# St. Matthew Island reindeer crash revisited: Their demise was not nigh—but then, why did they die?

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*Abstract*: Twenty-nine yearling reindeer (*Rangifer tarandus*) were released on St. Matthew Island in the Bering Sea Wildlife Refuge in 1944: 24 females and five males. They were reported to have increased to 1350 reindeer by summer 1957 and to 6000 by summer 1963. The 6000 reindeer on St. Matthew Island in summer 1963 were then reduced by 99% to 42 by summer 1966. The evidence suggests that after growing at a high average annual rate of $\lambda = 1.32$ for 19 years, the entire die-off occurred in winter 1963–64, making it the largest single-year crash ever recorded in any *R. tarandus* population. Although a supposedly meaningful decline in successful reproduction and early survival of calves was originally reported for the population between 1957 and 1963, our reevaluation indicates this is an error resulting from the wrong sample being used in the between-year comparison. The quantitative data indicate no meaningful change occurred, and the calf:cow ratio was about 60 calves:100 cows in both 1957 and 1963. Calf production and survival were high up to the crash, and in the die-off population the age distribution (72%, 1–3 years old) and the sex ratio (69 males:100 females) reflected a still fast-growing *R. tarandus* population. All of these parameters do not support the hypothesis that the limited abundance of the absolute food supply was at a lethal level between 1957 and 1963 or in winter 1963–64. We now know from other studies that a high density of *R. tarandus* is not a prerequisite for a major single-year winter die-off. Existing population dynamics data do not support lack of lichens as a major causative factor in this single-year crash. If a decline had been caused by the limitation of the absolute food supply, it would have followed a multi-year pattern—it would not have been a single-year event. There was no evidence of a sudden, massive, island-wide loss of the absolute food supply, or that its nutritional value was inadequate for sustaining the reindeer. Mean weights of reindeer by sex and age class declined between 1957 and 1963, but only to levels similar to those of mainland reindeer. The reindeer population on St. Matthew Island undoubtedly was or soon would have been seriously influenced by heavy use of the lichens and the future did not bode well for continued population growth. Although the food supply through interaction with climatic factors was proposed as the dominant population-regulating mechanism, a general acceptance that only density-dependent food-limitation was necessary to cause the crash remains strong in some quarters. We challenge this; we believe that the winter weather was the all-important factor that led to the premature, extreme, and exceptionally rapid, near total single-year loss of 99% of the reindeer on St. Matthew Island in winter 1963–64.

Key words: climate, forage, growth rates, introduced population, *Rangifer tarandus*, single-year die-off, weather.

## Introduction

Growth of populations of reindeer and caribou (*Rangifer tarandus*) and other large ungulates can be regulated by limitation of the absolute food supply, especially in the absence of exceptionally severe weather years and heavy predation or hunting pressure (e.g., Riney, 1964; Caughley, 1970; Leader-Williams, 1980; Skogland, 1986; Fowler, 1987).

Our intent here is not to challenge regulation of a population through density-dependent limitation of its absolute food supply per se, but to suggest that such regulation of *R. tarandus* populations is often overemphasized and accepted uncritically without adequate proof. In fact, both biotic and abiotic limiting factors, in the absence of density-dependent

limitation of the absolute food supply, can and do play a dominant sporadic or periodic functional role in population setbacks.

Twenty-nine yearling reindeer were released on St. Matthew Island in 1944. Klein (1959, 1968) estimated that they increased about 46-fold by 1957 and 207-fold by 1963. The reindeer population then crashed, leaving only 42 reindeer alive when he returned to St. Matthew Island in summer 1966 (Klein, 1968). He believed that the entire 99% die-off of 6000 reindeer occurred in winter 1963–64, making it the largest single-year crash known for any *R. tarandus* population. Klein (1968: 366) concluded that the "Food supply then, through interaction with climatic factors, was the dominant population-regulating mechanism for reindeer on St. Matthew Island." However, this statement does not unambiguously identify which factor specifically caused the crash of reindeer on St. Matthew Island. We believe the St. Matthew Island crash has been commonly referenced (e.g., Haber & Walters, 1980; Reimers, 1982; Gates *et al.*, 1986; Adamczewski *et al.*, 1988; Leader-Williams, 1988; Ouellet *et al.*, 1996) and widely used in discussion as an example of density-dependent population regulation that can often be expected to occur in *R. tarandus* populations. This inference has created a serious shortcoming in understanding the true relationship between *R. tarandus* and its environment.

