

Aggression and Coexistence in Female Caribou

FLOYD W. WECKERLY¹ and MARK A. RICCA²

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ABSTRACT. Female caribou (*Rangifer tarandus*) are highly gregarious, yet there has been little study of the behavioral mechanisms that foster coexistence. Quantifying patterns of aggression between male and female, particularly in the only cervid taxa where both sexes grow antlers, should provide insight into these mechanisms. We asked if patterns of aggression by male and female caribou followed the pattern typically noted in other polygynous cervids, in which males display higher frequencies and intensity of aggression. From June to August in 2011 and 2012, we measured the frequency and intensity of aggression across a range of group sizes through focal animal sampling of 170 caribou (64 males and 106 females) on Adak Island in the Aleutian Archipelago, Alaska. Males in same-sex and mixed-sex groups and females in mixed-sex groups had higher frequencies of aggression than females in same-sex groups. Group size did not influence frequency of aggression. Males displayed more intense aggression than females. Frequent aggression in mixed-sex groups probably reflects lower tolerance of males for animals in close proximity. Female caribou were less aggressive and more gregarious than males, as in other polygynous cervid species.

Key words: Aleutian Islands, group size, social interactions, Cervidae, *Rangifer tarandus*, sex

RÉSUMÉ. La femelle caribou (*Rangifer tarandus*) est très grégaire et pourtant, très peu d'études ont été faites sur les mécanismes du comportement qui favorisent la coexistence. Des modèles quantificateurs d'agression entre le mâle et la femelle, particulièrement chez le seul cervidé où les deux sexes possèdent des bois, devraient permettre d'en savoir plus sur ces mécanismes. Nous nous sommes demandé si les modèles d'agression entre la femelle et le mâle caribou ressemblaient aux modèles d'agression généralement remarqués chez d'autres cervidés polygynes, pour lesquels les mâles affichent une fréquence et une intensité d'agression plus grandes. De juin à août 2011 et 2012, nous avons mesuré la fréquence et l'intensité d'agression au sein de groupes de tailles diverses, et ce, au moyen de l'échantillonnage centré de 170 caribous (64 mâles et 106 femelles) sur l'île Adak de l'archipel des Aléoutiennes, en Alaska. Les mâles des groupes du même sexe et des groupes mixtes, et les femelles de groupes mixtes affichaient une plus grande fréquence d'agression que les femelles se trouvant dans des groupes du même sexe. La fréquence d'agression n'était aucunement influencée par la taille du groupe. L'intensité d'agression des mâles était plus grande chez le mâle que chez la femelle. L'agression fréquente dans les groupes mixtes est probablement représentative de la plus faible tolérance des mâles à la présence d'animaux à proximité. Les femelles caribou étaient moins agressives et plus grégaires que les mâles, à l'instar d'autres espèces de cervidés polygynes.

Mots clés : îles Aléoutiennes, taille des groupes, interactions sociales, cervidés, *Rangifer tarandus*, sexe

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INTRODUCTION

Female caribou (*Rangifer tarandus*) can form groups numbering more than 1000 animals (Pruitt, 1960), and forming such large groups must require them to use behaviors that facilitate coexistence (Rutberg, 1986; Thouless and Guinness, 1986; Weckerly, 1999). Insight into how females coexist in groups might be gleaned from intersexual patterns in aggression. Males are more aggressive than females in a number of polygynous ruminants (Clutton-Brock et al., 1982; Weckerly et al., 2001; Richardson and Weckerly, 2007). The role of aggression in determining and maintaining individual social rank varies between the sexes.

