at the time of capture since exact age would not be known. However, given a possible correlation between age and mass in bighorn females (Cote, 2001; Favre et al., 2008; Festa-Bianchet et al., 1996) a measure of mass taken at the time of capture could be used in an interaction with horn length and would decrease the error inherent if estimates of age were used. Furthermore, in a population such as this one where the age of the sheep was already know a linear hierarchy could likely be determined with only a few sessions of photographing sheep horns with a remote measuring device such as the one used in this study.

Data analysis relating to my third prediction, which was that high ranked individuals would have more protected positions in bedded groups and would be the leaders of groups, produced some interesting results. The relationship between rank and bedded positions was significant in the 2008 study year. High ranking individuals had fewer immediate neighbours. This is contrary to the expectation that high ranking individuals would have the advantage of interior positions, and thus protection from predation while bedded. Interior individuals are considered to be at lower predation risk than peripheral individuals (Krause and Ruxton, 2002). One possible explanation for high ranked ewes having less protected bedded positions could be related to a correlation between rank and leadership. A leading ewe would be the first to sit down and all following ewes may sit in protected positions relative to those that are already bedded. However, in 2009, there was no correlation between rank and bedded position. This discrepancy suggests that further research is needed on the topic.

Another possible advantage a high ranked sheep might have is to be a group leader. My analysis of leadership data resulted in a positive correlation between rank and leadership in 2008 and 2009; high ranked ewes were leading groups. A sheep that is leading the group in a direction she chooses while grazing can choose to go in the direction that best suits her needs at that time. She is at the front of the group so she has first access to patches of food, she can go to water or a saltlick whenever she needs. She can decide when the group will rest, when they will stand to graze again or move to another location. The other members of the group do not have the choice to go where their greatest need is because they would lose the relative safety of their group.

In the analysis of leadership and bedded position, rank values used were relative to the other members in the subgroup of the population. This resulted in mean values for leadership and number of neighbours for a given rank of an individual in a group. This was done because in a subgroup a lower ranked individual may be the highest rank in that subgroup and rank is affecting only those individuals in the subgroup. The other correlations, such as number of interactions initiated, reproductive success and ewe survival, were not group dependent and therefore rank values used were relative to the whole population.

The analysis of the correlation between rank and reproductive success showed mixed results. In 2007 and 2008 the trend in the data suggested higher offspring survival in higher ranked ewes. However, the trend was the opposite in 2009 and the results were not significant I cannot conclude that there is a reproductive advantage associated with high rank. This is a similar finding as in previous studies (Festa-Bianchet, 1991; Eccles and Shackleton, 1986), in which there was also no significant correlation between rank and ewe survival. Both papers suggest the reason is that the food sources utilized by the sheep could not be defended because of their ubiquitous nature. The same explanation was suggested in a study of mountain goats (Fournier and Festa-Bianchet, 1995) in which dominant female goats did not forage more efficiently than subordinate goats, and dominance status did not affect the amount of time devoted to alert behaviour. Food is widely available in Sheep River Provincial Park; even in the winter, the south facing slopes of the foothills are frequently not covered by snow and the sheep can easy access their food there. With access to food all around there would be little incentive to compete over it. If food were in a more patchy distribution, an individual that established dominance over others for access to the best patches of food may derive more of a reproductive benefit from being dominant because she is able to maintain a higher body condition than her subordinates but controlling the patchy resources.

The trend in this study's data was for higher survival in lower ranked individuals. Given that previous studies have found that dominance rank in bighorn ewes was primarily correlated with age (Festa-Bianchet, 1991), it may be that older individuals in this population, that have gained rank over the years, reached the end of their lives and passed on. Perhaps there is a different analysis that could have been used to test the correlation between rank and ewe survival that would avoid the possibility of the results simply showing the autocorrelation between age and ewe survival.

The results of the reproductive success and survival analysis suggest no fitness consequences to being high or low rank among female ewes.

These findings are contrary to those regarding female red deer *(Cervus elaphus)*. Differences in dominance rank among red deer females were related to their breeding success (Clutton-Brock et al., 1986). Lifetime reproductive success of dominant females was significantly greater than subordinates, and they produced more sons (the sex with higher variance and thus potential in reproductive success). This difference in reproductive success was also the product of a tendency for dominants to calve more frequently and for their offspring to have a higher probability of surviving to maturity. Dominance in red deer females thus appears to increase their reproductive fitness. Female rank in these ungulate species seems to suggest that dominance accrues some increase in reproductive fitness and, in some cases, an increase in body condition which could also contribute to increased reproductive success or survival.

I also explored the possible costs associated with being a dominant ewe. One such cost that may arise is in the time, and thus energy, spent asserting dominance over subordinates. The significant correlations between rank and the number of agonistic interactions initiated in 2008 and 2009 shows that higher ranked ewes were initiating more interactions. The 2007 data were not significant but the trend in the data was the same as the other years. Ewes may use more energy as a result of frequent assertions of dominance and time spent in dominance struggles is time that could be spent grazing or surveying for predators. Although leading a group can be an advantage, it may also be considered a cost of dominance because when leading a group the individual is in a peripheral position and may be more vulnerable to predation (Krause and Ruxton, 2002). It has been observed that cougars may hide and wait for a group of sheep to approach them at which time it would attack the leading sheep of the group (Festa-Bianchet, 2006). If this behaviour is common among cougars or other predators it could be considered a disadvantage of leadership and high rank given that higher ranked ewes do not seem to gain interior bedded positions and are often on the perimeter of groups when leading.