Unfortunately, many biologists have focused on the high density of reindeer at the time of the St. Matthew crash as a supposed prerequisite for the crash and have accepted Klein's (1968: 366) statement that "… the relatively poor condition of the reindeer going into the winter [1963–64] as a result of competition for high quality summer forage during summer 1963 …." as factual—when in fact there are no quantitative measures to support this supposition. Leader-Williams (1988) subsequently made a detailed comparison between reindeer introduced to South Georgia and those introduced to islands around the world, especially to Alaskan islands, and particularly to St. Matthew and St. Paul islands. In doing so, he perpetuated the same points that we challenge herein, as he did no reanalysis of the data for those points. The inference that reindeer on St. Matthew Island would not have crashed if population density had not been high and food had not been depleted remains strong.

We argue that neither the state of the absolute food supply nor the condition of the reindeer going into the winter of 1963–64 played a major role in either the single-year precipitous decline or in the magnitude of that crash. There are examples of caribou populations with low mean densities and some with relatively high mean densities before the initiation of a single-year crash where the absolute food supply was adequate but made relatively unavailable due to extremely unfavorable snow or ice conditions. This paper is not meant to be a general review of population dynamics of *R. tarandus* populations on islands; rather, our sole aim is to address what really caused the St. Matthew Island reindeer crash in winter 1963–64 and what in fact dictated the number of animals that survived it. We are not expanding this consideration to multi-year declines of reindeer or caribou populations and, especially, not to large mainland *R. tarandus* populations. We consider only this one isolated event and compare it to other isolated events in island environments, to explain the St. Matthew Island reindeer crash.

In reevaluating the reindeer crash on St. Matthew Island in winter 1963–64, we have the benefit of hindsight and good documentation from a number of new studies of different reindeer and caribou herds over the past 36 years. Our intent is to clarify and expand the ecological considerations associated with Klein's (1959, 1968) findings, not to criticize the original interpretation. We review the evidence from Klein (1959, 1968) and come to the conclusion that only the winter weather was the all-important factor that caused the crash. We hope that this paper will stimulate others to further evaluate limiting factors influencing *R. tarandus* population growth with adequate consideration given to the many factors that influence population size (e.g., Valkenburg *et al.*, 1996; Whitten, 1996; Boertje & Gardner, 2000).

## Materials and methods

The subarctic oceanic island of St. Matthew is 332 km$^2$ (128 mi$^2$), lying in the north-central Bering Sea at 60°30'N, 172°30'W. Although multi-year weather records are available only from St. Paul and Nunivak islands about 400 km away, the St. Matthew Island climate is similar to those islands, being subarctic maritime characterized by cool and humid summers but with a relatively long plant growing season compared to interior mainland and arctic island ranges. Winter snowfall is relatively heavy, and strong winds and above-freezing temperatures are common. Klein (1968: 360) describes the island as arctic tundra low-lying vegetation—only a few grasses and forbs annually exceed 30 cm in height. The only common shrubs are decumbent willows (*Salix* spp.). He also noted that the vole (*Microtus abbreviatus*) and the arctic fox (*Alopex lagopus*) were the only native land mammals found there before the introduction of reindeer.