Male-male competition for access to females during the mating season drives male aggression both within and outside that season (Weckerly, 2001; Weckerly et al., 2001). Male aggression can also be intense, so physical contact during interactions can lead to serious and potentially fatal injuries (Geist, 1986). Female aggression, in contrast, is often associated with conflicts over resources. Since food resources for ruminants are usually diffusely distributed across the landscape and temporally variable as well, resource defense should not have large fitness consequences (Rutberg, 1986; Thouless and Guinness, 1986). Moreover, female aggression is typically characterized by a lack of physical contact (Rutberg, 1986; Thouless and Guinness,

¹ Department of Biology, Texas State University, San Marcos, Texas 78666, USA; fwll@txstate.edu

² U.S. Geological Survey, Western Ecological Research Center, 1 Shields Avenue, The Barn, Davis, California 95616, USA; current address: USGS-WERC, 800 Business Park Drive, Suite D, Dixon, California 95620, USA

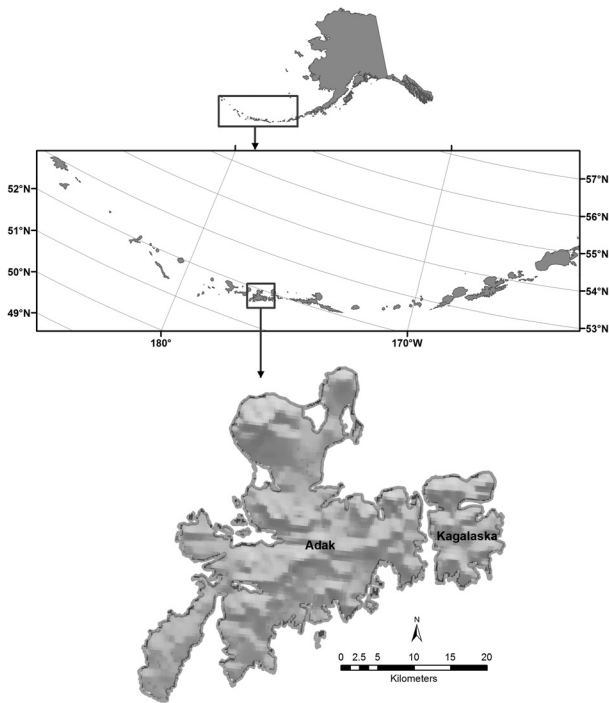


FIG. 1. Map of Adak Island and the nearest adjacent island, Kagalaska, located in the Aleutian archipelago of Alaska.

1986; Weckerly, 1999; Richardson and Weckerly, 2007). Perhaps female aggression is often less intense because females that engage in aggression incur lower fitness benefits compared to males.

Prior work examining aggression in female caribou has chiefly focused on why females evolved antlers (Espmark, 1964; Barrette and Vandal, 1986; Holand et al., 2004). Caribou is the only cervid in which males and females possess antlers. Predation seems to be an unlikely reason because females grow new antlers each year. During the four to five months that it takes to develop a new set of antlers, females cannot use growing antlers to assist in repelling attacks from predators or as signals of weapons to predators (Crisler, 1956; Stankowich and Caro, 2009). It is more likely that antlers evolved in association with intraspecific aggression for the purpose of resource defense (Barrette and Vandal, 1986; Espmark, 1964; Holand et al., 2004), yet the potential consequences of antlers to social dynamics or the means by which female caribou mitigate costs to coexistence have not been examined. Moreover, interference competition for resources can intensify as group size increases and spacing between individual animals concomitantly decreases (Hirotani, 1990; Fournier and Festa-Bianchet, 1995; Robinson and Kruuk, 2007). Hence, the frequency of aggression among female caribou should be positively coupled to group size.

We asked whether the level of aggressive behavior affects the ability of gregarious female caribou to coexist by estimating the frequency and intensity (i.e., involves physical contact) of aggressive behaviors displayed by males and females. If female coexistence occurs as documented

in other polygynous cervids, then males should display greater frequency and intensity of aggression than females. Intersexual patterns of aggression should also be influenced by group size and group type. Caribou form three kinds of groups: aggregations composed of males age one year or older (male-only); groups of females that may contain juveniles (female); or groups that contain male and female adults and often juveniles (mixed-sex) (Cameron and Whitten, 1979; Gates et al., 1986; Heard and Ouellet, 1994). We expected that group size would be positively correlated to frequency of aggression, but that males and females would display higher frequencies of aggression in mixed-sex compared to same-sex groups. Higher frequency of aggression in mixed-sex groups is expected because of the greater potential for aggression instigated by males that are in close proximity to conspecific animals (Weckerly, 2001; Weckerly et al., 2001). Finally, if females are more gregarious than males, then male-only groups should be smaller than female and mixed-sex groups.

