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Dynamics of an Introduced Caribou Population

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ABSTRACT. Caribou (*Rangifer tarandus groenlandicus*) were hunted to extinction on Southampton Island (Northwest Territories, Canada) by 1953. In 1967, 48 caribou were captured on neighbouring Coats Island and released on Southampton Island. We documented the population dynamics, group size and composition, and distribution of caribou from introduction to 1991, based on aerial and ground survey data. The number of one-year-old and older caribou grew from 38 in 1967 to 13 700 (SE = 1600) in 1991. The corresponding annual growth rate was 27.6%, with no indication of any decline in the rate with increasing population density. Contrary to models describing the irruption of ungulates, the population dispersed rapidly after introduction to use all suitable habitats. Southampton caribou did not show high winter mortality in some years as did caribou on neighbouring Coats Island, where caribou density was higher, suggesting that the effect of adverse weather on the dynamics of northern insular caribou populations is dependent on animal density.

Key words: caribou, *Rangifer*, population dynamics, irruption, distribution, Northwest Territories

RÉSUMÉ. Dans l'île Southampton (Territoires du Nord-Ouest [Canada]) le caribou (*Rangifer tarandus groenlandicus*) a fait l'objet d'une chasse jusqu'en 1953, date de son extermination. En 1967, on a capturé 48 caribous dans l'île Coats avoisinante et on les a relâchés dans l'île Southampton. On documente la dynamique, la taille et la composition des groupes ainsi que la distribution du caribou depuis son introduction jusqu'en 1991, en s'appuyant sur des données obtenues à l'aide de relevés aériens et terrestres. Le nombre des caribous âgés d'un an et plus est passé de 38 en 1967 à 13 700 (erreur-type = 1600) en 1991. Le taux de croissance annuel correspondant était de 27,6 p. cent et ne comportait aucune indication dénotant une baisse du taux accompagnant une augmentation de la densité de population. Contrairement à des modèles décrivant l'explosion du nombre d'ongulés, la population de caribous s'est dispersée rapidement après l'introduction de cet animal, pour occuper tous les habitats disponibles. On n'a pas enregistré certaines années chez le caribou de Southampton une forte mortalité comme cela a été le cas pour le caribou de l'île Coats avoisinante, où la densité des animaux était plus élevée, ce qui donne à penser que les répercussions de conditions climatiques défavorables sur la dynamique du caribou insulaire du Nord dépendent de la densité de la population.

Mots clés: caribou, *Rangifer*, dynamique des populations, explosion démographique, distribution, Territoires du Nord-Ouest

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INTRODUCTION

Caribou (*Rangifer tarandus groenlandicus*) and wolves (*Canis lupus*) were common on Southampton Island until the early 1900s, but caribou were rare by 1935, wolves were extinct by 1937, and the last caribou died in 1953 (Parker, 1975; Mikitok Bruce, pers. comm. 1989). In 1967, 48 caribou (19 cows, 7 yearling females, 2 female calves, 6 bulls, 6 yearling males, and 8 male calves) were captured from neighbouring Coats Island and released on Bell Peninsula, Southampton Island (Fig. 1) (Manning, unpubl.). The typical response by a population after such introductions is an irruption, which follows a well-defined sequence of four stages (Riney, 1964; Caughley, 1970). However, the outcome has differed among introduced *Rangifer* populations. Leader-Williams (1988) summarized results of introductions of caribou and reindeer to islands, or isolated portions of islands, throughout the world. Out of 31 introductions, 5 failed initially, whereas the remainder entered irruptive oscillations. Of these 26, 11 have been considered successful, seven unsuccessful, 5 too recent to categorize, 1 uncertain, and 2 probably successful, including the Southampton Island population. None of these populations experienced heavy hunting pressure. Island size, latitude, and previous caribou habitation did not seem to influence success. Successful introductions occurred only when vascular species rather than lichens were the dominant winter forage (Leader-Williams, 1988).

In the Arctic, little is known about the ecology of introduced herds (Leader-Williams, 1988), but because caribou on Southampton Island rely heavily on lichens in winter (see Ouellet, 1992), a substantial depletion of winter food resources, followed by a dramatic population crash, must be considered the most likely outcome unless management