On 20 August 1944, 29 yearling reindeer, 24

Table 1. Total quantitative data available from Klein (1959, 1968) for determining the size and sex and age composition of the St. Matthew Island reindeer population in 1957 and 1963.

| Year | Parameters | Sample | N | Calves | Yearlings | Cows | Bulls |
|------|-----------|--------|---|--------|-----------|------|-------|
| 1957 | Total count | A | 1226 | ?[a] | ? | ? | 300 |
| | Calf sample | B | 910 | 267 | ? | ? | none |
| | Yearling sample | C | (218)[b] | 75 | 45 | 99 | none |
| | Population estimate | D | 1350 | 280 | 190 | 470 | 410 |
| 1963 | Calf:cow ratio | E | 1652[c] | 60 calves:100 cows | | | |
| | Yearling:cow ratio | F | 705[c] | 26 yearlings:100 cows | | | |
| | Population count | G | 6000 | ? | ? | ? | ? |
| 1966 | Skeletal sample[d] | H | 241 | 48 | 56 | 86 | 51 |

[a] "?" values not reported in Klein (1959, 1968).
[b] Reported by Klein (1959) as "218" but 75 + 45 + 99 = 219.
[c] No numbers were reported for calves, yearlings, cows, or bulls in the two 1963 samples or in the 1963 total population count.
[d] Skeletal sample was collected by Klein (1968) in summer 1966: he assumed it was representative of the 1963–64 die-off population.

female and five male, were released on the island. Only 105 reindeer are known to have been harvested on St. Matthew Island between 1944 and 1964, all during the 1957–63 period.

Klein (1959, 1968) recognized five sex and age classes: calves, female yearlings, male yearlings, cows, and bulls. We report the quantitative values obtained in 1957, 1963, and 1966 by Klein (1959, 1968) and our calculations of sample compositions, calf:cow and yearling:cow ratios, percent calves, percent yearlings, and also our corrections to some values used by Klein (1968).

The main focus of Klein's (1959, 1968) studies was the investigation of the vegetation on St. Matthew Island and its changes from 1957 to 1963, with some follow-up in 1966. Information on population dynamics was secondary to the above studies. However, those population data are what allows a reader to interpret and evaluate the 1968 report—and it is impossible to do so without also reading the 1959 report in detail and comparing the two. Therefore, we have carried out a detailed comparative review of both papers to provide a fuller assessment along with a reasonable alternative evaluation for what in fact caused the crash event.

Counts of reindeer made in summers 1957 and 1963 do not lend themselves directly to a complete evaluation of the sex and age composition of the entire population (Tables 1 and 2). The population data obtained by direct count for the reindeer in 1957 and 1963 were fragmentary and require calcu-

lations and estimation to attain a fuller set of values. Even then, little sex and age information can be extracted for reindeer in summer 1963, so the skeletal sample obtained by Klein (1968) in summer 1966 representing the 1963–64 die-off population must be relied upon.

Klein (1959) made three counts in 1957: the first is termed a 'total count' (Table 1: A-see sample column in table) and the other two are referred to as the 'calf sample' (Table 1: B) and the 'yearling sample' (Table 1: C). Klein (1968) then produced the 'population estimate' (Table 1: D) by inflating the total count by 10% and rounding to the nearest multiple of 10. The only count of any sex or age class in the total count was of bulls, so the number of non-bulls in the total count is 926 (1226 - 300). Therefore, to reproduce the values for the total population estimate in Klein (1959), we calculated the numbers of calves, yearlings, and cows as follows: calves equal the number of calves in the calf sample times the total count minus the number of bulls divided by the size of the calf sample (272 = 267 × 926/910); yearlings equal the number of yearlings in the yearling sample times the total count minus the number of bulls divided by the size of the yearling sample (190 = 45 × 926/219); and the number of cows equal the total count minus the number of bulls minus the summation of the number of calves and yearlings (464 = 926 - 272 - 190). The number of calves, yearlings, cows, and bulls in the population estimate is then obtained by inflating the number of calves and cows calculated for the total count to the next multiple of 10 (Table 1: D), holding the yearlings at their calculated value for the total count and inflating the number of bulls in the total count by 37% (0.367 = (410 - 300)/300). Klein (1959) believed that most of the missing animals were bulls: he counted 300 in the total count and estimated 410 in the population estimate; therefore, he extrapolated an additional 110 bulls. The remaining 14 animals among the 124 extrapolated were calculated to be eight calves and six cows. There were no bulls in the calf and the yearling samples in 1957 and bulls in the total count are underrepresented by

