

ANTLERS ON FEMALE CARIBOU: BIOGEOGRAPHY OF THE BONES OF CONTENTION

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Abstract. Functional explanations for horns and antlers on female ungulates are conflicting. We tested the hypothesis that such appendages serve in intraspecific competition for resources by analyzing the tendency for female caribou to carry antlers across a 1000 km wide gradient. We predicted that females in populations experiencing more intense or more protracted interference competition, reflected as greater depth and duration of snow cover, would exhibit greater propensity to bear antlers. Among 15 herds in Newfoundland and Labrador, Canada, the percentage of antlered females was correlated positively with average annual snowfall and mean snow depth at the end of March, and negatively with population density. Our results support the hypothesis that antlers on females provide functional advantages in interference competition for winter food, but that antler possession may decline in instances of higher animal densities and diminished nutritional state.

Key words: antlers; caribou; horns; interference competition; Labrador; Newfoundland; *Rangifer tarandus*; snow cover; ungulates.

INTRODUCTION

Horns and horn-like organs on ungulates likely have intrigued humans for millennia. Although scientific studies have traditionally focused on males, less attention has been devoted to the adaptive significance of horns and antlers on females. The evolution and ontogeny of these organs demand a functional explanation: horns on female ruminants have evolved independently at least 11 times (Roberts 1996), and the physiological cost of antler and horn development is appreciable (Clutton-Brock 1982, Kiltie 1985). Nonetheless, the functional advantages of horn possession to females remain unresolved. Conflicting explanations have included defense against predators (Packer 1983), mimicry of male offspring (Estes 1991), and competition for resources (Geist 1977, Clutton-Brock 1982, Roberts 1996).

Caribou and reindeer (*Rangifer tarandus*) could serve as a decisive test of these ideas. Caribou are unique among the Cervidae in the possession of antlers by females, although the species is not monomorphic: the percentage of antlered females can vary markedly across populations (Bergerud 1971, Reimers 1993). The annual antler cycle also tends to vary according

to sex, age class, and fertility status (Bergerud 1976). Mature males shed their antlers shortly after the rut in late autumn, presumably to reduce the energetic burden of carrying this 7–15 kg mass, whereas females and young males tend to retain their antlers through the winter. Antler casting for barren females and juveniles is typically in early spring, and for pregnant females, near the time of parturition in late May or early June (Bergerud 1976). A genetic basis for the trait is implied by the year-to-year stability of antler carrying within populations and within individual females (Bergerud 1971).

In functional explanations of antlers, observers of caribou have stressed the role of resource competition. During winter, caribou uncover subnivean foods by “cratering,” i.e., pawing through the snow cover (Brown and Theberge 1990), an activity that is energetically demanding (Fancy and White 1985). Because antlered females are capable of displacing larger, but unantlered, males in disputes over feeding patches (Espmark 1964, Barrette and Vandal 1986, 1990), the more localized winter foods of *Rangifer*, compared to other cervids, may confer advantages to antlered females and their calves (Kojola 1989) while procuring and defending these resources (Espmark 1964, Henshaw 1969, Bergerud 1976, Reimers 1993). Nevertheless, it remains unclear why antler possession by females is not universal within *Rangifer* (Kiltie 1985,

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Reimers 1993). Indeed, intraspecific polymorphisms for female horn possession are virtually unexplored (cf. Roberts 1996), even though such analysis might resolve the rival interpretations, as well as avoid the potentially masking effects of vast genetic differences (Jarman 1983) from interspecific analyses.