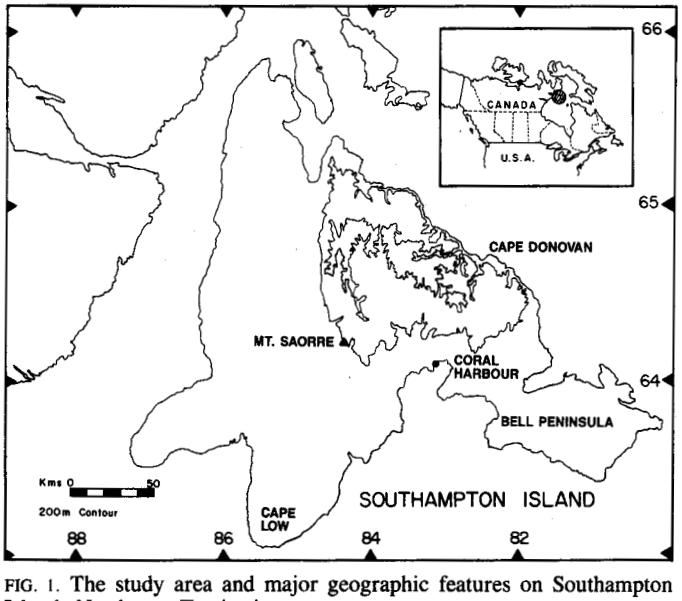

FIG. 1. The study area and major geographic features on Southampton Island, Northwest Territories.

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action is taken to prevent it. In this paper we document the population dynamics, distribution, and social organization of a caribou population from introduction in 1967 to 1991 and recommend ways to reduce the probability of a population crash.

STUDY AREA

Southampton is a 43 000 km² island lying at the north end of Hudson Bay (Fig. 1). It is almost always surrounded by open water, even in winter. The west half and most of the southeast (Bell Peninsula) of the island consist of low, flat limestone plains dominated by *Dryas* barrens and sedge meadows (Parker, 1975). The remainder of the island is steep to rolling Precambrian shield dominated by *Alectoria* and *Cetraria* lichens and heaths. An abrupt escarpment north of Mount Soarre divides these two geological formations. The cold waters of Hudson Bay contribute to a cold, windy climate similar to that found on arctic islands of higher latitude. The average wind speed is 20 km/h. Mean annual temperature is −11°C, with mean daily temperatures above freezing only in July and August. Snow cover persists from mid-September until mid-June. Precipitation averages 13 cm of rain and 133 cm of snow per year, twice that at Baker Lake, which is located on the mainland at the same latitude (Parker, 1975).

METHODS

In November 1978, a stratified systematic aerial strip transect survey was performed to estimate caribou numbers. The survey was flown in a DeHavilland Beaver, 120 m above ground level, with an observer on each side counting caribou of all ages within a 400 m wide strip. Between 25 June and 12 July 1983 flights in a Cessna 337 fixed-wing aircraft and a Bell 206 helicopter covered all parts of the island, providing data on both distribution and composition.

Between April 1980 and April 1984, eight trips were made by snowmobile to determine caribou group composition. Observers drove through the areas of known caribou distribution and recorded the age and sex of all animals seen.

In late June 1987, caribou numbers were estimated using a stratified random block design. A Bell 206B helicopter was flown at various speeds and altitudes, depending on viewing conditions. Observers in the rear seat reported all caribou they saw to a navigator. Each animal seen, including those detected by the navigator and the pilot, was approached more closely so that its age and sex could be determined. The census zone was divided into five strata, each receiving differential coverage, based on local knowledge, habitat characteristics, population density information obtained from a reconnaissance flight, and previous census data.

In March 1990, a systematic aerial strip transect survey was performed to estimate caribou numbers and distribution. The survey was flown in a Cessna 337 fixed-wing aircraft at 120 m above ground level with an observer on each side counting caribou of all ages within a 400 m wide strip. A late June census in 1991 followed the same methodology as in 1987. However, to allocate the effort more efficiently and to cover the entire island, the two strata defined as low density (strata 4 and 5) were surveyed using an aerial strip transect design and flown with a Cessna 337 fixed-wing aircraft.

Caribou counted in June and July 1983, June 1991 (strata 4 and 5), and during snowmobile trips in April 1980 and 1981 were classified as either calves (<1 year old) or older animals. No composition data were recorded in November 1978 or March 1990. During snowmobile trips in November 1981, May 1982, December 1982, April 1983, November 1983, and during the April 1984 census conducted by helicopter, older animals (>1 year old) were also classified as males or females.

In June 1987 and 1991 (strata 1 to 3), caribou were classified as either calves (<1 month old), yearlings (1 year old), cows (≥2 years old), bulls (≥2 years), or unknowns. Calves were distinguished by their small size and reddish colour. Yearlings had short faces and small bodies. Many bulls could be recognized by their large antlers, but sex determination of small-antlered animals was based on external genitalia. One-year-old or older caribou that could not be classified to age or sex were allocated proportionally among classified bulls, cows, and yearlings. In 1987 only 45 of 1237 caribou could not be classified and in 1991 only 21 of 2360.

The Jackknife technique (Cochran, 1977) was used to determine the mean and variance of the age and sex ratios. Calculation of population estimates and their standard errors followed Jolly (1969; see also Caughley, 1977). Aggregation size was defined using Jarman's measure of typical group size, i.e., the group size experienced by the average individual (Jarman, 1974).

