Journal of Wildlife Management 74(3):395–404; 2010; DOI: 10.2193/2008-384

*Management and Conservation Article*

# Body Size Variations in Caribou Ecotypes and Relationships With Demography

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**ABSTRACT** In many vertebrates size is one of the most influential and variable individual characteristics and a strong determinant of reproductive success. Body size is generally density dependent and decreases when intraspecific competition increases. Frequent and long-distance movements increase energy expenditures and, therefore, may also influence body size, particularly in highly mobile species. Caribou (*Rangifer tarandus*, also known as reindeer) exhibit tremendous variation in size and movements and thus represent an excellent candidate species to test the relationships between body size, population size, and movements. We analyzed body measurements of adult female caribou from 7 herds of the Québec-Labrador Peninsula, Canada, and we related their morphology to population size, movements, and annual ranges. The herds represented 3 ecotypes (migratory, montane, and sedentary). Ecotypes and herds differed in size (length), shape (roundness), and movements. The sedentary ecotype was larger and moved 4 to 7 times less than the migratory ecotype in the 1990s. At the start of a demographic growth period in the early 1960s, migratory caribou from the Rivière-George (hereafter George) herd had longer mandibles than caribou of the sedentary ecotype. Mandible length in the George herd declined in the 1980s after rapid population growth, while individuals performed extensive movements and the herd's annual range increased. Migratory caribou then became shorter than sedentary caribou. After the George herd decline in the 1990s, mandible length increased again near levels of the 1980s. Caribou from the migratory Rivière-aux-Feuilles herd later showed a similar decline in mandible length during a period of population growth, associated with longer movements and increasing annual range. We hypothesize that the density-dependent effect observed on body size might have been exerted through summer habitat degradation and movement variations during herd growth. Our study has 2 important implications for caribou management: the distinctiveness of different populations and ecotypes, and the correlations between population trajectories and changes in body condition and habitat.

**KEY WORDS** annual range, caribou, Labrador, migration, morphology, movement, Québec, *Rangifer tarandus*.

In vertebrates, body size is one of the most influential life-history traits and is intricately correlated with many morphological, physiological, behavioral, and environmental characteristics. It is therefore one of the most difficult traits to study in animal ecology (Wikelski 2005). The selective advantage of large size occurs both under natural (e.g., survival) and sexual (e.g., mating success) selection processes (Andersson 1994). Size is therefore one of the most influential and variable individual characteristics and a strong determinant of reproductive success (Le Boeuf 1974, Calder 1996, Côté and Festa-Bianchet 2001). Body size is also influenced by climatic factors (Post et al. 1997, Rodriguez et al. 2006) and population density (Meldgaard 1986, Pettorelli et al. 2002, Toïgo et al. 2006, Zedrosser et al. 2006). Although studies have shown that population density influences body size, little is known about the underlying mechanisms. A decrease in quality or in quantity of food and a resulting increase in intraspecific competition have often been identified as generating the effect of density on body size (Clutton-Brock et al. 1982, Zedrosser et al. 2006, Simard et al. 2008), but other mechanisms, such as increased movements and associated energy expenditures, may also be involved.

Across its circumpolar range, caribou (*Rangifer tarandus*, also known as reindeer) exhibits tremendous variation in morphology and is the most variable of all deer species (Geist 1998). Morphological variation in caribou is thought to be due to the great differences in environments where this species is found, including harsh arctic deserts, temperate forests, tundra-taiga, snow-bound boreal forest, and alpine habitat (Thomas and Everson 1982, Kuzyk et al. 1999). This wide range of environmental conditions may influence caribou morphological characteristics such as body size (Thomas and Everson 1982, Kuzyk et al. 1999), coat color and pattern (Geist 1998), leg length (Klein et al. 1987), and antler shape and presence (Schaefer and Mahoney 2001), and may also shape its ecology and behavior (Bergerud 2000, Côté et al. 2002).

Bergerud (1996, 2000) proposed to use the concept of ecotypes to classify caribou populations or herds according to different life-history strategies and ecological conditions. Caribou in the sedentary ecotype (hereafter sedentary caribou or herds) remain south of the tree line, disperse at calving, and perform small seasonal movements in the boreal forest. Sedentary caribou have been designated as threatened under the Species at Risk Act in Canada (Committee on the

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Status of Endangered Wildlife in Canada [COSEWIC] 2002, Schmelzer et al. 2004). Caribou in the migratory ecotype (hereafter migratory caribou or herds) move north of the tree line, aggregate at calving, and undertake seasonal migrations of thousands of kilometers through tundra, taiga, and boreal forest. Caribou in the montane ecotype (hereafter montane caribou or herds) undertake small altitudinal migrations in alpine environments.

Although the ecotype concept is widely used in caribou conservation (e.g. COSEWIC 2002), little evidence currently supports the distinctiveness of ecotypes. Using DNA microsatellites, Courtois et al. (2003) and Boulet et al. (2007) confirmed genetic differences among caribou ecotypes. It is unknown, however, whether variations in genetics translate into differences in morphology or in other characteristics. Movements are very different among ecotypes, and we hypothesize that the energetic costs of movements may affect caribou body size. Migration likely evolved in caribou, as in many invertebrate and vertebrate species, in response to ecological opportunities related to forage quality, predation risk, or seasonality (Fryxell and Sinclair 1988, Alerstam et al. 2003, Hebblewhite and Merrill 2007). If these opportunities or factors promoting, but also limiting, migration change according to variations in population demography, then caribou migratory behavior might also be variable (Mahoney and Schaefer 2002, Hinkes et al. 2005). The potential effect of migration or movements on body size may then change with population demography.

Our goal was to investigate variations in morphology and movements across 3 caribou ecotypes in 7 herds according to changes in population size. We hypothesized that population size and the cost of migration, as estimated by the herd's daily movement rate, negatively affected body size of caribou. We predicted that 1) at high density, migratory caribou would be smaller than sedentary caribou and move longer distances; 2) movements and annual range would be positively related to herd size in migratory caribou; and 3) increases in movements and annual range during herd growth would be negatively related to caribou body size in migratory caribou.