METHODS

Study Area

Caribou were studied on Adak Island in the central part of the Aleutian archipelago, Alaska, USA (Fig. 1). Adak is a large (725 km²) and mountainous island composed of maritime tundra. Natural predators and mosquitoes were absent on Adak Island but caribou could be hunted by anyone with an Alaska hunting license. Vegetation communities consist of grass-forb meadows, dwarf shrub-dominated heaths, and windswept fell-fields. The climate is maritime, characterized by cool (5°–10°C) foggy summers and frequent cyclonic storms, with temperatures typically near freezing in the winter. Annual precipitation is about 160 cm. Caribou were introduced to Adak Island in the late 1950s by the U.S. Navy (Jones, 1966) and the caribou population fluctuated between 200 and 600 animals through the late 1990s, when the naval facility on Adak shut down. Subsequently, population size irrupted to 2750 animals in 2005 and then leveled off at approximately 2900 animals in 2012 (Ricca, 2013).

Data Collection and Analyses

We used focal animal sampling to collect data on aggressive interactions from 15 June to 21 August in 2011 and 2012. During the summer, group sizes can be large, the antlers of both males and females are in the same state (developing or in velvet), and elevated male aggression due to mating behavior should not occur (Pruitt, 1960; Leader-Williams and Ricketts, 1982; Gates et al., 1986; Heard and Ouellet, 1994; Weckerly et al., 2001). We selected a focal animal (a male or female more than one year old) from a group within 400 m that we could see unobstructed by terrain (75% of observations were made from a distance of 225–400 m). Males were identified by the penis sheath,

TABLE 1. Numbers of focal observations and aggressions displayed by caribou during summer 2011 and 2012, by month and by group type. For mixed-sex groups, separate numbers are presented for males and females.

	Month			Group type			
	June	July	August	Male-only	Female	Mixed-sex	
						Male	Female
Observations	89	32	49	52	65	12	41
Aggressions	34	26	24	31	18	13	22

testicles, and urination posture. We observed the focal animal through spotting scopes or binoculars (7×–20× magnification) for at least four (and up to 13) minutes. We recorded the following information: 1) study day (the day of the study, counting from June 15 as day 1); 2) close proximity (the time during which a focal animal was within one body length of other caribou); 3) the number and type of aggression behaviors displayed by the focal animal; 4) group size; and 5) group type (same-sex or mixed-sex). We recorded study day because the variation in forage distribution from June to August should influence both group size and the proximity of animals to each other (Weckerly, 2001; Lung and Childress, 2007; Robinson and Kruuk, 2007). We recorded the size of caribou groups whenever it was possible to classify the group type, even if we were unable to collect focal observations. A same-sex group was composed of females (could include juveniles less than 1 year of age) or males, and a mixed-sex group included both female and male adults. We did not encounter any animals older than 1 year without antlers.

Aggressive interactions occurred between two caribou and were classified according to descriptions in Weckerly (1999). Aggressive behaviors not including physical contact were hard stares, head shakes, ears-back grimace, sniffs, and charges. Intense aggressions involved physical contact and included bites, scissor kicks, and rear-and-flail behavior. If an aggression began without physical contact but progressed to physical contact, then the aggressive bout was recorded as intense. A group was defined as two or more caribou that displayed coordinated movement during focal observations.

