

The intrinsic rate of increase of reindeer and caribou populations in arctic environments

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Abstract: The intrinsic rate of increase of an animal population, r_m , is specific to the environment in which it is measured. Previous estimates of maximum growth rates for reindeer and caribou *Rangifer tarandus* populations were based on introductions to islands with cool oceanic climates. The mean intrinsic rate of increase of 6 populations was 0.26 ranging from 0.21 on St Paul Island in the Bering Sea to 0.29 in the Barff herd on South Georgia. I calculated r_m for two *Rangifer* populations introduced to arctic environments to determine the effect of environmental severity on the intrinsic rate of increase. Reindeer on the Belcher islands increased at $r_m = 0.28$ and caribou on Southampton Island increased at $r_m = 0.23$ (mean = 0.26). The lower primary productivity and longer duration of snow cover in arctic environments did not affect the intrinsic rate of increase.

Key words: increase of populations

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Introduction

The intrinsic rate of increase of an animal population, r_m , is worth knowing for a variety of practical and fundamental purposes e.g., to compare the favourability of different environments (Begon et al. 1986), to estimate sustained yield hunting limits (Caughley and Birch 1971), and to indicate potential population regulation mechanisms (Bergerud 1980, 1983, Caughley and Krebs 1983, Tanner 1975). r_m is best estimated by measuring the growth of a newly established population increasing from minimal density with unlimited resources (Caughley and Birch 1971).

Because birth rates and survival rates are unlikely to be the same everywhere an organism

lives, r_m relates only to the environment within which it was measured (Birch 1948). Published estimates of maximum population growth rates in *Rangifer* have all been from island environments with cool oceanic climates (ie., 4-5 months with snow cover). In this paper I present data on the growth rates of two *Rangifer* populations introduced to islands with arctic climates (ie., 8-9 months with snow cover) and compare the intrinsic rates of increase in the two environments.

Study areas

Southampton Island covers 43 000 km² and lies at the north end of Hudson Bay, Northwest Territories, Canada. The vegetation consists of

Dryas barrens, sedge meadows and lichen heaths (Parker 1975). The 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. The Belcher island archipelago, 900 km to the southeast, covers 2800 km². Mosses, dwarf shrubs, lichens and sedges predominate (J. Edmonds unpublished). Snow cover persists for about 8 months of the year. Both Southampton and the Belcher islands are usually surrounded by open water even in winter.

Caribou (*Rangifer tarandus groenlandicus*) and wolves (*Canis lupus*) coexisted on Southampton Island until the early 1900's (Parker 1975). After the establishment of a Hudson's Bay Company trading post in 1924 and the unlimited availability of ammunition, caribou numbers quickly declined from overhunting. Caribou were rare by 1935 and extirpated between 1950 and 1955. Wolves also declined to extinction, presumably from lack of prey. No natural recolonization of caribou occurred. In 1967, 48 caribou (*R. t. groenlandicus*, 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 Southampton (Manning unpublished). One wolf was shot on Southampton in 1979 but no other sightings have been reported. Hunting was prohibited until 1978 when a quota of 25 males/yr was permitted. The quota was increased to 50 males/yr in 1980 and to 50 males plus 20 females/yr in 1984.

Native caribou disappeared from the Belcher islands in the late 1800's (Ferguson 1985). Again, no recolonization of caribou occurred and in March 1978, 60 semi-domestic reindeer (*R. t. tarandus*, 50 adult cows and 10 adult bulls) were taken from Tuktoyaktuk, NWT and released on Flaherty I, the largest island in the archipelago. Those animals were allowed to range freely. There are no wolves on the Belcher island and no animals were shot.

Methods

The intrinsic rate of increase can be calculated only when a population has a stable age and sex distribution (Caughley and Birch 1971). However, the age and sex composition of a cohort of ungulates introduced to unoccupied areas in the hope of establishing a new population is usually biased toward adult females. In those situations the actual rate of increase (r) of an introduced population is always greater than the intrinsic rate calculated from those data.

I took distorted age and sex ratios into account by simulating the population dynamics of each herd with a simple bookkeeping model. Initial conditions were determined by the number of the animals introduced by age and sex. Calf survival (from birth to age one) was varied as required, to achieve the final population size. The model was based on the following assumptions; 1) there was an equal sex ratio at birth, 2) calf survival was equal in both sexes, 3) adult survival was 100% in both sexes, 4) all adult (yearling and older) females produced one calf each year, and 5) all rates were constant through time. Data from Southampton Island were consistent with those assumptions. All 44 females (including 10 yearlings) in 1988 and 1989 collections were pregnant. Equal survival of the Sexes can be inferred from the even sex ratio found in 1987 (104 adult males: 100 adult females; Heard unpublished); Simulation was continued until the age distribution stabilized at which time λ , the finite rate of population change, was determined as N_t/N_{t-1} . The $\log_e \lambda$ for each population was considered an estimate of the intrinsic rate of increase for *Rangifer*.