Social interactions are expected to be most intense where resources are clumped (Jarman 1974). For foraging caribou, snow cover carries important consequences: it restricts the extent of suitable feeding areas, heightens the energetic investment into each crater, and thus magnifies the potential for interference competition (Barrette and Vandal 1986, Schaefer and Messier 1995). We surmised, therefore, that among populations, increased depth or duration of snow cover would reflect increased scope for interference competition for food and, hence, greater benefits to antler possession by females. Several lines of evidence support this contention. The season of snow cover is typically associated with larger group sizes in caribou (Fuller and Keith 1981, Darby and Pruitt 1984, cf. Skogland 1989, Stuart-Smith et al. 1997, Rettie and Messier 1998) and snow depth is correlated with more frequent agonistic interactions (Vandal and Barrette 1985) and greater energetic expenditure, expressed as the rate of pawing while foraging (Skogland 1978, Schaefer and Messier 1995). For example, Vandal and Barrette (1985) reported that feeding antagonism was nearly absent when caribou did not crater, i.e., at snow depths <25 cm. We predicted, as a corollary of the resource defense hypothesis, that the propensity for female caribou to bear antlers would be positively related to snow depth and duration. At the same time, because antler possession may reflect proximate nutritional status (Bergerud 1976, Thing et al. 1986), we anticipated a negative relationship with population density (Reimers 1993).

Here, we report a biogeographic analysis of antler possession by females among populations of woodland caribou (*R. t. caribou*) across a 1000-km gradient in Newfoundland and Labrador, Canada (Fig. 1). The region exhibits superb contrasts of the snow environment and the percentage of antlered female caribou. In the northwest, animals contend with some of the highest recorded snow depths while cratering (Brown and Therberge 1990); in the southeast, caribou frequently experience years with little or no snow cover. At the same time, these herds display large variations in the percentages of females carrying antlers (Bergerud 1971) and in population densities (Mahoney 2000).

METHODS

Our study populations represented one subspecies, and all tended to reside in treeless environments during winter. The number of females, ≥ 1 yr old, with and without antlers was tallied during aerial and ground

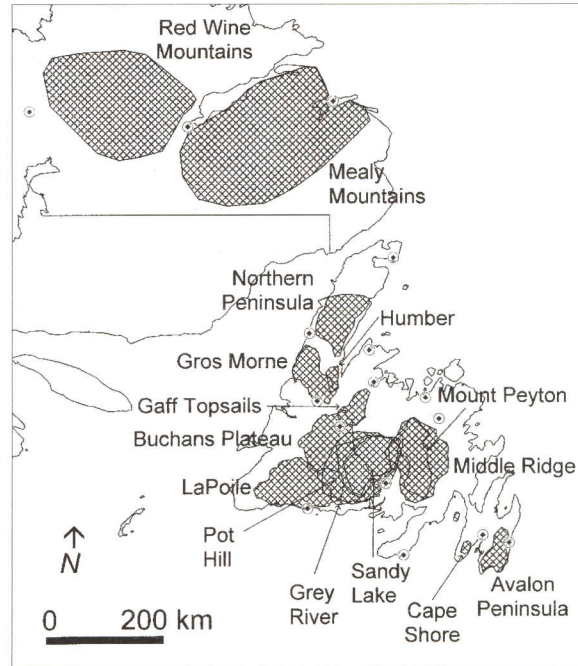


FIG. 1. Caribou populations (shaded regions) and meteorological stations (point locations) in Newfoundland and Labrador, Canada, used in the study.

classifications intermittently from 1957 to 1999, during October through April (Table 1). Female caribou exhibit little tendency to cast antlers during this time of year (Bergerud 1976). Observations from the air were conducted using a helicopter; those on the ground were made with a spotting scope or binoculars. For two herds, Grey River and Northern Peninsula, data were from Bergerud (1971). The data were pooled across years; the total numbers of females classified per herd varied from 160 to 2503 (Table 1).

Population sizes were based on 1–5 aerial censuses per herd, using either strip, block, or mark–resight procedures, or total enumerations (Mahoney 2000), coincident with the periods of observation of antler possession. Population density was computed as the ratio of average population size to the maximum area of herd occupancy (Table 1).

Observations of snow conditions were annual averages, 1961–1990, from Environment Canada (1993). Each herd was paired with observations from the meteorological station nearest the center of its range, or with the average from the two most proximate stations if the herd's range did not encompass a station (Fig. 1). The percentages of females with antlers were compared to the total snowfall, snow depth at the end of March, and the number of months in which snow cover was ≥ 25 cm deep at the end of the month. The 25 cm

TABLE 1. Observations of female antler possession and population densities of caribou herds in Newfoundland and Labrador, Canada.