## STUDY AREA

The annual ranges of the herds we studied in the Québec-Labrador Peninsula (50°–62°N, 56°–80°W) encompassed an area of about 1.2 million km$^2$ north of 50°30′N (Fig. 1) extending into 4 large vegetation biomes from the south to the north: boreal forest, taïga, forest tundra, and arctic tundra (Payette 1983). The tree line marked the transition from forest to arctic tundra and generally stretched from east to west along 58°N (Couturier et al. 1990). About half of the precipitation in the peninsula fell as snow (Couturier et al. 1990) with an increasing gradient from the arctic tundra to the boreal forest (Fig. 1).

We studied 4 sedentary, 2 migratory, and 1 montane herds that we delineated based on data from radiocollared animals monitored over the last 20 years (Fig. 1). Sedentary caribou of the peninsula lived in low density herds between 50°N and 53°N, but they have been found as far as 54°N (Boulet et al. 2007) and 49°N in isolated groups (Courtois et al. 2003). From east to west, we investigated 4 sedentary herds: 1) the Mealy Mountains herd (hereafter Mealy) underwent a marked decline between the 1950s and 1970s from a few thousand caribou to only a few hundred, but during our study the herd population was stable or slightly increasing at about 2,600 caribou (Otto 2002); 2) the Red Wine Mountains herd (hereafter Red Wine) sharply declined from 751 sedentary caribou in 1981 to 87 in 2003 (Schaefer et al. 1999, Schmelzer et al. 2004); 3) the Lac Joseph herd (hereafter Lac Jos) was approximately 1,100 sedentary caribou (Jung et al. 2000), but this was lower than historical records (Saint-Martin 1987); 4) the Jamésie herd (hereafter Jamésie) was estimated at approximately 600 sedentary caribou (D. St-Pierre, Québec Ministère Ressources naturelles et Faune, unpublished data), but the precise annual range of the herd was unknown (approx. range shown on Fig. 1).

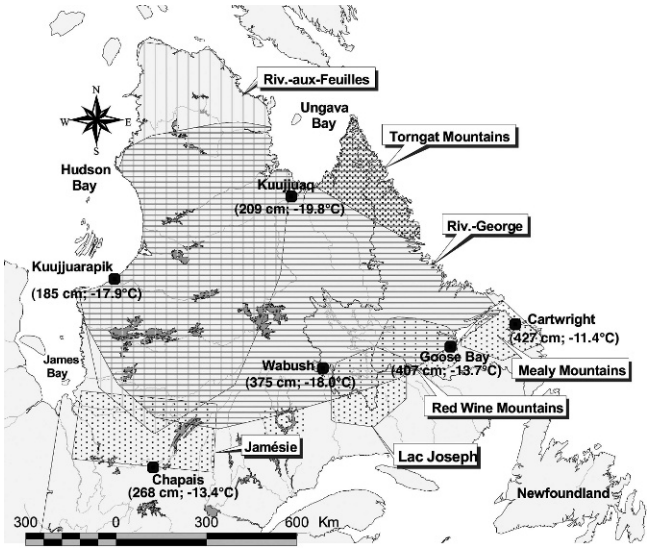


**Figure 1.** Multi-annual ranges of the migratory Rivière-George (Riv.-George) caribou herd (horizontal shading, 1991–2003), the migratory Rivière-aux-Feuilles (Riv.-aux-Feuilles) herd (vertical shading, 1993–2003), 4 sedentary herds (Lac Joseph, Mealy Mountains, Red Wine Mountains [following Schmelzer et al. 2004], and Jamésie [approx. annual range]), and the montane Torngat Mountains herd (Schaefer and Luttich 1998) in the Québec-Labrador Peninsula, Canada. Snowfall (cm) and daily minimum temperature (° C) averages in winter (Nov–Apr) from 1962 to 2002 are shown under the weather station name (meteorological data from Environment Canada, www.climate.weatheroffice.ec.gc.ca, accessed 8 Nov 2009).

Since the 1980s the 2 herds of migratory caribou of the Québec-Labrador Peninsula became successively the largest herd in the world (Mallory and Hillis 1998, Couturier et al. 2004). In the migratory ecotype, we studied the Leaf River herd, which was locally known as Rivière-aux-Feuilles herd (hereafter Feuilles), and the George River herd, which was known as the Rivière-George herd (hereafter George). In their annual migrations, these 2 herds occupied all of the peninsula land north of 53°N, although they have been seen as far south as 50°30′N during recent winters. The 2 migratory herds underwent major population fluctuations in the last 2 centuries (Boudreau et al. 2003, Payette et al.

2004). In the 1880s Feuilles and George herds were abundant but populations declined thereafter and remained extremely low until the 1950s (Low 1896, Elton 1942). Aerial population surveys have shown that the George herd had as few as 5,000 caribou in 1956 (Banfield and Tener 1958) and 15,000 in 1958 (Bergerud 1967), but reached 776,000 caribou in 1993 and 385,000 in 2001 (Couturier et al. 2004). The Feuilles herd increased from 56,000 caribou in 1975 to 276,000 in 1991, and to >628,000 in 2001 (we used the lower confidence limit in 2001, see Couturier et al. 2004). We assumed that the Feuilles herd increased during our study, and we assumed the George herd increased until 1989 but decreased after that. We based our assumptions on herd size estimates and their confidence intervals, annual ranges, demographic parameters (Crête et al. 1996), and dendroecological (Boudreau et al. 2003) and lichen abundance analyses (Boudreau and Payette 2004).

Seasonal ranges of the 2 migratory herds were well known from a satellite radiotracking program that began in the 1980s (Couturier et al. 2004, Boulet et al. 2007). The 2 migratory herds were managed as distinct populations because they aggregate on different calving grounds more than 800 km apart (Boulet et al. 2007). Historical information suggests that females have been gathering on these calving grounds since the end of the 19th century (Low 1896, Elton 1942). Migratory and sedentary ecotypes shared part of their ranges in winter (Boulet et al. 2007).

The only montane herd of the peninsula lived in the alpine habitat of the Torngat Mountains (Schaefer and Luttich 1998). We studied the Torngat Mountains herd (hereafter Torngat) that was probably less than a few thousand caribou (S. Couturier, Québec Ministère Ressources naturelles et Faune, unpublished data). This small montane herd shared most of its seasonal ranges with the large George herd, except in winter. Using radiotelemetry, Schaefer and Luttich (1998) confirmed the distinctiveness of the Torngat herd. Boulet et al. (2007) found that the Torngat, George, and Feuilles herds were genetically similar, but they were different from the 4 sedentary herds.