A general linear mixed-effects model was used to assess factors that affected the proportion of time that the focal animal spent within one body length of another caribou (Pinheiro and Bates, 2000). We used mixed-effects models to account for uncertainty about whether the same animal was measured multiple times in large groups (mean number of focal observations per group = 3.33, range = 1–14). Therefore, group was the random factor. Group size, group type, and sex were fixed factors, as were the potentially confounding influences from day of study and length of the focal observation. To accommodate heteroscedasticity in our response variable, we created two indicator variables and binned each data point into one of three percentile ranges (0–33, 34–66, 67–100) on the basis of the value of the response variable. These indicator variables were then used to estimate separate residual variances for each bin in our mixed-effects model (Pinheiro and Bates, 2000).

We used a generalized linear mixed-effects model with a binomial error structure to estimate the probability of aggression and to assess the factors that influenced aggression (Faraway, 2006). We used a binomial error structure because only one aggressive behavior was detected in 95% of the focal observations during which aggressions occurred. Group was the random factor, and the fixed factors were group size, group type, sex, proximity, day of study, and length of the focal observation.

We used the ratio of two proportions to test for intersexual differences in the intensity of aggression. For both males and females we calculated the proportion of focal observations in which aggressions involved physical contact. The 95% confidence interval of the male:female ratio was estimated from 10 000 bootstrapped samples (Manly, 2007). A confidence interval greater than 1.0 indicated that males showed more intense aggressions. We did not assess differences between group types in intensity of aggression because so few observations included intense aggressions (males 10, females 4).

Group size was estimated with a generalized linear model that had a negative binomial distribution (Stauffer, 2008). Solitary caribou were considered a group size of one. Predictors were group type and day of study.

RESULTS

We collected 170 focal observations from 54 groups in all regions of Adak Island (Table 1). The mean duration of focal observations was 8.11 minutes \pm 2.17 SD. One or more aggressions were detected in 59 focal observations, and we observed a total of 84 aggressions.

Our measure of close proximity, the proportion of observation time that a focal animal spent within one body length of other caribou, was unaffected by any predictor we considered because confidence intervals included zero (Table 2). In contrast, probability of aggression was least for females in female groups, intermediate for males in male-only groups, and highest for both males and females in mixed-sex groups (Table 3, Fig. 2). We did not detect an influence of group size on probability of aggression across the range of observed group sizes in our data. Probability of aggression was highest during the early summer and increased with proportion of time spent in close proximity, but it was not influenced by the length of the focal observation.

Intense aggression was more frequent in males than in females. The frequency of intense aggression (involving

TABLE 2. Parameter estimates and 95% confidence bounds of a general linear mixed-effects model predicting the proportion of focal observation time that the animal spent within one body length of other caribou. For sex and group type, the reference category was female in same-sex group. Values are reported using abbreviated scientific notation (e.g., -0.0000678 or $-6.789 \cdot 10^{-5}$ was -6.789^{-5}).

Coefficient	Estimate	Lower	Upper
Intercept	-6.786^{-5}	-2.942^{-3}	2.806^{-3}
Group size	-1.514^{-5}	-1.223^{-5}	4.252^{-5}
Same-sex			
Male	-1.749^{-4}	-1.974^{-3}	1.625^{-3}
Mixed-sex			
Female	-1.120^{-3}	-3.113^{-3}	8.718^{-4}
Male	-7.767^{-4}	-3.055^{-3}	1.501^{-3}
Study day ¹	-1.451^{-6}	-4.334^{-5}	4.044^{-5}
Observation length	1.209^{-4}	-1.497^{-4}	3.916^{-4}

¹ Day of observation between 15 June (Day 1) and 21 August (Day 68).

TABLE 3. Parameter estimates and 95% confidence bounds of a generalized linear mixed-effects model with a binomial error structure predicting the probability of aggression of caribou. For sex and group type, the reference category was female in same-sex group.