Caribou herd	Year(s) of antler observations	Total no. females classified	Females with antlers (%)	Population density (no. animals/km ²)
Avalon Peninsula	1964, 1966, 1968, 1994–1996	2503	2.7	0.61
Buchans Plateau	1994–1999	1429	12.0	0.32
Cape Shore	1994–1997	803	3.0	1.96
Gaff Topsails	1994–1996	772	10.0	1.79
Grey River	1957–1967†	n/a†	36.0	0.15
Gros Morne	1994–1995, 1997	682	52.5	0.65
Humber	1997	160	45.6	0.70
La Poile	1994–1997	1759	20.6	0.88
Mealy Mountains	1975, 1977, 1981, 1985, 1987	1340	94.4	0.03
Middle Ridge	1993–1994, 1997	1791	24.7	1.40
Mount Peyton	1994, 1996	368	41.8	0.36
Northern Peninsula	1957–1967‡	n/a‡	88.0	0.02
Pot Hill	1994, 1996	377	17.5	0.69
Red Wine Mountains	1981, 1996–1998	292	98.3	0.02
Sandy Lake	1994–1995	472	22.2	0.21

† From Bergerud (1971); observations on an unknown number of animals (n/a, not available) from five years, 1957–1967.

‡ From Bergerud (1971); observations on an unknown number of animals from one year, 1957–1967.

depth is the approximate threshold above which caribou must restrict their foraging by cratering (Vandal and Barrette 1985). Because of non-normality, we log-transformed population density and March snow depth, and arcsine-transformed (Krebs 1999) the percentage of antlered females before conducting multiple regression and correlation analyses with Statistica (StatSoft 1999).

RESULTS

The percentage of females bearing antlers was related positively with snowfall, depth, and duration (Fig. 2). Antler possession was correlated with total annual snowfall ($r = 0.889$, $P < 0.0001$), snow depth at the

end of March ($r = 0.876$, $P < 0.0001$), and the number of months with ≥ 25 cm snow cover ($r = 0.746$, $P = 0.0014$). We surmise that depth or duration of snow cover, compared to snowfall, may be a more accurate depiction of the scope for interference competition. The climate of much of Newfoundland is maritime; mid winter snow melt is not uncommon. March snow depth and the number of months with ≥ 25 cm snow cover reflect the length of the snow cover season, and thus may better convey the duration of interference competition among foraging caribou.

Population density was related negatively with female antler possession ($r = -0.857$, $P < 0.0001$; Fig. 2) as well as with measures of snow cover. Our pre-

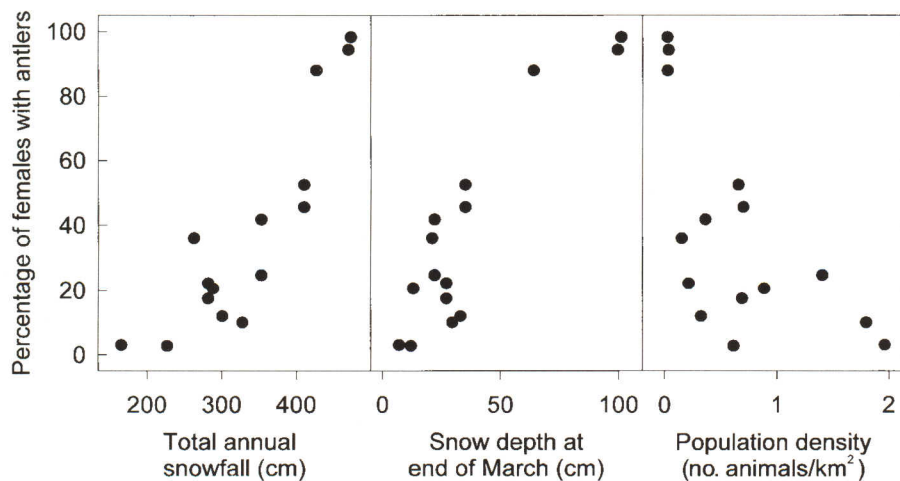


FIG. 2. Percentage of Newfoundland–Labrador female caribou bearing antlers in relation to average total annual snowfall, mean snow depth at the end of March, and caribou population density.