# METHODS

### Morphological Data

We measured body length (contour length from the upper lip to the last vertebrae of the tail), heart girth (circumference behind the forelegs and shoulder hump), and hind foot length (from tip of hoof to heel) on live animals between 1983 and 2005 (no data in 1989–1992). In 1983–1988, 1993, and 2001–2003, we collected mandibles of migratory caribou from hunters and scientific culls. We measured mandible length with an electronic caliper to the nearest 0.1 mm from the process angularis to the anterior part of the fresh dentary bone. We estimated age of live caribou from tooth wear and replacement, using known-age mandibles. We aged harvested caribou by counting cementum annuli of the first incisors (Miller 1974). We tested the 2 methods of aging by comparing a sample of mandibles. For the analyses of body length, heart girth, and hind foot length, we used adult females ≥2.5 years old because most of the growth is completed at that age (Parker 1980, 1981), and for mandible length measurements, we selected female and male caribou ≥4 years old and ≥5 year old, respectively (Parker 1980, 1981; Holthe and Lassen 1984). We did not repeat any measures on the same individual. Laval University Animal Care Committee approved the study (protocol 2008015-2) and the capture methods met the principles and guidelines of the Canadian Council on Animal Care.

### Movements and Annual Ranges

We captured caribou using darts or nets fired from a helicopter. The Argos satellite telemetry system (CLS America Inc., Largo, MD) monitored movements of 5 herds (George, Feuilles, Torngat, Red Wine, Lac Jos) from June 1986 to December 2003. In the movement analyses we only included animals that we tracked for a minimum of 12 months to avoid the potential bias of season. We only used movement data for adult females because the number of radiotracked males was too small in some years. We checked satellite telemetry positions for error based on a custom filtering tool similar to Austin et al. (2003). Duty cycle ranged from 1 day to 5 days for individual satellite collars, and we excluded successive locations >12 days apart. After filtering, 88% of locations were from 3-day to 5-day intervals. From the distance moved and duration between successive locations, we calculated daily movement rates (km/day). We computed mean daily movement rate (hereafter movements) for the snow-bound winter season (26 Dec–30 Apr; Bergman et al. 2000), and for the rest of the year (hereafter other seasons) when snow was not ecologically limiting.

From 1971 to 1987, the annual range of the George herd was estimated from very high frequency (VHF) radiotelemetry and aerial surveys (Messier et al. 1988, Vandal et al. 1989). We used filtered Argos locations of both sexes to compute the annual range of the George herd from 1986 to 2003 and the Feuilles herd from 1993 to 2003 with 95% Kernels estimated by the Animal Movement extension (Hooge and Eichenlaub 1997) in ArcView 3.1 (ESRI Inc., Redlands, CA).

### Statistical Analyses

Using the Factor Analysis procedure, we performed a canonical correlation model to test for morphological differences among herds. We used the principal components method and extracted the first 2 variates. We plotted these canonical variates on a 2-dimensional graph to assess morphological separation between herds. We represented the herd centroid and its 95% confidence ellipse for each herd. We considered 2 herds significantly different if no overlap occurred between ellipses. We used General Linear Models and post hoc Tukey tests or *t*-tests to identify differences between herds or time periods for morphological measurements. To avoid pseudo-replication, we fitted General Linear Mixed Models (GLMM) with identification number as a random factor on movement data to assess differences among herds, years, or time periods. We fitted a GLMM with cohort as a random factor on mandible data to

**Table 1.** Hind foot length, heart girth, and body length measurements (cm, means, SE, and *n*) of adult female caribou (≥2.5 yr old, $n = 593$) recorded between 1983 and 2005 from 7 herds and 3 ecotypes from the Québec-Labrador Peninsula, Canada. General linear model (GLM) results are presented. Values followed by the same letter did not differ significantly according to a Tukey post hoc comparison.

| | | | | Hind foot length | | Heart girth | | Body length | |
|---|---|---|---|---|---|---|---|---|---|
| Ecotype | Herd[a] | Yr | *n* | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE |
| Migratory | George | 1983–2002 | 344 | 55.6 A | 0.1 | 114.0 A | 0.4 | 186.6 A | 0.5 |
| | Feuilles | 2000–2002 | 104 | 55.6 A | 0.2 | 108.6 B | 0.6 | 184.2 A | 0.9 |
| Montane | Torngat | 2001 | 14 | 53.6 B | 0.8 | 122.4 CD | 1.8 | 200.3 B | 2.1 |
| Sedentary | Red Wine | 1993–2002 | 42 | 60.6 CD | 0.4 | 124.2 C | 1.2 | 209.2 C | 1.8 |
| | Lac Jos | 1998–2002 | 38 | 61.6 C | 0.3 | 117.3 AD | 0.9 | 205.6 BC | 1.1 |
| | Jamésie | 2003–2004 | 24 | 61.5 C | 0.3 | 119.9 CD | 1.5 | 200.9 B | 2.3 |
| | Mealy | 2002–2005 | 27 | 59.6 D | 0.6 | 123.5 C | 0.9 | 208.1 BC | 1.2 |
| GLM | | | | $F_{6,586} = 106.4$<br>$P < 0.001$<br>$r^2 = 0.52$ | | $F_{6,586} = 40.8$<br>$P < 0.001$<br>$r^2 = 0.30$ | | $F_{6,586} = 96.4$<br>$P < 0.001$<br>$r^2 = 0.50$ | |

[a] George: Rivière-George herd; Feuilles: Rivière-aux-Feuilles herd; Torngat: Torngat Mountains herd; Red Wine: Red Wine Mountains herd; Lac Jos: Lac Joseph herd; Jamésie: Jamésie herd; Mealy: Mealy Mountains herd.

test for differences among migratory herds. We analyzed mandible data based on the year of birth (i.e., on the cohort). To compare our data with the means reported in Bergerud (1967) and Parker (1980, 1981), we subtracted 5 from their year of collection to approximate the mean year of birth. We presented means ± standard errors, and we set significance level at $\alpha = 0.05$. We conducted all analyses with SPSS 11 for Macintosh (SPSS Inc., Chicago, IL).