Coefficient	Estimate	Lower	Upper
Intercept	-2.123	-3.982	-0.274
Group size	0.006	-0.012	0.023
Same-sex			
Male	1.171	0.273	2.070
Mixed-sex			
Female	1.658	0.458	2.858
Male	2.188	0.598	3.779
Close proximity	2.958	0.618	5.297
Study day	-0.029	-0.054	-0.005
Observation length	0.110	-0.069	0.289

physical contact) was 0.16 (95% CI: 0.078–0.25) for males and 0.04 (0.009–0.075) for females. Intense aggression was 4.0 times more likely in males than in females (95% CI:1.42–21.57).

To quantify gregariousness, we recorded group sizes for 19 male-only, 27 female, and 23 mixed-sex groups. Minimum, quartiles, and maximum group sizes, respectively, were: 1, 2, 6, 9, and 20 for male-only; 2, 6, 11, 16, and 57 for female; 3, 10, 17, 32, and 161 for mixed-sex group types. Group sizes were smallest for male-only, intermediate for female, and largest for mixed-sex groups (Table 4, Fig. 3). Also, group sizes were larger during early summer than in late summer for all group types.

DISCUSSION

Female caribou coexist as documented in other polygynous cervids (Weckerly et al., 2001). Females displayed lower frequencies of aggression than males in same-sex

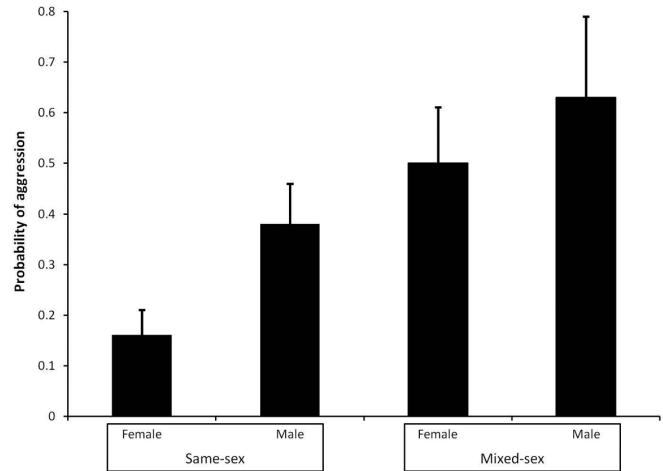


FIG. 2. Predicted probabilities of aggression (narrow bars show 1 standard error), for male and female caribou in same-sex and mixed-sex groups. Probabilities were predicted using the means of group size (18), time of close proximity (0.1), study day (28), and observation length (8.11 min).

TABLE 4. Parameter estimates and 95% confidence bounds of a generalized linear model (assuming a negative binomial distribution) predicting group size. For group type the reference category was male-only.

Coefficient	Estimate	Lower	Upper
Intercept	2.483	2.027	2.938
Group type			
Female	0.549	0.086	1.012
Mixed-sex	1.558	1.049	2.066
Study day	-0.018	-0.028	-0.008

groups and were less likely than males to exhibit intense aggression. These patterns of aggression by females probably promote coexistence among females. Not surprisingly, sizes of female groups were larger than male-only groups.

Males and females were in close proximity to other caribou for similar amounts of time regardless of group type, yet the probability of aggression remained greater for males. Males that are in close proximity are more apt to engage in aggression because that proximity might signal a readiness to participate in aggression or a lack of submission (Weckerly et al., 2001). A consequence of the greater probability of aggression by males in proximity is social incompatibility between males and females, which might explain the high frequencies of aggression in mixed-sex groups.