Table 2. Comparisons made for evaluating the 1957 and 1963 St. Matthew Island reindeer population parameters: see Table 1 for raw data from Klein (1959, 1968).

| Studies | Parameter | 1957 Sample source[a] | 1957 versus 1963 | | 1963 Sample source[a] |
|---|---|---|---|---|---|
| | | | 1957 | 1963 | |
| Klein | % Calves | C | (34%)[b] | 20% | H |
| | % Calves | B | 29%[b] | | |
| | % Calves | D | 21% | | |
| | Calves:100 cows | C | 75:100[b] | 60:100. | E |
| | Yearlings:100 cows | C | 45:100[c] | 26:100[d] | F |
| This study | % Calves | D | 21% | 20% | H |
| | Calves:100 cows | D | 60:100 | 56:100 | H |
| | Yearlings:100 cows | D | 40:100 | 65:100[e] | H |

[a] See Table 1 for raw data from sample source.
[b] Biased high for calves.
[c] Biased slightly high for yearlings.
[d] Questionable value: most likely biased low for yearlings.
[e] Questionable value: most likely biased high for yearlings.

37% compared to the population estimate; so, we assume that the most accurate calf:cow and yearling:cow ratios come from the population estimate in 1957 (280/1350 and 190/1350, respectively).

The calf:cow ratio was obtained from the larger of the two samples in 1963 and the yearling:cow ratio from the smaller sample (Table 1: E and F). The 1963 total population count was obtained directly from the aerial survey results (Table 1: G). Klein (1968) did not report the numbers of calves, yearlings, cows, and bulls in the 1963 total population count or the two samples that the calf:cow and yearling:cow ratios come from in 1963. Both ratios can be derived from the 1966 skeletal sample of the 1963–64 die-off population (Table 1: H). Proportional representation of calves, yearlings, cows, and bulls can only be calculated from the skeletal sample (Klein, 1968).

*Defining crash*
The term 'crash' has been used loosely over the years to equate to virtually all marked downturns in population size. This use is common, regardless of the number of years involved in the downturn. Perhaps, most importantly, no due notice is given to the annual magnitudes of changes in population size during these "crash" events. This is true, even if annual changes vary from losses to temporary annual gains, as long as the end result is a major reduction in the size of the population. This seriously detracts from any ecologically or biologically accurate evaluation of the differences in a rapid population crash versus a prolonged population decline often lasting more than a decade, following an extended period of moderate to high population growth (*cf.* Caughley, 1970).

Merriam Webster's Collegiate Dictionary (10th ed.) defines a 'crash' as "a sudden decline (as of a population), marked by a concerted effort and effected in the shortest possible time." We define a 'population crash' as a single-year event where 30% or more of a population is lost in that year. We argue that the term crash should be restricted to describe only annual events that exceed the 30% level of decline. We would define an 'extreme population crash' as a single-year event where ≥ 50% of the animals die. Annual crashes occurring over three consecutive years are known (Miller, 1998; Gunn & Dragon, 2002; Miller & Gunn, 2003a, b). To refer to a major loss of animals that takes place over a decade or more as a crash is misleading. This is true even if the end result is essentially the same. More than anything else, it is the rapidity, sporadic infrequency, and unpredictability of a crash event that sets it apart from a protracted downturn and marked decline that takes place over a series of years after and as a consequence of an extended continual period of appreciable overall population growth.