## RESULTS

We measured 593 adult female caribou to test for body size differences between herds and ecotypes. To investigate long-term changes in size, we analyzed 379 mandibles collected since the 1960s in the 2 migratory herds. Comparing the 2 aging methods, we found a high correlation between the tooth wear and cementum methods ($r = 0.825$, $n = 65$, $P < 0.001$). We studied movements and annual ranges from satellite locations recorded between 1986 and 2003 of 241 caribou in 5 herds: 171 (24 M, 147 F) caribou in the George herd, 42 (8 M, 34 F) caribou in the Feuilles herd, 6 caribou (6 F) in the Torngat herd, 13 caribou (13 F) from the Red Wine herd, and 9 caribou (9 F) from the Lac Jos herd. We monitored individual caribou for an average of 2.5 years, but we followed some animals for up to 10 years.

### Differences in Morphology Among Herds and Ecotypes

Hind foot length, heart girth, and body length all differed between herds (Table 1). Tukey comparisons revealed that sedentary caribou were significantly larger than migratory caribou. Hind foot length, heart girth, and body length were about 5 cm, 10 cm, and 20 cm larger, respectively, for sedentary animals than for migratory ones. From 2000 to 2002 data were available for both migratory herds and heart girth ($t = 4.6$, $P < 0.001$) and body length ($t = 4.2$, $P < 0.001$) were longer in the George ($n = 150$) than in the Feuilles herd, whereas hind foot was slightly shorter ($t = -2.0$, $P = 0.041$; Tables 1, 2).

The first canonical variate was highly positively correlated with hind foot ($r = 0.934$) and body length ($r = 0.710$), but not much with heart girth ($r = 0.217$), and was therefore an indication of animal length or size. The second canonical variate was weakly correlated with hind foot length ($r = 0.147$), moderately correlated with body length ($r = 0.504$), but strongly correlated with heart girth ($r = 0.953$). We interpret the second variate as an indication of animal roundness or shape. Both variates explained 86% of the variance, suggesting a good representation of the variability in the data. A 2-dimensional plot of size and shape for each herd indicated a wide separation between the 3 ecotypes (Fig. 2). There was a total separation between most herds except the Lac Jos and Jamésie, and the Red Wine and the Mealy herds. For the size variate, the 3 northern herds were not different from each other, but caribou in the northern herds were shorter than those from the 4 southern sedentary herds (Fig. 2). Among sedentary herds, Lac Jos caribou were the longest and Mealy the shortest, although there was some overlap on the size axis. Caribou from Lac Jos and Jamésie were more slender in shape than those from Mealy and Red Wine. Although similar in size, George and Feuilles were different in shape, the latter being more slender.

### Long-Term Changes in Migratory Caribou Body Size

Body measurements showed significant long-term changes in adult female caribou from the George herd in 5 sampling periods from 1983 to 2002 (Table 2). We did not note any time trend in hind foot length and heart girth, but post hoc comparisons indicated that body length was longer in 1993–2002 than in 1983–1986 (Table 2). Female mandible length of the George herd decreased between cohorts born in 1973 and 1984 ($Y = -1.68X + 3{,}606$, $r^2 = 0.15$, $P < 0.001$, $n = 117$; Fig. 3A). The annual mean plummeted to 270 mm for the cohort born in 1984 (Fig. 3A), which is much smaller than the mean of 288.5 ± 1.3 mm ($n = 58$) for females born in the late 1950s (Bergerud 1967) or the mean of 283.0 ± 1.0 mm ($n = 74$) for females born in the mid-1970s (Parker 1980, 1981). Mandible length of adult females from the Mealy herd born in the late 1950s was 281.5 ± 1.1 mm on average ($n = 128$, Fig. 3A), which was smaller than for the George herd at that time (Bergerud 1967). However, female mandible length of the George herd increased to a mean of 279.9 ± 0.9 mm ($n = 52$) for the cohorts born in 1991 to 1998, after the herd had initiated its decline (Fig. 3A). Average mandible length of George males ≥5 years old was

**Table 2.** Hind foot length, heart girth, and body length measurements (cm, means, SE, and *n*) of adult female caribou (≥2.5 yrs old) of the Rivière-George herd ($n = 344$) recorded between 1983 and 2002 from the Québec-Labrador Peninsula, Canada. General linear model (GLM) results are presented. Values followed by the same letter did not differ significantly according to a Tukey post hoc comparison.

| | | Hind foot length | | Heart girth | | Body length | |
|---|---|---|---|---|---|---|---|
| Yr | *n* | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE |
| 1983–1984 | 41 | 55.9 AB | 0.3 | 115.3 AC | 1.1 | 183.1 A | 1.4 |
| 1985–1986 | 55 | 55.7 AB | 0.3 | 117.7 A | 1.0 | 181.8 A | 1.1 |
| 1987–1988 | 65 | 56.1 A | 0.2 | 113.0 BC | 0.8 | 186.8 AC | 0.9 |
| 1993–1998 | 33 | 56.0 AB | 0.3 | 115.5 AC | 1.5 | 189.1 BC | 1.6 |
| 2000–2002 | 150 | 55.1 B | 0.2 | 112.3 C | 0.5 | 188.7 BC | 0.6 |
| GLM | | $F_{4,339} = 3.9$<br>$P = 0.004$<br>$r^2 = 0.04$ | | $F_{4,339} = 7.0$<br>$P < 0.001$<br>$r^2 = 0.08$ | | $F_{4,339} = 10.0$<br>$P < 0.001$<br>$r^2 = 0.11$ | |

308.4 ± 1.5 mm ($n = 72$) and 309.5 ± 3.7 mm ($n = 8$) for animals collected in 1987–1988 and 2003, respectively. From Bergerud (1967), we computed a mean mandible length of 321.4 ± 1.2 mm ($n = 249$) and 313.2 ± 2.3 mm ($n = 25$) for males ≥4 years old (note the age difference with our data) collected in 1963–1965 from the George and the Mealy herds, respectively. For the Feuilles herd (Fig. 3B), female mandible length decreased from the cohort of 1982 to that of 1999 ($Y = -0.78\ X + 1{,}822$, $r^2 = 0.10$, $P = 0.005$, $n = 78$). The slopes of the regression of female mandible length on cohort did not differ between the 2 migratory herds (both confidence intervals overlapped), indicating similar rates of decline through time (George: 1973–1984; Feuilles: 1982–1999). Using GLMM analysis on data from the second period of our study of mandible length (cohorts 1991 to 1998), we found female mandibles were 3.5 ± 1.4 mm ($F_{1,110} = 5.9$, $P = 0.017$) longer for the George ($n = 51$) than the Feuilles herd ($n = 66$).