When more than two population estimates were available, I calculated the final population size and the actual growth rate from a linear regression of \log_e population size on time where the line was constrained to pass through the known number introduced.

I considered the period of increase on St

Paul and St George islands from the time of introduction until hunting began.

Results

The number of caribou on Southampton Island was estimated at 1200 ± 340 , 11 years after they were introduced and at 5400 ± 1130 nine years later (Heard unpublished). The actual rate of growth (r) was 0.25 and the intrinsic rate of increase was 0.23.

In March 1982, four years after the introduction, the number of reindeer on the Belchers was estimated at 287 (Ferguson 1985), an observed growth rate of $r = 0.39$ and r_m was 0.28.

Discussion

The mean intrinsic rate of increase of the two *Rangifer* populations introduced into arctic environments was 0.26; the same as the mean intrinsic rate of increase of 6 populations introduced to islands with cool oceanic climates (Table 1). Therefore lower primary productivity and the longer duration of snow cover in the arctic environments did not affect the intrinsic rate of increase, suggesting that reindeer and caribou can do well as long as the energetic costs of obtaining food (e.g., cratering) are compensated for by the energy derived from their forage.

The theoretical maximum rate that caribou can increase is 0.31 given a litter size that is al-

Table 1. Maximum rates of increase for reindeer and caribou populations where r is the actual rate of increase and r_m is the intrinsic rate of increase; the rate at which the population would have increased if it had had a stable sex and age distribution.

Population	Years of increase	Number of counts	r	r_m	Climate	Source of data
Theoretical				.31		
Barff (R)	10	4	.34	.29	M	1
Brunette I (C)	5	6	.37	.27	M	2
Belcher I (R)	4	2	.39	.28	A	3
St George I (R)	6	7	.35	.26	M	4
Adak I (C)	8	2	.26	.25	M	5,6
St Mathew I (R)	13	2	.30	.25	M	7
Southampton I (C)	20	3	.25	.23	A	8
St Paul I (R)	7	8	.30	.21	M	4

R=reindeer, C=caribou

M=maritime/cool oceanic, A=arctic

1 Leader-Williams 1988

2 Bergerud 1971

3 Ferguson 1985

4 Scheffer 1951

5 Jones 1966

6 Hemming 1970

7 Klein 1968

8 Heard unpublished

ways one, a 1:1 sex ratio at birth, caribou never become pregnant as calves (4 month old animals), no mortality until 20 years old when they all die, and 100% pregnancy among yearling and older cows. The theoretical maximum for reindeer is somewhat higher because occasionally they give birth to twins (Godkin 1986) and calves can become pregnant (Reimers 1972). The theoretical maximum rate of increase of

reindeer and caribou could be higher than 0.31 if pre-natal sex ratios are biased toward females as Skogland (1986) found for favourable environments. Neither the pre-natal nor adult sex ratios were greatly distorted on Southampton Island where pre-natal sex ratios were 9 males: 12 females and 10 males: 12 females in 1988 and 1989 collections respectively (Heard unpublished). Intrinsic rates of increase for reindeer and caribou approach the theoretical maximum of 0.31 (Table 1).

The actual rate of increase of reindeer on St Mathew, St Paul and St George islands had often been incorrectly cited as r_m (eg., Caughley and Krebs 1983, Leader-Williams 1988). When introduced cohorts are biased toward adult females, r is always greater than r_m and the difference is usually substantial (Table 1). On St Mathew I for example, 24 yearling females and 5 yearling males were introduced in 1944. By 1957 they had increased to 1350 (Klein 1968), an actual rate of increase of 0.30. Correcting for the distorted sex ratio indicates that the herd grew from 24 females to 685 females, a rate of increase of 0.26, assuming an even sex ratio of recruits ($1350 - 29 = 1321$ recruits; $1321 \times 0.5 = 661$ female recruits; $661 + 24 = 685$ females). After correcting for the unstable age distribution using the simulation model, the estimate of r_m was further refined to 0.25 (Table 1).

Bergerud (1971) adjusted for the distorted sex ratio of caribou introduced to Brunette Island by assuming that population composition would approach the mean sex ratio for the species at equilibrium which is only 56 males: 100 females (Bergerud 1971). My model of the Brunette population indicated that mortality was only 5%/yr for all ages and both sexes combined, providing little room for substantial differential mortality between the sexes. Therefore I believe Bergerud should have assumed an even sex ratio.

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