There are a number of density-dependent relationships that could cause a major protracted population decline; however, we know of no possible density-dependent mechanism that could or would cause an extreme single-year crash in the first year of a decline. On the other hand, some density-independent abiotic factors could have and have caused exceptionally large annual winter die-offs and crashes among island populations of reindeer and caribou (e.g., Reimers, 1977, 1982, 1983; Gates *et al.*, 1986; Adamczewski *et al.*, 1988; Stimmelmayr, 1994; Ouellet *et al.*, 1996; Miller & Gunn, 2003a, b). Biotic factors (predation, disease, and parasites) could act to dampen or reverse population growth in a density-independent or density-dependent fashion, but most likely would not affect a rapid near-total single-year decline in a population.

*Defining starvation*

We use the term 'starvation' to mean death by extreme and prolonged undernutrition. Some ruminal contents may be present but not of adequate quality to sustain life.

## Reevaluation of population status in relation to density-dependent food limitation

*Calf to cow and yearling to cow ratios*

Klein (1968: 352) states "In the 1957 counts, the ratio of fawns to adult females was obtained from a sample of 910 animals and the ratio of yearlings to adult females from a sample of 218 [actually 219] reindeer. In these samples there were 75 fawns and 45 yearlings per 100 adult females." The stated value of "75 fawns ... per 100 adult females" cannot be reproduced from the 1957 sample of 910 reindeer (Table 1: B). The only explanation based on existing data is that the 75 fawns per 100 adult females reported by Klein (1968: 352) was inadvertently taken from the smaller 1957 sample of 219 reindeer with 75 calves and 99 cows (see Table 1: C). This error creates a false impression that there was a documented major decline—when there was not.

Of particular importance in determining which sample must have been used is the fact that no measure of cows is provided in the 1957 sample of 910 reindeer; as a result, no ratio of calves:100 cows can be calculated directly from that sample (Table 1: B). It can be extrapolated indirectly from other information provided in the 1959 report. When the extrapolation is made, the calf:cow ratio is only 60 calves:100 cows (Table 2). Notably, Klein (1959: 7) rejected and did not use the small sample of 219 to calculate a calf:cow ratio because he believed it was biased. Calves were markedly overrepresented, as there were no bulls present in the sample (Table 1: C) and the total population estimate yielded a ratio of only 60 calves:100 cows.

The three measures of the number of yearlings:100 cows that can be obtained from the 1957 data are all similar: there were 40 yearlings:100 cows from the values for the total herd of 1350 animals (Klein, 1959: Table 2); 41 yearlings:100 cows from the extrapolated sex and age composition of the total count of 1226 reindeer; and 45 yearlings:100 cows from the sample of 219 reindeer. We believe the 40 yearlings:100 cows is the best measure in 1957, as it is drawn from the total population estimate (Table 1: D; Table 2).

In 1963, Klein (1968: 352) reports 60 calves:100 cows from a sample of 1652 reindeer and 26 yearlings:100 cows from a sample of 705 reindeer (Table 1: E and F). In the 1966 skeletal sample,

which Klein (1968) said was representative of the 1963 population, there were 56 calves:100 cows. When the calves in the skeletal sample are arbitrarily adjusted by 10%, in accordance with Klein's (1968) suggestion of underrepresentation for calves, this ratio rises to about 61 calves:100 cows in the 1963 population.

The 1957 yearling sample indicates that the number of yearlings to cows ranged between 40 and 45 yearlings:100 cows. In the 1966 skeletal sample, there were about 65 yearlings:100 cows (Klein, 1968). This certainly suggests a greater representation of yearlings than the 40–45 yearlings:100 cows obtained in 1957. Most importantly, it is also 2.5 times greater than the value obtained by Klein (1968: 352) from his sample of 705 reindeer in 1963. This puts both the yearling:cow counts obtained in summer 1963 and the 1963 yearling:cow count obtained from the 1966 skeletal sample into serious question. Even the average of 26 yearlings and 65 yearlings would still provide a value of 46 yearlings:100 cows; therefore, the number of yearlings to cows in 1963 most likely was similar to those values from 1957.