To summarize some of the major findings of this study, I could not show that the ewes in this population form linear dominance hierarchies. The best predictors of sheep rank are age and mass. There are no fitness consequences associated with the ranks that were observed and, if anything, the disadvantages of high rank may outweigh the advantages. This leads me to believe that having a dominance hierarchy among the ewes may have evolved as a benefit for all individuals in the population in that having an individual to follow promotes group cohesion which can have other advantages including anti-predator and foraging efficiency advantages. This may be similar to the findings of a study involving African elephants (*Loxodonta africana*). The study shows that the elephants formed linear age/size related hierarchies; older larger females consistently dominated younger smaller females. The hierarchy may aid in reducing the rate of conflict within the group and also the risk of injury so the hierarchy may reduce the uncertainty and lessen the severity of agonistic interactions (Archie et al., 2005).

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APPENDIX A - Antagonistic interactions (n=154) recorded between September 2007 - May 2009.

Initiator ID	Winner ID	Loser ID	Type of Interaction	Initiator ID	Winner ID	Loser ID	Type of Interaction
640	640	334	chase off	332	332	334	displacement
685	685	640	displacement	709	709	733	displacement
733	733	618	displacement	709	709	733	displacement
314	314	332	displacement	709	709	733	displacement
724	724	334	displacement	709	709	725	displacement
618	618	605	displacement	709	709	733	displacement
725	725	733	displacement	709	709	725	displacement
725	725	724	displacement	282	282	612	displacement
596	596	334	displacement	314	314	332	displacement
709	709	332	displacement	733	733	315	displacement
734	734	319	displacement	618	618	334	displacement
734	734	319	displacement	315	315	618	displacement
598	598	282	displacement	618	618	334	displacement
598	598	332	displacement	733	733	334	displacement
671	671	333	displacement	733	733	315	displacement
733	733	596	displacement	315	315	332	displacement
709	709	640	displacement	733	733	334	displacement
315	315	316	displacement	734	734	640	displacement
316	316	334	displacement	734	734	671	displacement
724	724	605	displacement	734	734	630	displacement
315	315	630	displacement	734	734	640	displacement
314	314	624	displacement	671	671	640	displacement
630	630	334	displacement	725	725	315	displacement
630	630	334	displacement	640	640	315	displacement
709	709	334	displacement	640	640	618	displacement
709	709	334	displacement	640	640	618	displacement
316	316	624	displacement	725	725	605	displacement
709	709	334	displacement	624	709	624	eye rub
671	671	686	displacement	?	725	733	fighting for grazing patch
605	605	334	displacement	671	671	334	fighting for grazing patch
671	671	733	displacement	725	725	315	front kick
630	630	332	displacement	640	640	316	horn butt
733	733	624	displacement	316	316	686	horn butt
316	316	624	displacement	733	733	282	horn butt
725	725	333	displacement	328	328	334	horn butt
640	640	624	displacement	733	733	328	horn butt
333	333	334	displacement	733	733	334	horn butt
671	671	709	displacement	733	733	334	horn butt

Initiator ID	Winner ID	Loser ID	Type of Interaction	Initiator ID	Winner ID	Loser ID	Type of Interaction
314	314	328	horn butt	333	333	332	horn clash
315	315	328	horn butt	640	640	332	horn clash
605	605	334	horn butt	733	733	624	horn clash
640	640	259	horn butt	315	315	605	horn clash
596	596	333	horn butt	315	315	328	horn clash
725	725	733	horn butt	315	315	328	horn clash
725	725	332	horn butt	709	709	598	horn clash
618	618	332	horn butt	?	709	640	horn clash
259	259	791	horn butt	?	709	640	horn clash
259	259	624	horn butt	640	640	315	horn clash
709	709	316	horn butt	709	709	332	push
640	640	605	horn butt	709	709	733	push
733	733	333	horn butt	734	734	314	push
725	725	709	horn butt	?	333	332	rub horns
596	596	314	horn butt	671	671	334	threatened
282	282	334	horn butt	671	671	686	threatened
328	328	334	horn butt	315	315	332	threatened
598	709	598	horn butt	640	640	334	threatened
709	709	315	horn butt	640	640	618	threatened
624	624	630	horn butt	640	640	618	threatened
671	671	605	horn butt	640	640	332	threatened
640	640	724	horn butt	314	314	334	threatened
733	733	596	horn butt	733	733	333	threatened
314	314	630	horn butt	685	685	334	threatened
733	733	624	horn butt	333	333	334	threatened
598	598	328	horn butt	725	725	332	threatened
314	314	334	horn butt	709	709	332	threatened
640	640	332	horn butt	725	725	332	threatened
640	640	315	horn butt	624	624	334	threatened
618	618	332	horn butt	734	734	332	threatened
640	640	315	horn butt, horn clash	724	724	334	threatened
733	733	724	horn clash	709	709	733	threatened
709	725	709	horn clash	333	333	334	threatened, horn butt
709	725	709	horn clash	332	332	733	?
724	724	725	horn clash	282	282	610	?
640	640	315	horn clash	333	333	334	displacement
725	725	259	horn clash	734	734	640	horn butt

725	725	596	horn clash
709	709	596	horn clash
?	725	733	horn clash
733	733	640	horn clash