TABLE 2. Partial correlation coefficients of predictor variables with the proportion of female caribou bearing antlers.

Variable being controlled	Population density	Total annual snowfall	Months with ≥ 25 cm snowcover	Snow depth at end of March
Population density		0.879 ($P < 0.0001$)	0.411 ($P = 0.144$)	0.634 ($P = 0.0148$)
Total annual snowfall	-0.843 ($P = 0.0002$)	
Months with ≥ 25 cm snowcover	-0.708 ($P = 0.0046$)
Snow depth at end of March	-0.562 ($P = 0.036$)	

dictor variables were thus potentially confounded. When we statistically removed the effect of population density, the percentage of females with antlers remained positively correlated with total annual snowfall and March snow depth (Table 2). Conversely, when we controlled for variation in snow conditions, the negative correlation between the percentage of females with antlers and population density remained (Table 2).

DISCUSSION

For caribou, an important effect of snow cover is to confine foraging to patches, thereby enhancing the scope for antagonistic displacements (Vandal and Barrette 1986, Schaefer and Messier 1995). Feeding craters, microsites where caribou excavate the snow cover and gain access to subnivean food, become energetic investments into monopolizable resources (Henshaw 1969). Antler possession in caribou is the most reliable predictor of the incidence and outcome of contests over craters (Barrette and Vandal 1986), which increase in frequency with snow depth > 25 cm (Vandal and Barrette 1985). Hence, our results, demonstrating significant relationships between snow conditions and antler carrying (Fig. 2, Table 2), support the hypothesis that antlers may be advantageous to females in interference competition for winter food. On the other hand, antlers might confer fewer benefits where resources are not economically defensible. Accordingly, where much of the caribou winter diet consists of arboreal lichens, a resource that is more uniformly distributed and that does not entail cratering, female antler possession might be expected to decline (Barrette and Vandal 1986, Geist 1998).

Antler renewal is energetically expensive (Clutton-Brock 1982, Kiltie 1985). Frequency of antler possession by females often shows a negative relationship with the quality of winter range (Bergerud 1976, Thing et al. 1986, Reimers 1993). In our study area, lower percentages of antler-bearing females were linked to higher population densities (Fig. 2), presumably a reflection of the heightened nutritional stress of antler growth. Indeed, at the extremes of densities in our study

area (Avalon Peninsula and Red Wine Mountains herds; Table 1), population size was related inversely to body size, condition, and antler carrying (J. A. Schaefer and S. P. Mahoney, unpublished data). Reimers (1993) also reported that antlered females became rarer in instances of higher animal densities, diminished dressed weights, and reduced body size. Where snow cover is predictably shallow or brief, antlers may thus represent a luxury organ for female caribou in poorer nutritional state.

Evidence from *Rangifer tarandus* proves additionally valuable in evaluating rival hypotheses of horn-like organs on females. As proposed by Packer (1983), such appendages might aid female ungulates in defending against predators. Unlike other deer, caribou were assumed not to hide their fawns, and hence were assumed to be more likely to engage in active defense. More recent evidence, however, demonstrates that hiding offspring is not uncommon for caribou dams (Chubbs 1993; S. P. Mahoney, unpublished data), and observations of active defense are rare (Estes 1991). Similarly, antlers as means to mimic juvenile male offspring and to guard against aggression by dominant males (Estes 1991) cannot account for the somewhat different chronology of antler casting between the sexes (Bergerud 1976). Especially during late winter and early spring, polished antlers on females will help to distinguish, not mask, them from young stags.

Intraspecific combat remains the sole well-substantiated function for antlers (Clutton-Brock 1982, cf. Markusson and Folstad 1997), and is supported by recent phylogenetic evidence that female horns and their analogues serve as weapons in intraspecific, often intrasexual, competition for resources (Roberts 1996). As noted by Roberts (1996:415), antlers on *Rangifer* seem to represent "the most convincing evidence of female weaponry being used in contest for limited feeding sites." The biogeography of antler possession lends additional support to this idea.

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