### Movements and Annual Ranges

Movements differed among herds in winter ($F_{4,123} = 37.5$, $P < 0.001$), other seasons ($F_{4,128} = 235.5$, $P < 0.001$), and year-round ($F_{4,118} = 215.7$, $P < 0.001$; Table 3). Movements of the migratory herds were approximately 4 to 7 times higher than those of the sedentary herds, whereas the montane ecotype was intermediate. To investigate temporal variations in movements of migratory herds, we split the database into 4 periods based on data availability and demographic phases. Movements differed between periods for the George herd in winter ($F_{3,289} = 17.3$, $P < 0.001$), other seasons ($F_{3,303} = 12.1$, $P < 0.001$), and year-round ($F_{3,401} = 38.6$, $P < 0.001$; Table 3). Movements in winter for the George herd decreased by 39% from 1987–1989 to 1993–1998 during the herd decline, whereas for other seasons, movements decreased by 16% during the same periods. During herd growth, movements in the Feuilles herd increased by 34% in winter from 1993–1998 to 1999–2002 ($F_{1,244} = 15.4$, $P < 0.001$), but it did not change during other seasons ($F_{1,314} = 1.5$, $P = 0.217$) or year-round ($F_{1,280} = 1.1$, $P = 0.292$). For the periods 1993–1998 and 1999–2002, the analysis of movements in winter showed significant herd ($F_{1,77} = 16.9$, $P < 0.001$), period ($F_{1,1291} = 11.7$, $P = 0.001$), and herd*period ($F_{1,1291} = 10.8$, $P = 0.001$) effects as

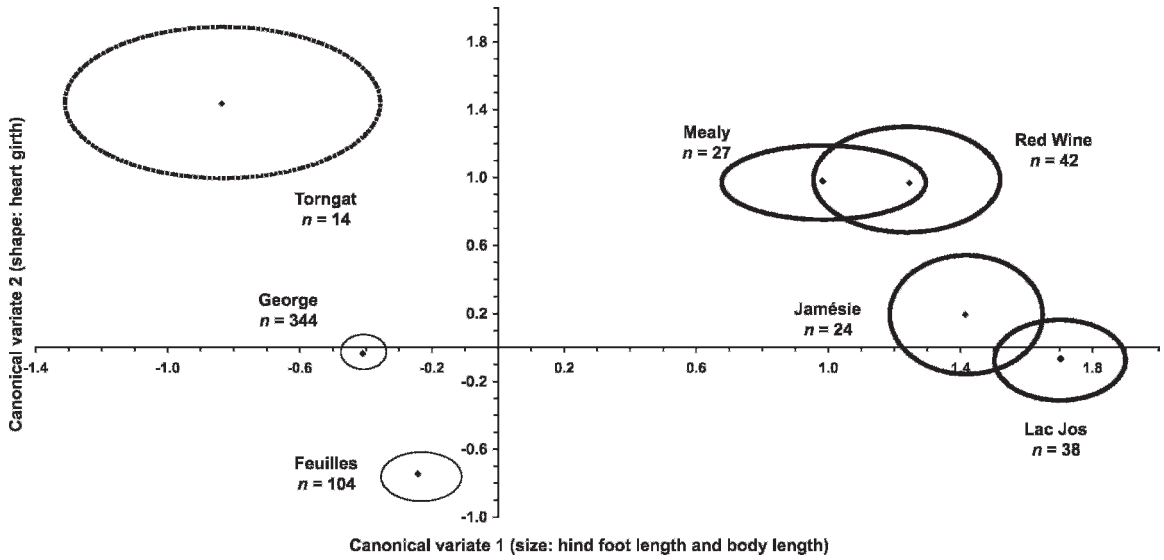


**Figure 2.** Canonical correlation plot of variate scores of body measurements recorded between 1983 and 2005 for 7 caribou herds from the Québec-Labrador Peninsula, Canada, including herd centroids and 95% confidence ellipses. Three ecotypes are represented: sedentary (bold), migratory (regular), and montane (dashed). Variate 1 indicates size (hind foot length and body length), and variate 2 indicates shape (heart girth).

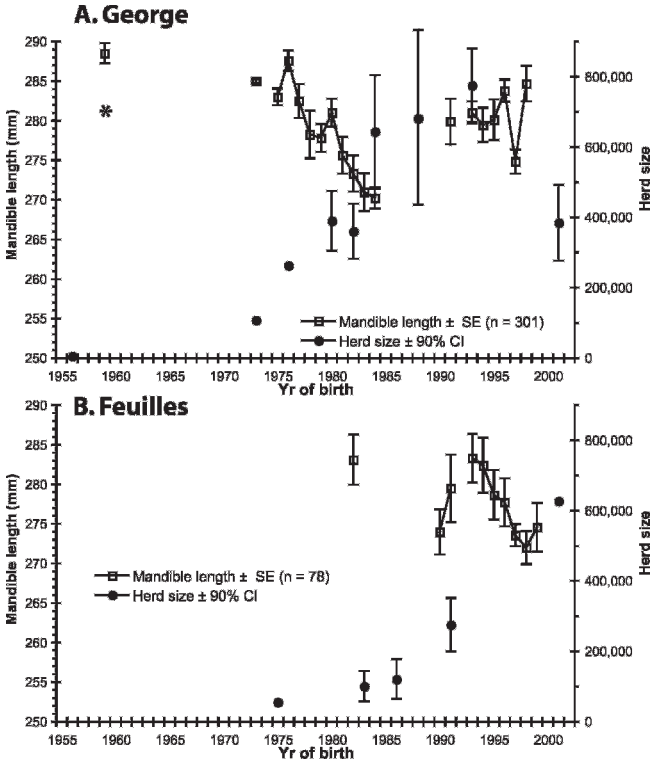


**Figure 3.** Mandible length (mean ± SE) of adult female caribou (≥4 yr old) and herd size ($n$ ± 90% CI) in 2 migratory herds of the Québec-Labrador Peninsula, Canada: (A) Rivière-George herd (George) and (B) Rivière-aux-Feuilles herd (Feuilles). Note that adult mandible length is plotted against year of birth. For George, data for the cohorts of 1959 and 1975 are from Bergerud (1967) and Parker (1980), respectively. The mean for the sedentary Mealy Mountains herd in 1959 is indicated by a star. The value of the lower confidence limit of herd size is shown for the Feuilles herd in 2001 (see Couturier et al. 2004).