RESULTS

Population Estimates

The 1978 census provided an estimate of 1200 ± 340 (S.E.) caribou (including calves) for the island (Table 1). In 1987, there were 5400 ± 1130 caribou including calves, and 4000 ± 660 of these animals were 1 year old or older. The number of caribou increased to 9000 ± 3200 (including calves) by March 1990 and to 13 700 ± 1600 caribou ≥1 year old by June 1991.

The number of caribou ≥1 year old on Southampton Island grew from 38 to 13 700 in 24 years (Fig. 2a). The population growth rate averaged 27.6%/yr (r^2 = 0.986), based on regression analysis where the curve was constrained to pass through the known number of 1-year-old and older caribou introduced in 1967 (Fig. 2b). When a correction factor was used to account for the skewed sex ratio of the introduced population (Heard, 1990), the intrinsic growth rate was found to be 26.2%/yr (r^2 = 0.998).

Caribou density increased almost 5 times within the core distribution area (the shaded areas in Fig. 3: 1983, 1990, and 1991) from 0.25/km² in 1987 to 1.22/km² in 1991 (strata 1, 2, and 3; Table 1), but there was no indication of any decline in the rate of growth with increasing population density (Fig. 2a,b). Parker (1975) predicted that the island's carrying capacity is 40 000. If the herd was increasing logistically, where each individual added to the population reduces the rate of increase by an equal amount (Krebs, 1978:186),

TABLE 1. Estimated number of caribou on Southampton Island, Northwest Territories, between 1978 and 1991

Survey date	Stratum number	Stratum area (km²)	Number of sample units	Sampling intensity (%)[1]	Number of calves (SE)	Number of caribou ≥4 mo old (SE)[2]
Nov 78	1	2471	8	13		231 (163)
	2	1594	7	13		564 (219)
	3	2908	9	13		387 (210)
	Total	6973	24			1181 (344)
Jun 87	1	1150	7	51	39 (23)	313 (65)
	2	1933	10	50	326 (6)	1244 (103)
	3	4425	10	25	330 (165)	1304 (194)
	4	6389	6	12	662 (512)	1162 (618)
	5	2144	2	11	9 (8)	9 (8)
	Total	16041	35		1366 (544)	4033 (659)
Mar 90	1	28462	18	4		9319 (3235)
Jun 91	1	1536	8	32		3242 (699)
	2	3802	10	17		3854 (951)
	3	3808	10	17		4048 (909)
	4	11187	13	4		1230 (300)
	5	22799	7	2		1304 (448)
	Total	43132	48			13676 (1584)

[1]Total area of sample units flown within the stratum divided by the stratum area.
[2]SE of the total population estimate equals the square root of the sum of the squares of the SEs (i.e., the variances) for each stratum (Jolly, 1969; Caughley, 1977).

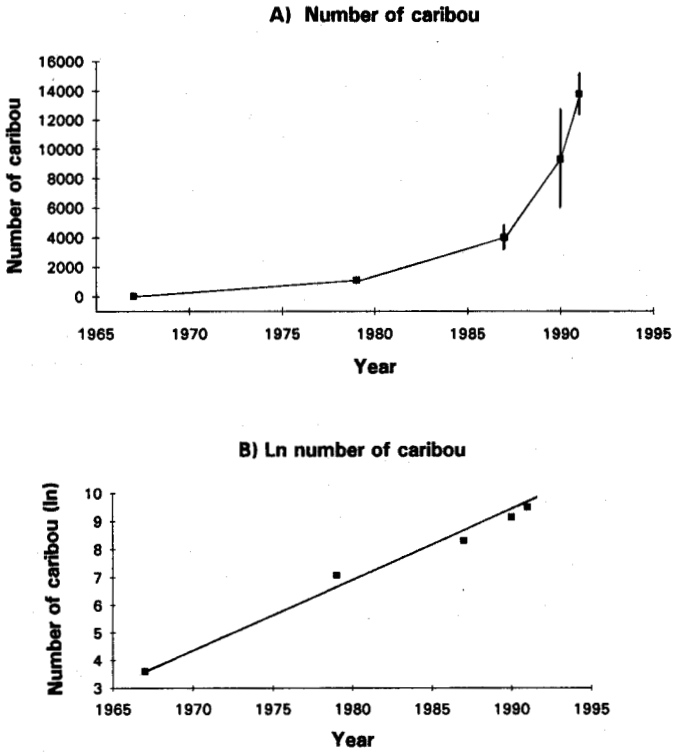

FIG. 2. The increase in the number of 1-year-old and older caribou since the introduction of 38 in 1967 to Southampton Island, Northwest Territories. (A) The estimated number of caribou with vertical bars representing one standard error on either side of the estimate. (B) The natural logarithm of the estimated number of caribou (y) regressed against the number of years since introduction (x) and the curve constrained through the known number introduced in 1967 ($y = 3.638 + 0.244\,x$; $r^2 = 0.986$, $P < 0.001$).

then the 1991 population size would have been 10 000, which is less than the minimum of the 95% confidence interval (10 600 – 16 800) around our 1991 estimate.