There is an unexplained contradiction in the acceptance of the 1966 skeletal sample as representative of the sex and age composition of the 1+yr-old segment of the 1963 population (Klein, 1968). We do not understand why the low 1963 yearling:cow ratio from the sample of 705 animals was used instead of the much larger yearling:cow ratio obtainable from the 1966 skeletal sample that Klein (1968) said was supposedly representative of the 1963–64 die-off population. Given the lack of evidence for a significant reduction in proportional representation of calves and yearlings from 1957 to 1963, the low value obtained for yearlings in the 1963 sample of 705 reindeer and the high value obtained from the skeletal sample are enigmas. It seems highly questionable that either the low contribution of yearlings in the sample of 705 or the high contribution from the skeletal sample was truly representative of the relative occurrence of yearlings in the entire herd of 6000 reindeer in 1963. It is more reasonable to believe the true value fell somewhere in between. Thus, there is no quantitative evidence to support meaningful breeding depression or reduced early survival between 1957 and 1963 or even in 1963 only, particularly in terms of the pending crash of the population and the required 28% average annual rate of population increase from 1957 to 1963.

*Observed rates of population growth and required annual rates of increase*

The observed rate of growth during the 13 years from 1944 to 1957 required an average annual rate
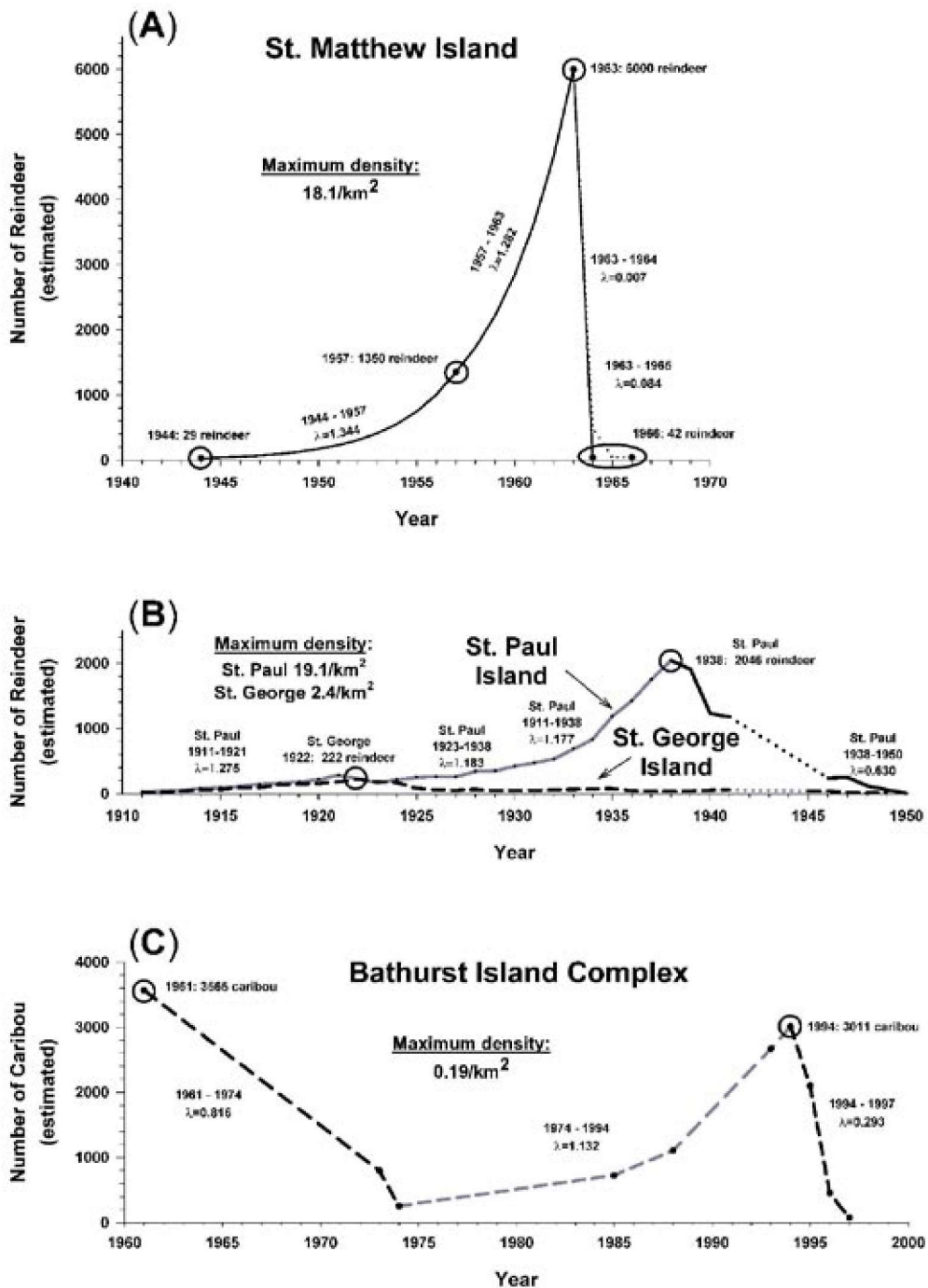
Fig. 1. (A) Assumed population growth of St. Matthew Island reindeer herd: a high-density introduced reindeer popula-
tion experiencing a single-year crash (after Klein, 1968: Fig. 2; data sources Klein, 1959, 1968); (B) Assumed
population growth of St. Paul Island and St. George Island reindeer herds: St. Paul—a multi-year decline of a
high-density introduced reindeer population with continued decline at low densities; and St. George—an intro-
duced reindeer population 'locked in' at relatively low densities (data from Scheffer, 1951: Table 1; Fig 1); and
(C) Assumed population growth of Bathurst Island complex indigenous Peary caribou population: the fall, rise,
and consecutive 3 years of single-year crashes of an extremely low-density Peary caribou population (data from
Tener, 1963; Miller *et al.*, 1977; Miller, 1987, 1989, 1995, 1998; Gunn & Dragon, 2002).