movements increased between periods for the Feuilles herd but not for the George. Movements in winter were 1.7 ± 0.3 km/day higher for the Feuilles compared to the George herd. A similar analysis for other seasons revealed a significant relationship with herd ($F_{1,61}$ = 7.2, $P$ = 0.009), and the Feuilles movements were 0.6 ± 0.3 km/day higher than those of the George. However, we did not detect a relationship between period or herd*period ($P$ > 0.078). Movements were 0.7 ± 0.6 km/day higher in winter ($F_{1,55}$ = 4.5, $P$ = 0.039) and 0.4 ± 0.6 km/day higher during other seasons ($F_{1,81}$ = 4.1, $P$ = 0.045) in the Red Wine herd than in the Lac Jos herd, while year or herd*year were not significant ($P$ > 0.135).

We found similar annual range estimates from satellite and VHF methods. In 1986 range estimates for the George herd were 330,000 km$^2$ from satellite data and 362,000 km$^2$ for VHF radiotelemetry data. In 1987 range estimates for the George herd were 398,000 km$^2$ from satellite data and 394,000 km$^2$ from VHF radiotelemetry data (Fig. 4A; Vandal et al. 1989). The annual range of the George herd increased in the 1970s–1980s and reached a maximum at 606,000 km$^2$ in 1989, and it declined thereafter to reach 257,000 km$^2$ in 2002 (Fig. 4A). The annual range of the Feuilles herd increased steadily from 218,000 km$^2$ in 1993 to 573,000 km$^2$ in 2003 (Fig. 4B).

## DISCUSSION

We found that body size and shape, as well as movements, were highly variable between ecotypes and herds of caribou. Our results supported our first prediction that the migratory ecotype, at high population numbers, has a smaller body size than the sedentary ecotype. Our empirical data also confirmed the ecotype definition and indicated that the migratory ecotype moves 4 to 7 times more extensively than the sedentary ecotype. We confirmed our second prediction for both migratory herds and found that movements and annual ranges were positively related to herd size. Schaefer and Mahoney (2003) also previously reported that population range tended to increase with the abundance of migratory caribou. We found that within the migratory ecotype, body size (mandible) and shape (heart girth; Fig. 2) were larger in the George than in the Feuilles herd, but movements and annual ranges were smaller, which confirms our third prediction. Our findings suggest that the influence of herd size on body size and shape is acting over time through movement variations, particularly during the snow-bound winter, as changes in movements were greater in that season. We cannot fully rule out that the influence of

**Table 3.** Daily movement rates (km/day, means, SE, and $n$) based on satellite telemetry between 1987 and 2002 during winter (26 Dec–30 Apr), other seasons, and year-round for 5 caribou herds of 3 ecotypes of the Québec-Labrador Peninsula, Canada. Ecotypes include migratory (George and Feuilles), montane (Torngat), and sedentary (Red Wine and Lac Jos). Number of monitored caribou and satellite fixes ($n$) are shown.

| | | | Winter (km/day) | | | Other seasons (km/day) | | | Yr-round (km/day) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Herd[a] | Yr | No. of caribou | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $n$ |
| George | 1987–1989 | 10 | 6.4 | 0.3 | 481 | 11.8 | 0.3 | 928 | 9.9 | 0.2 | 1,409 |
| | 1990–1992 | 27 | 5.0 | 0.2 | 1,105 | 11.0 | 0.2 | 2,610 | 9.2 | 0.1 | 3,715 |
| | 1993–1998 | 51 | 3.9 | 0.1 | 2,988 | 9.9 | 0.1 | 5,779 | 7.8 | 0.1 | 8,767 |
| | 1999–2002 | 35 | 4.1 | 0.1 | 1,756 | 9.7 | 0.1 | 3,408 | 7.8 | 0.1 | 5,164 |
| | 1987–2002 | 82 | 4.3 | 0.1 | 6,330 | 10.2 | 0.1 | 12,725 | 8.2 | 0.1 | 19,055 |
| Feuilles | 1993–1998 | 18 | 4.4 | 0.2 | 944 | 10.6 | 0.2 | 2,350 | 8.8 | 0.1 | 3,294 |
| | 1999–2002 | 14 | 5.9 | 0.2 | 939 | 10.4 | 0.2 | 1,713 | 8.8 | 0.2 | 2,652 |
| | 1993–2002 | 23 | 5.1 | 0.1 | 1,883 | 10.5 | 0.1 | 4,063 | 8.8 | 0.1 | 5,946 |
| Torngat | 1988–1999 | 6 | 2.1 | 0.1 | 464 | 3.4 | 0.2 | 862 | 2.9 | 0.1 | 1,326 |
| Red Wine | 1995–2000 | 13 | 1.4 | 0.1 | 893 | 2.1 | 0.1 | 1,444 | 1.8 | 0.1 | 2,337 |
| Lac Jos | 1998–2002 | 9 | 0.9 | 0.1 | 529 | 1.6 | 0.1 | 1,012 | 1.3 | 0.1 | 1,541 |

[a] George: Rivière-George herd; Feuilles: Rivière-aux-Feuilles herd; Torngat: Torngat Mountains herd; Red Wine: Red Wine Mountains herd; Lac Jos: Lac Joseph herd; Jamésie: Jamésie herd; Mealy: Mealy Mountains herd.