Distribution

The November 1978 and June 1987 surveys covered only those areas where Inuit hunters had reported seeing caribou, but the June-July 1983, the March 1990, and the June 1991 surveys were designed to document the distribution of caribou over the entire island (Fig. 3). Caribou expanded their distribution between 1978 and 1983, but distribution did not continue to increase thereafter. During all three island-wide surveys, caribou were seen along the ridge north of Mount Soarre, on the coast of Bell Peninsula and Cape Low, and in the upland areas north of Coral Harbour. Caribou were rarely seen far from the coast of Bell Peninsula and Cape Low, west of the ridge north of Mount Soarre, or in the high country along the northeast coast. Therefore, there did not appear to be any density-dependent changes in caribou distribution between 1983 and 1991. There did not seem to be a difference between winter and summer distribution, but deep snow (see Ouellet, 1992) may have forced the animals to avoid the northeast coast in winter. We found no indication from our many conversations with Inuit hunters or from caribou observations incidental to other research to question these conclusions about range expansion and seasonal distribution.

Most bulls were found around Cape Low and Coral Harbour, but both bulls and cows were seen on Bell Peninsula and on the east coast south of Cape Donovan. Based on the two late June distribution surveys, cows did not appear to concentrate on a particular calving ground. Yearlings were found in all areas used by adults of both sexes.

Group Size and Composition

In all samples, typical group size (≥ 1-year-old caribou) of aggregations with calves was larger than groups that did not contain calves (Table 2). The only seasonal pattern to

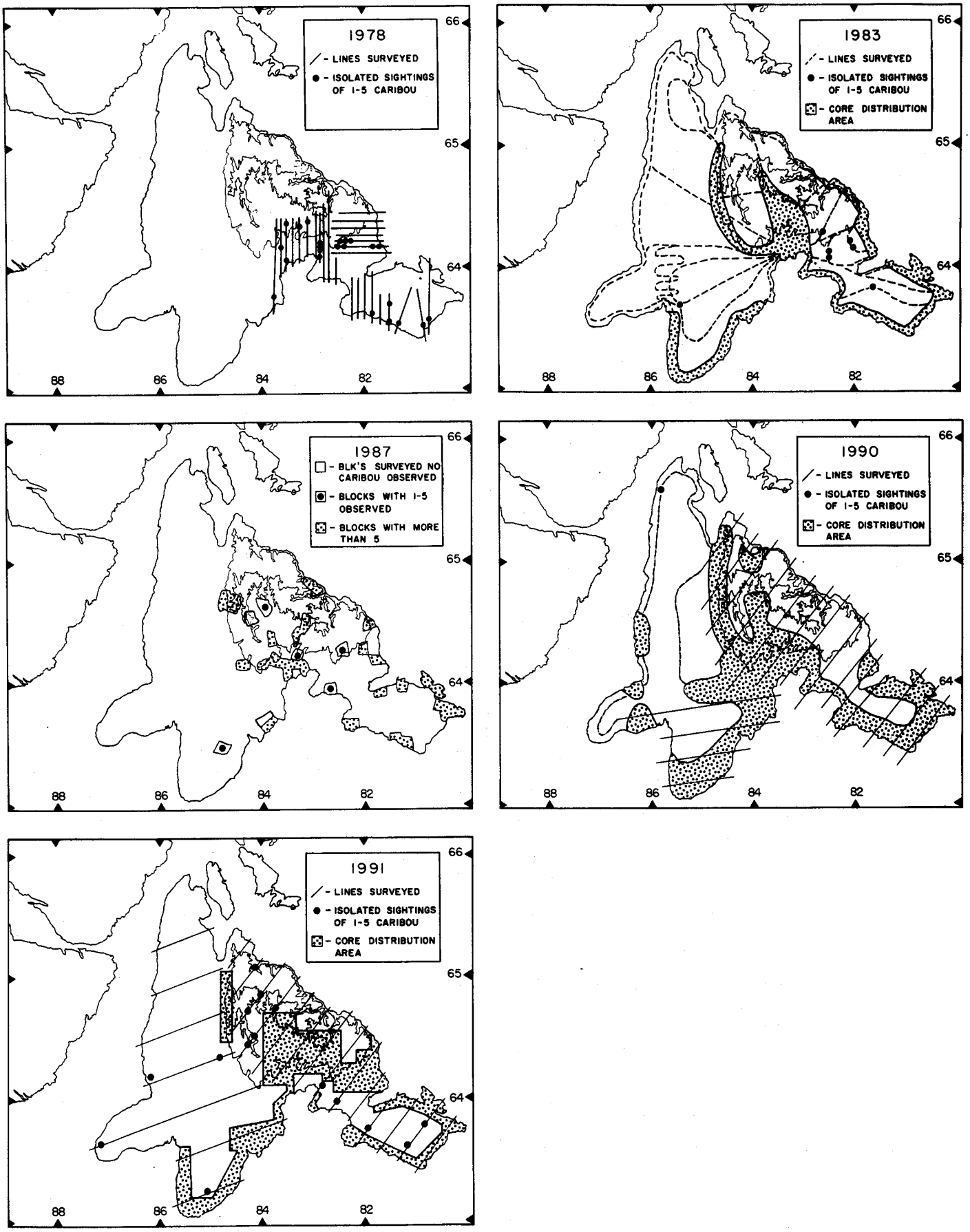

FIG. 3. Distribution of caribou observed on Southampton Island, Northwest Territories, in 1978, 1983, 1987, 1990, and 1991.