It is unlikely that greater aggression in mixed-sex groups is due to larger group sizes because we found no influence of group size on frequency of aggression for any group type. Positive associations between group size and frequency of aggression, which in turn decreases foraging efficiency, have been detected for same- and mixed-sex groups of Alaskan moose (*Alces alces gigas*, Molvar and Bowyer, 1994) and white-tailed deer (*Odocoileus virginianus*, Grenier et al., 1999). Perhaps the reason group size was not influential in our study is that proximity of caribou to one

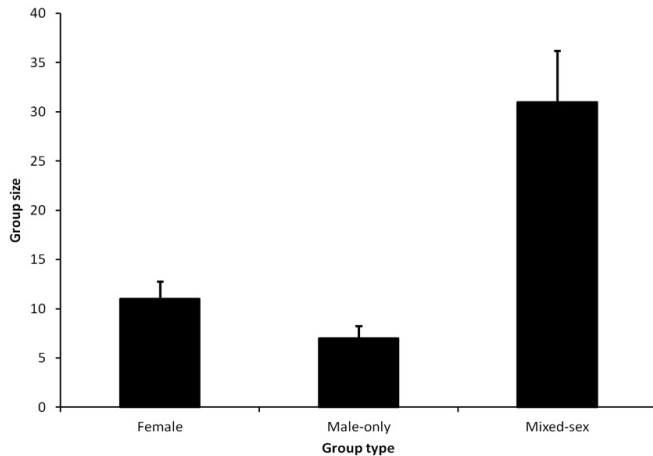


FIG. 3. Predicted group size means (and 1 standard error bars) for same-sex and mixed-sex caribou groups. Mean group size was predicted using the mean of study day.

another had more bearing on the probability of aggression. The influence of animal proximity on aggression has been well documented in other ruminants (Côté, 2000; Robinson and Kruuk, 2007; Weckerly, 2001). Group size probably does influence aggression when it is positively related to proximity among animals, which did not occur in our study, or when the species is less gregarious.

The inverse relationship between study day and frequency of aggression probably reflects an increase in animal physiological condition throughout summer. Males and females in early summer are in poor condition after subsisting on scarce supplies of nutritious forage during winter and spring (Parker et al., 2009), and females with young also have high energetic costs from lactation (Klein, 1990). Also, green-up of tundra vegetation begins during early summer, and competition for nutritious, green forage is probably keener at that time than later in summer. In June 2012, competition for nutritious, green forage might have been particularly keen because winter snowmelt was later than usual (Ricca, 2013).

Although higher male and female aggression in mixed-sex groups compared to same-sex groups is consistent with female coexistence, as found in other polygynous cervids, another possible explanation exists for our findings. Antlers on female caribou evolved presumably to defend discrete food patches in winter (Barrette and Vandal, 1986; Schaefer and Mahoney, 2001; Holand et al., 2004). Females crater through snow to access lichen (*Cladonia*) patches and then defend these “lichen pits” from males and other females. Defense of lichen pits between similar-sized females involves aggression with little physical contact (Barrette and Vandal, 1986; Holand et al., 2004). However, females can use their antlers to defend lichen pits from larger, antlerless males (Barrette and Vandal, 1986; Espmark, 1964; Lincoln and Tyler, 1994). Males typically cast their antlers by early winter, but gravid females do not cast their antlers until parturition in the spring. The increased aggression by males and females in mixed-sex groups in summer may be

a carry-over from social interactions that developed in winter, when resources were more limited (Rutberg, 1986).

Female caribou are less aggressive and more gregarious than males in summer. Coexistence with other females benefits them by reducing the risk of predation, and younger females can follow more experienced ones who select the birthing sites (Gunn and Miller, 1986; Loe et al., 2006). Female coexistence is probably facilitated by displaying lower frequency of aggression and engaging in less intense aggression. Lower levels of aggression by females may also be coupled to hormonal regulation of the antler cycle. Testosterone has an overriding influence on the timing of the antler cycle in males, whereas estradiol governs the female antler cycle (Lincoln and Tyler, 1994, 1999). Circulating levels of estradiol are highest during gestation. Since circulating concentrations of testosterone influence levels of aggression (Barboza et al., 2004) and females have much lower levels of testosterone than males throughout the year, lower female aggression is not surprising. Aggression by female caribou in summer is of low intensity and probably does not impair female gregariousness.

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