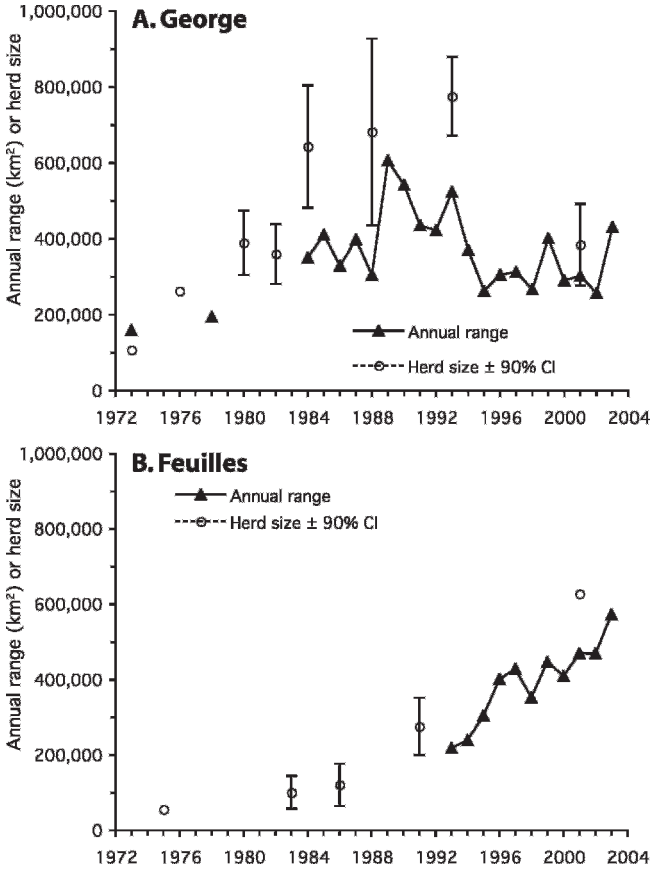


**Figure 4.** Annual population range (km$^2$) and herd size ($n \pm 90\%$ CI) of 2 migratory herds of caribou from the Québec-Labrador Peninsula, Canada: (A) Rivière-George herd (George) and (B) Rivière-aux-Feuilles herd (Feuilles). Range data from 1971 to 1975 (plotted in 1973) and from 1976 to 1980 (plotted in 1978) are from Messier et al. (1988), and data for 1984 and 1985 are from Vandal et al. (1989). The value of the lower confidence limit of herd size is shown for the Feuilles herd in 2001 (see Couturier et al. 2004).

movements on body size could also be a correlate of another density-dependent process, such as summer habitat deterioration generated by increases in herd size (Couturier et al. 1990, Crête and Huot 1993). However, like Messier et al. (1988), we hypothesize that movements may not simply be a correlate of a higher-level process but could be involved directly in population regulation. On one hand, greater movements represent increased energy expenditures (Fancy and White 1985) that appear to influence caribou body size from the first year of life (Couturier et al. 2009*b*) to adulthood (this study), which may eventually affect survival and reproduction. On the other hand, although migration clearly imposes energetic costs, limited nutrition opportunities may also stimulate migration.

### Ecotype and Herd Distinctiveness

Our canonical correlation analysis of caribou size and shape revealed the distinctiveness of ecotypes and a complete separation between most herds. Strong differences in movements also confirmed the ecotype distinction. These results are similar to the conclusions of Courtois et al. (2003) and Boulet et al. (2007) about genetic differences between sedentary and migratory caribou herds. Our data therefore empirically support the ecotype concept and the herd identification used in management. However, our results can be of environmental or genotypic origin (see also Klein et al. 1987). Hind foot, mandible, and total body lengths are measures of frame size referring to high-priority growth tissue that are normally heritable (Wilson et al. 2005) but that also clearly depend on environmental conditions (Zannèse et al. 2006*a*). Frame size is generally indicative of nutrition early in life, whereas girth may reflect body condition and be more related to the recent past (Côté et al. 1998).

The shorter leg length that we observed in the 2 migratory herds supports the northward pattern of reduction in leg length reported by Klein et al. (1987) among North American caribou herds from sedentary, to migratory, and to high-arctic herds. This decreasing northward cline is likely due to various selective mechanisms such as nutritional constraints, the energetic efficiency of foraging through snow at various depths, the efficiency of locomotion during long migrations, and fleetness related to predator avoidance (Klein et al. 1987).

### Herd Size Influence on the Body Size of the Migratory Ecotype

Pettorelli et al. (2002) demonstrated that population density during the spring of birth accounted for 35% of the cohort variation in adult body size in roe deer (*Capreolus capreolus*). The length of the metacarpus and the age at which juvenile fallow deer (*Dama dama*) achieve total ossification is also sensitive to changes in animal's population density (Serrano et al. 2007). Our results on the migratory ecotype also confirmed that body size was negatively related to herd size. Mandible length has often been used as a body size index in ungulates (Lowe 1972, Holthe and Lassen 1984, Zannèse et al. 2006*b*), and it has been shown to respond to variations in demography (Hewison et al. 1996, Lyberth et al. 2007). Meldgaard (1986) reported a decrease of 10 mm in mandible length in 30 years when a reindeer herd increased to a historically high level. Mandible of muskoxen (*Ovibos moschatus*) males responded more heavily to density and environment than those of females, possibly because of directional sexual selection for increased body size in males (Lyberth et al. 2007). Our limited dataset on males did not support these findings, because caribou mandibles varied similarly in both sexes.

Crête and Huot (1993) showed that adult females from the George herd were smaller in 1988 than those from the less abundant Feuilles herd. After demographic changes, we reported that adult females from the Feuilles herd became smaller than those from the less abundant George herd. Crête and Huot (1993) also found that George calves weighed less in summer than those from the Feuilles herd in 1988 (19.6 kg vs. 28.5 kg, corrected to 30 July), but this pattern was reversed in 2001 (23.2 kg vs. 22.2 kg; Couturier et al. 2006). Those rapid changes in body size appear to partly depend on herd size because both migratory herds showed the same negative decreases at different times.

The negative influence of population numbers on body size may be partly related to the deterioration of summer

habitat (Couturier et al. 1990, 2009*a*; Crête and Huot 1993). In a long-term analysis of Newfoundland caribou, Mahoney and Schaefer (2002) also reported a decrease in adult body size coincident with herd growth, and they surmised that this response may reflect increased density-dependent competition for summer forage. The crucial influence of summer range condition for both George and Feuilles herds is illustrated by positive effects of summer habitat quality on caribou calf body mass (Couturier et al. 2009*b*) and on adult body proteins in the fall (Couturier et al. 2009*a*). However, the importance of summer habitat is not universal in *Rangifer*. Studies in montane wild reindeer in Norway indicated that winter food limitation lowered adult body size, fat reserves, and birth mass (Skogland 1990). Habitat, however, may not be the only factor involved in the determination of caribou body size. We have shown that movements and annual ranges in migratory herds were positively related to herd size, and we reported elsewhere that movements negatively affected calf body mass (Couturier et al. 2009*b*). During population growth, the increase of movements is negatively related to calf mass and likely influences the size reached at adulthood as well. Variations in adult body size have often been explained by factors acting early in life during the somatic growth period (Post et al. 1997, Gaillard et al. 2003, Solberg et al. 2004, Yom-Tov et al. 2007).