TABLE 2. Typical group size of caribou ≥ 1 year old recorded on Southampton Island, Northwest Territories, between 1981 and 1991

Date	Number of groups	Number of caribou ≥ 1 year old	Size of largest group	Typical[1] size of groups[2]			SE
				With calves	Without calves	All	
Nov 81	25	353	58	30.5			1.02
	4	7	4		2.7		0.61
	29	360	58			30.0	1.02
May 82	24	134	18	9.1			0.46
	43	132	10		4.3		0.21
	67	266	18			6.7	0.29
Dec 82	28	141	11	6.8			0.25
	10	37	6		4.0		0.19
	38	178	11			6.2	0.22
Apr 83	21	109	18	8.6			0.54
	24	98	12		6.1		0.31
	45	207	18			7.4	0.33
Jun-Jul 83	227	227	22	8.2			0.38
	305	305	17		5.0		0.26
	532	532	22			6.4	0.23
Nov 83	35	274	38	14.5			0.67
	10	40	8		5.3		0.39
	45	314	38			13.3	0.61
Apr 84	38	218	29	13.0			0.69
	42	106	6		3.4		0.16
	80	324	29			9.9	0.53
Jun 87	92	450	28	9.9			0.36
	261	787	14		5.3		0.13
	353	1237	28			7.0	0.17
Mar 90	280	1215	50			12.0	0.39
Jun 91	246	1509	60	15.8			0.39
	320	851	13		4.3		0.10
	566	2360	60			11.6	0.28

[1]*Sensu* Jarman, 1974.
[2]In all instances, the number of caribou ≥ 1 year old in groups that also contained calves was larger than those groups without calves (Mann-Whitney *U*-test, $P < 0.001$) using a two-tailed test.

group size variation was that groups with calves were largest in November, which is just after the rut. Excluding November groups, there was a positive linear relationship between typical group size of "all" groups and population size, where population size was interpolated from the census results (Fig. 2) for the years when there was no census ($r^2 = 0.713$, $n = 8$, $P = 0.008$).

Mixed groups of cows and bulls were most common in November, closest to the rutting period, and least numerous in June, after calving (Table 3). Calves appeared to begin leaving cow groups when they were 10 months old. All calves were in cow or mixed sex groups in November and December and in the spring of May 1982 and April 1983. In April 1984, however, we found greater sexual segregation among adults (Table 3), and 28% of the calves were in bull groups. By June, when there was even greater sexual segregation among adults, more calves (now yearlings) had segregated from their mothers. By late June 1987, 78% of the yearlings were in all-yearling or bull groups, and by late June 1991 the corresponding value was 49% (see Table 2 for sample sizes).

Population Composition

The large variation among surveys in the estimated sex ratio (Table 4; Fig. 4) was biologically impossible and undoubtedly arose because the sexes were segregated and sampling was not always representative. The calf:female ratio depended in part on the sex ratio of the sample, because calves associated with males after April (see above). Therefore, calf production and survival (i.e., recruitment) estimates were unbiased only when we obtained an accurate estimate of the sex ratio.

The 1987 survey was the best estimate of population composition because it was done from a helicopter and

TABLE 3. Percentage of caribou groups in different seasons that were made up of cows only, bulls only, or both cows and bulls on Southampton Island, Northwest Territories, between 1981 and 1991

Date	Group composition (%)[1]		
	Cows	Bulls	Mixed (cows and bulls)
Nov 81	7	7	86
May 82	43	15	42
Dec 82	42	24	34
Apr 83	49	13	38
Nov 83	27	11	62
Apr 84	37	41	21
Jun 87	33	54	2
Jun 91	49	45	6

[1]Group composition was based on the sample sizes reported in Table 2.

TABLE 4. Age and sex composition of caribou recorded on Southampton Island, Northwest Territories, between 1981 and 1991

Date	Calves:100 females[1] (SE)	Males:100 females (SE)
Nov 81	85 (1.1)	59 (2.6)
May 82	23 (0.6)	49 (1.4)
Dec 82	48 (1.1)	86 (3.4)
Apr 83	24 (0.7)	59 (2.5)
Nov 83	61 (0.8)	89 (1.1)
Apr 84	77 (2.0)	186 (5.4)
Jun 87[2]	69 (3.9)	104 (19.3)
Jun 91[2]	22 (4.3)	43 (19.3)

[1]Composition was based on the sample sizes reported in Table 2.
[2]"Calves" were 12 months old (i.e., yearlings).