of increase of $\lambda = 1.34$ (Fig. 1A). This is considerably greater than population growth rates in established, free-ranging, indigenous caribou populations (e.g., Davis *et al.*, 1980, Western Arctic Herd, 14%, 1976–79; Messier *et al.*, 1988, George River Herd, 14%, 1955–84, and 11%, 1970–84), although Valkenburg *et al.* (2000) did record similar high mean rates of increase for shorter periods of time among four of seven herds of *R. t. granti* translocated in Alaska.

As reported by Leader-Williams (1980), reproduction and survival at the theoretical maximum annual rate of increase could have meaningfully altered the realized average annual growth rate. Klein (1968: 352) suggested that "Under the assumed ideal range conditions on St. Matthew Island at the time of the release, the introduced nucleus herd probably increased at a rate approaching the theoretical maximum during the years immediately following." If so, and the theoretical maximum was realized with no mortality among calves and the 1+ yr olds in the first two years of pristine range conditions, the introduced herd would have grown at 83% from 1944 to 1945 and at 68% from 1945 into 1946. The sex ratio was highly skewed in favor of females at 24 to five in summer 1944. By summer 1946 under this scenario there would have been 89 reindeer and the sex ratio would have become balanced at about 60 females:40 males, assuming no mortality and a 50:50 sex ratio among calves. For the following 11 years, an average annual rate of increase of 28% would be all that would be necessary to get to the population estimate of 1350 in 1957. This is the growth rate documented by Klein (1968: $\lambda = 1.28$) for the 6 years from 1957 to 1963. This would suggest that after an initial two-year increase at the maximum rate of population growth, it would be necessary for the reindeer population to average only 28% per year—not 34%— to reach 1350 by 1957 and 6000 by 1963. Under this scenario, there could be no meaningful change in the reindeer's capability to sustain themselves on the absolute food supply, in the relative availability of that food supply for the reindeer up until the crash, or in annual rates of reproduction, survival, or mortality during those last 17 years. If so, there is no support for advanced limitation of the absolute food supply being in place.