### Costs of Migration and Movements

Migration may increase access to high quality food or reduce the risk of predation (Hebblewhite and Merrill 2007), but it also bears an energetic cost that may be reflected in the body condition of animals (Alerstam et al. 2003). Few studies have investigated the possible cost of migration on body size and the underlying mechanisms involved. Studying the body characteristics of 11 caribou herds from the sedentary ecotype, Kuzyk et al. (1999) rejected the hypothesis that migration is a selective force on sedentary and montane caribou leg length as suggested by Klein et al. (1987), but Kuzyk et al. also suggested that migration may be a selective force in the migratory ecotype that undertakes long movements.

Migration behavior would only be a detriment to body size and growth if it diverts energy and nutrients from somatic growth. Food limitation may impair growth of calves in utero and in early life. We have shown elsewhere that range quality in June is an important factor influencing the mass of calves at birth and in the fall (Couturier et al. 2009*b*). High environmental demands from deep snow may further exacerbate lower birth mass and subsequent growth (Adams 2005, Couturier et al. 2009*b*). In addition, the proportional cost of horizontal travel increases with decreasing body size, that is, a small calf would expend proportionately more energy than its mother when both animals cover the same distance (Fancy and White 1985, Robbins 1993). Young animals may therefore be more sensitive to the cost of migration, which may also subsequently reduce their adult size.

We hypothesized that the costs of migration or movements negatively influenced caribou body size. Testing this hypothesis between species is difficult, as even closely related species have different evolutionary histories. However, the presence of migratory and sedentary ecotypes makes it possible to test this hypothesis at the intraspecific level in caribou. We report 3 lines of evidence supporting the migration and movement cost hypothesis. First, movements and body size and shape appeared negatively correlated both at the ecotype and at the herd levels. Second, both migratory herds experienced similar temporal changes in body size, movements, and annual ranges following fluctuations in herd numbers. One interpretation is that long movements, particularly in winter in snow and when populations were abundant, were costly to calves and adult caribou and had a negative impact on their body size. We based our movement rates on the shortest distance between consecutive relocations that we recorded every 4 days on average; therefore, the rates would be considerably higher if an individual caribou was observed at a finer temporal scale (Schaefer and Mahoney 2003). Third, mandibles of caribou from the George herd were larger in the 1960s than those from the Mealy herd (Bergerud 1967). Banfield (1961) also noted that migratory caribou were larger than sedentary ones in Québec-Labrador. However, the opposite situation occurs during our study and migratory caribou are smaller than sedentary caribou. This switch in body size may be related to the cost of migration. In the 1950s, the George herd size was very low and animals apparently exhibited limited movements in a small area of northeastern Québec-Labrador (Banfield and Tener 1958, Bergerud 1967). During herd growth, we reported an increase in annual range until 1989 followed by a decline both in herd size and annual range (Fig. 4A). Associated with the range expansion and contraction, our results suggest that caribou movements changed accordingly (Fig. 4; see also Hinkes et al. 2005) and therefore likely resulted in variable energy expenditures and body size. Transition between residency and migration has been reported in vertebrates, and latent genetic features for migration can be activated or suppressed by ecological factors such as competition or predation (Alerstam et al. 2003, Hebblewhite and Merrill 2007). Mahoney and Schaefer (2002) and Hinkes et al. (2005) suggested that migratory behavior could change over time following variations in caribou herd size. We hypothesize that migratory behavior changed progressively during demographic changes of migratory caribou herds because of the depletion of forage on the summer range. When caribou numbers are low, migratory herds become more sedentary and use a smaller annual range but when numbers increase, migratory behavior is amplified and annual range increases.

## MANAGEMENT IMPLICATIONS

Our study has 2 important implications for caribou management: the distinctiveness of different populations and ecotypes, and the correlations between population trajectories and changes in body condition in the migratory ecotype. Our findings and those on genetic differentiation (Courtois et al. 2003, Boulet et al. 2007) support the separate listing of the sedentary ecotype under the

legislation for species at risk. Differences between caribou ecotypes have prominent implications for the conservation of the threatened sedentary ecotype, particularly in areas where both ecotypes are sympatric. We showed that it is possible to distinguish these two ecotypes using body size data. However, our results also suggest that phenotypic differences between ecotypes may reverse when migratory herds move less during low population number periods. Due to phenotypic variations between ecotypes, managers should monitor temporal variation in the body size of caribou, ideally at the same time as movement rates. Wildlife managers require reliable information on population size that is often obtained from expensive and irregular aerial surveys. In food-limited populations, managers need an assessment of population size relative to habitat quality to set management goals and harvest quotas. This relative assessment can be performed through the use of ecological indicators (Klein et al. 1987, Hewison et al. 1996, Zannèse et al. 2006*a*). For migratory caribou, we have shown elsewhere that calf body mass and body reserves of adult females can be used as ecological indicators to monitor population trends (Couturier et al. 2009*a*, *b*). Here, we reported long-term changes in body size of individuals from 2 migratory herds suggesting that body size monitoring might provide valuable information on the relationship between caribou abundance and their environment. We propose that monitoring a set of body condition indicators in relation to periodic population size surveys may offer an innovative approach to inform management decisions for migratory caribou and other ungulates.

## ACKNOWLEDGMENTS

Funding was provided by the Government of Newfoundland and Labrador, the Gouvernement du Québec, the Department of National Defense of Canada, Hydro-Québec, the Institute for Environmental Monitoring and Research, the Fonds pour les espèces nordiques – Fondation de la faune du Québec, Caribou Québec, Makivik, the Natural Sciences and Engineering Research Council of Canada, and Université Laval. We thank all those who helped with field and lab work, particularly D. Fiset, J.-Y. Lacasse, L. L'Italien, S. N. Luttich, F. Phillips, and J. A. Schaefer. Comments from 2 anonymous reviewers and C. Barrette, R. Hudson, J. Huot, S. Payette, and J. A. Schaefer greatly improved the manuscript.

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*Associate Editor: Hudson.*