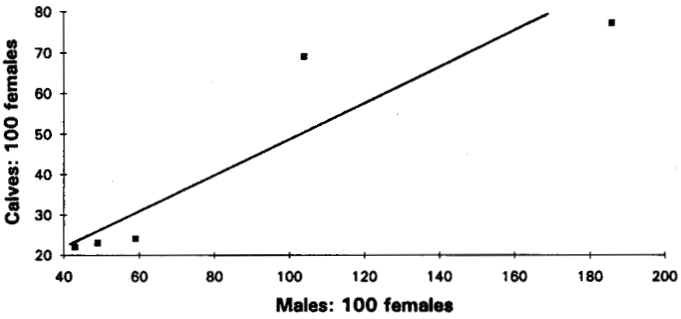

FIG. 4. The relationship between estimates of the ratio of 10- to 12-month-old calves:100 females and the sex ratio (males:100 females) in samples of caribou classified on Southampton Island, Northwest Territories ($y = 5.71 + 0.423\ x$; $r^2 = 0.84$, $P < 0.05$).

resulted in broader coverage than earlier ground surveys. The 1991 survey was also done from a helicopter but groups were larger than in 1987 and newborn calves could not be counted without causing excessive disturbance. The low sex ratio found during the 1991 survey may have been due to the relatively small fraction of the population that was sampled (i.e., blocks containing predominantly bulls did not happen to be selected), and the low yearling:cow ratio is consistent with that interpretation. In 1987, the calf:cow ratio for the entire island was estimated at 93 ± 1.3:100. The bull:cow ratio was estimated at 107 ± 27.5:100. Assuming an equal sex ratio among yearlings, the sex ratio among one-year-old and older caribou was 104 ± 19.3 males: 100 females.

Mortality

Natural mortality appeared to be low. One female tagged as a yearling when she was introduced to the island was shot when she was 3 months from being 19 years old. The maximum age previously reported for caribou was 17 years (Parker, 1981). Two other tagged caribou were almost 17 years old when they were shot.

Natural mortality of males was greater than that of females. Of the 17 deaths investigated between 1973 and 1991, 14 were males, 2 were females, and 1 was of unknown sex. The cause of death could be determined in 6 cases: a 2-year-old bull fell off a cliff, a 10-month-old male died from a sparring injury to the head, a middle-aged bull died from cancer (Gary Wobeser, pers. comm. 1987), 1 mature bull appear to have starved to death in late winter 1991, and 2 bulls died after locking antlers during the rut.

Since 1977, about 400 females and 1700 males have been killed by hunters. Hunting quotas were increased from 25 males per year beginning in 1977-78 to 300 males and 100 females in 1990-91. In addition, 198 caribou (51 males and 147 females) were collected between 1988 and 1991 for research purposes (Ouellet, 1992).

The population dynamics of the Southampton Island caribou herd was simulated with a population balance model (*sensu* Walters, 1986) to estimate the minimum survival rates needed to achieve the observed rate of population growth. The model used the estimated number of individuals of both sexes (calves, yearlings, and older caribou), fertility rate (based on Ouellet, 1992), and hunting losses. Mortality rates for the three categories of individuals (calves, 1-year-old and older males and females) were constant over time. There were no built-in density-dependent effects. Assuming 100% survival of individuals older than calves, the survival rate of calves must have been at least 72% to achieve the observed rate of growth. This survival rate must have been greater than that because natural mortalities of individuals other than calves were reported. Conversely, if calf survival was 100%, then adult survival must have been at least 92%.

DISCUSSION

Distribution and Social Organization

Herd size increased almost 100 times between 1967 and 1983, but because caribou expanded their range over the island, densities within the areas used remained relatively low. Because caribou distribution did not expand after 1983 even though herd size continued to grow, effective population density increased after 1983. These observations are contrary to the model proposed by Riney (1964) and Caughley (1970), which describes the behaviour of an introduced ungulate population. That model specifies that a zone of high density (i.e., at or near carrying capacity) will spread radially from the point of liberation. Because caribou did not continue to expand their range after 1983, it is likely that the remaining area is marginal or unsuitable for caribou, as suggested by Parker (1975). Parker (1975) predicted that caribou should use the mountainous areas north of Coral Harbour (lichen-heath felsenmeer range type) in winter and move to other range types in summer. However, there has been no seasonal change in distribution. Therefore, Parker's estimation of carrying capacity (40 000) may not be accurate.

Main and Coblentz (1990) argued that sexual segregation among ungulates is a consequence of sexual differences in reproductive strategies, primarily differences between how the sexes balance the trade-offs between foraging benefits and predation risks. Males attempt to maximize their body condition and therefore mating success, while females attempt to maximize the survival of their offspring. Because there are no predators on Southampton Island (nor were there any on Coats Island, where the Southampton stock originated), we first considered the possibility that sexual segregation was the result of differences in nutritional needs (e.g., males and females may have different needs for digestible energy and protein) or food availability (e.g., females may be able to

feed more selectively because of their smaller size). We doubt that either of those explanations applies to caribou on Southampton Island, because the sexes were not simply segregated to different parts of the island but also into same sex groups within an area. We suggest that sexual segregation in caribou on Southampton Island is a behavioural trait from earlier evolutionary times when caribou experienced predation.

Group associations observed in late June on Southampton Island were similar to large migratory caribou herds, with most yearlings associated with bulls or other yearlings (Kelsall, 1968). However, among the non-migratory caribou in the northeastern mainland of the Northwest Territories, most yearlings (81%) were associated with cows (Calef and Heard, 1980; Donaldson, 1981). Calef and Heard (1980) and Donaldson (1981) thought that persistent yearling-cow associations might be related to a non-migratory life history strategy, because the bond between cows and 10- to 12-month-old calves is usually broken during spring migration. Data for caribou on Southampton Island are inconsistent with that suggestion.

There was no evidence that seasonal differences in snow cover (i.e., winter vs. summer) affected group size on Southampton Island. The tendency for groups to be largest in November was also observed on Coats Island (Gates *et al.*, 1986), possibly because this period corresponds with the rutting season. Snow can reduce food availability and increase patchiness, and many foraging hypotheses suggest that group size should change in response to food availability and distribution (Clark and Mangel, 1984). On Coats Island (Gates *et al.*, 1986; D.C. Heard, unpubl. data) and on the western Queen Elizabeth Islands (Miller *et al.*, 1977), groups of caribou were smaller in winter than in summer and the availability of winter food is low. Because snow conditions were probably similar on both Coats and Southampton islands, we suggest that snow did not appear to influence group size on Southampton because food was more abundant (Ouellet, 1992).

Population Dynamics

From the time of introduction (1967) to 1991, the Southampton Island caribou herd was in the initial phase of irruption (*sensu* Caughley, 1970). Because there was no indication of decline in the rate of population growth with increasing density, the observed rate of growth is a good estimate of the intrinsic rate of growth (Caughley, 1977). The estimated intrinsic rate of increase (r_m) was 0.233 (lambda = 1.262). The intrinsic rate of population increase is specific to the environment in which it is measured (Caughley, 1977). This is the first intrinsic rate of increase estimate for a caribou population in an arctic environment. The intrinsic rate of increase exhibited by caribou on Southampton Island is similar to previous estimates of maximum growth rates (mean r_m = 0.26) for reindeer and caribou populations introduced to islands in cool oceanic climates (Heard, 1990).

High winter mortality was recorded on neighbouring Coats Island in the winters of 1974-75 and 1979-80, which Gates *et al.* (1986) attributed to severe snow conditions. The high rate of increase, the corresponding population model, and the absence of any reports by local people suggest that such losses were unlikely on Southampton Island. Thus, the simple relationship between snow condition and over-winter mortality rate is not supported here because these two populations probably experience comparable climate due to their close proximity. This finding, along with differences in winter food availability and body condition between these two populations (see Ouellet, 1992), suggests that the effect of adverse climatic conditions on population dynamics increases under resource limitation as proposed for reindeer by Skogland (1985, 1990). In other words, the effect of weather is not independent of animal density.

Management Implications

At the present rate of increase, the number of caribou on Southampton Island is doubling every three years. If the herd continues to increase geometrically, it will reach the island's predicted carrying capacity (Parker, 1975) of 40 000 within 5 years.

Some introduced *Rangifer* populations increased geometrically before crashing and remaining at very low levels because grazing reduced available food (Leader-Williams, 1988). Range damage is least likely to occur where graminoids are the staple food and most likely where the major food is lichens, as on Southampton Island. Associated with the increase in caribou density, there has been a decrease in lichen standing crop, and the impact of grazing on lichens is obvious in certain areas of the island (Ouellet, 1992). As lichens are not resilient to grazing (Ouellet, 1992; Ouellet *et al.*, 1993), we suggest that without intervention by people, growth of the Southampton Island caribou herd will probably end with a dramatic crash similar to those observed for other insular populations (Klein, 1968). The potential for a severe crash is accentuated because the herd is growing so quickly. A simulation model suggests that the amplitude of population fluctuations is related to population growth rate (Messier *et al.*, 1988).

The potential for overgrazing and its consequences to the caribou population can be reduced by changing hunting quotas. Hunting quotas were increased to 300 males and 100 females in 1989, but even if errors in sex identification by hunters were common, those kills would only slightly reduce herd growth rate. Hunting quotas were eliminated in 1992, and we recommended an annual kill of 1500 animals of each sex. A kill of 3000 animals may exceed the needs of the 475 Southampton Island residents. If so, hunters should select females, so that a smaller kill will have a greater reduction on the herd's growth rate.

Another way to stabilize caribou population size over the long term would be to promote the colonization of wolves on Southampton Island. Wolves were once part of the Southampton ecosystem but disappeared before the caribou were exterminated in the 1950s. Southampton Island is the only area in the Northwest Territories where wolves do not occupy their natural range (Heard, 1983). In December 1979, a wolf was shot on Southampton Island, but none has been reported since. If and when other wolves reach the island, wolves could be protected from hunting until they become

established. The presence of wolves may increase stability of caribou population size by preventing future irruptions, provide wolf hunting opportunities, and provide income for the residents of Coral Harbour through the sale of wolf hides. Predation would reduce the long-term sustained yield of caribou but not likely below the community's needs. Unless attitudes change, this may be irrelevant speculation, because our discussions with Coral Harbour residents indicate that few people would like to see wolves return to Southampton. Reestablishment of a wolf population on Southampton is not an option for stopping the present irruption, because the caribou herd is growing too quickly.

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REFERENCES

CALEF, G.W., and HEARD, D.C. 1980. The status of three tundra wintering caribou herds in northeastern mainland Northwest Territories. In: Reimers, E., Gaare, E., and Skjenneberg, S., eds. Proceedings of the Second International Reindeer/Caribou Symposium. Trondheim: Direcktoratet for vilt og ferskvannsfisk. 582-594.

CAUGHLEY, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51:53-72.

_____ . 1977. Analysis of vertebrate populations. New York: John Wiley & Sons.

CLARK, C.W., and MANGEL, M. 1984. Foraging and flocking strategies: Information in a uncertain environment. American Naturalist 123:626-641.

COCHRAN, W.G. 1977. Sampling techniques. 3rd ed. New York: John Wiley & Sons.

DONALDSON, J.L. 1981. Population and recruitment estimates for the Lorrillard and Wager caribou herds in 1977. Ottawa: Indian and Northern Affairs. Publication No. QS-8160-043-EE-AI, ESCOM Rep. No. A1-43.

GATES, C.C., ADAMCZEWSKI, J., and MULDERS, R. 1986. Population dynamics, winter ecology, and social organization of Coats Island caribou. Arctic 39:216-222.

HEARD, D.C. 1983. Historical and present status of wolves in the Northwest Territories. In: Carbyn, L.N., ed. Wolves in Canada and Alaska. Canadian Wildlife Service Report Series No. 45. 44-47.

_____ . 1990. The intrinsic rate of increase of reindeer and caribou in arctic environments. Rangifer, Special Issue No. 3:169-173.

JARMAN, P.J. 1974. Social organization of antelope in relation to their ecology. Behaviour 48:215-267.

JOLLY, G.M. 1969. Sampling methods of aerial census of wildlife populations. East African Agricultural and Forestry Journal 34:46-49.

KELSALL, J.P. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service. Monograph No. 3. Ottawa: Queen's Printer.

KLEIN, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management 32:350-367.

KREBS, C.J. 1978. Ecology: The experimental analysis of distribution and abundance. 2nd ed. New York: Harper and Row.

LEADER-WILLIAMS, N. 1988. Reindeer on South Georgia. Cambridge: Cambridge University Press.

MAIN, M.B., and COBLENTZ, B.E. 1990. Sexual segregation among ungulates: A critique. Wildlife Society Bulletin 18:204-210.

MESSIER, F., HUOT, J., LE HENAFF, D., and LUTTICH, S. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. Arctic 41:279-287.

MILLER, F., RUSSELL, R.H., and GUNN, A. 1977. Peary caribou and muskoxen on western Queen Elizabeth Islands, N.W.T., 1972-74. Canadian Wildlife Service Report Series No. 40.

OUELLET, J.P. 1992. Ecology of an introduced caribou population on Southampton Island, N.W.T., Canada. Ph.D. thesis, University of Alberta, Edmonton, Canada.

OUELLET, J.P., BOUTIN, S., and HEARD, D.C. 1993. Range impacts following the introduction of caribou on Southampton Island, Northwest Territories, Canada. Arctic and Alpine Research 25:136-141.

PARKER, G.R. 1975. An investigation of caribou range on Southampton Island, Northwest Territories. Canadian Wildlife Service Report Series No. 33.

_____ . 1981. Physical and reproductive characteristics of an expanding woodland caribou population (*Rangifer tarandus caribou*) in northern Labrador. Canadian Journal of Zoology 59:1929-1940.

RINEY, T. 1964. The impact of introductions of large herbivores on the tropical environment. International Union of Conservation of Nature Publication, New Series, 4:261-273.

SKOGLAND, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology 54:359-374.

_____ . 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. Oecologia 84:442-450.

WALTERS, C. 1986. Adaptive management of renewable resources. London: Macmillan.