*Changes in body weight between 1957–63 and 1963 range conditions*
There was a general reduction in body weight by sex and age class after 1957 (Klein, 1968: Table 2), but this may not equate to reduced biological performance. It does not follow that the reduced weights were critical to future reproductive success or survival of those reindeer: statistical significance

is not in itself a measure of biological meaningfulness, especially when the statistical differences are based on such small samples (e.g., Yoccoz, 1991; Steidl *et al.*, 2000; Anderson *et al.*, 2001; Guthery *et al.*, 2001). It is the nutritional state and physical condition of the individual that matters, not total body mass. The reported decline in body weight is in itself unconvincing; given the small sample sizes for all reindeer and especially for the young animals, and given that only the mean values are presented with no measures of variation. Although individual body weights dropped to a level similar to those of reindeer on the mainland of Alaska (Klein, 1968), we contend that the sex and age composition argues more strongly for no large change in production and survival from 1957 to 1963 or 1963–64. Two 1963 calves were pregnant (Klein, 1968), suggesting no reduction in forage sufficient to markedly reduce reproductive rates.

Even though the lichen mat component of the food supply had been seriously reduced on St. Matthew Island by summer 1963, Klein (1968: Tables 8 and 9) reported 16–21% protein in summertime rumen samples. These protein values are high compared to other published values (e.g., Nieminen & Heiskari, 1989) and are adequate for nutrition, breeding, and reproduction. The overall average annual rates of population growth from 1944–63, the reported percentages of 1963 calves still alive in winter 1963–64, and the sex and age composition of 1+ yr-old animals estimated in the die-off population do not indicate any major slowdown in population growth before the crash. All of these population parameters actually suggest the potential for continued high rates of population growth.

## Alternative explanation and associated ecological implications

*Extreme weather restricting forage availability in winter 1963–64*
Klein (1968: 354) reported "The winter of 1963–64 on the islands of the Bering Sea was one of the most severe on record from the standpoint of the amount and duration of snow on the ground and extreme cold." The magnitude of a single-year crash is virtually independent of any density-dependent relationship between the reindeer and their absolute food supply before the weather event took place. That is, it is the severity, extent, and duration of the unavailability of the forage caused by exceptionally severe snow conditions that dictated the number of animals that would survive – not the starting density or nutritional condition of the animals in this particular situation.

Our position does not completely rule out the possibility that the state of the absolute forage supply at the time of the extreme weather contributed somewhat to at least the initial acceleration of deaths during the crash. However, the important point is that the single-year crash would have occurred regardless of the abundance of the absolute food supply. This is true because the absolute food supply had to be rendered unavailable island-wide for a long enough time to create lethal conditions of this magnitude (i.e., 99% loss), regardless of the abundance of the absolute food supply, the initial density of the reindeer, or the condition of those reindeer.

Reindeer in relatively poor nutritional condition entering such an exceptionally stressful time might die sooner than 'healthy' reindeer, but when the extremely severe condition persists long enough, the end result is the same and most animals will die. An important question is whether the St. Matthew Island reindeer population would have necessarily crashed in 1963–64, especially to the same degree, if it had not experienced exceptionally prolonged, unfavorable snow conditions. We believe the answer is—no! The lichen mat component of the forage had received heavy reindeer use on some wintering areas on St. Matthew Island as early as 1957, but sedges and grasses actually had increased (Klein, 1959, 1968).

Another important question is whether the reindeer would have crashed in 1963–64 under the same weather extremes but with the lichen mat component still abundant? We believe the answer is—yes! The lichen loss over the several years before the crash did not greatly reduce calf births, survival of calves to yearlings, or winter survival of reindeer of either sex and all ages. We believe that the estimated decline in growth from 34% (1944–57) to 28% (1957–63) per year does not reflect a population suffering extreme nutritional stress, nor a meaningfully dangerous depression in population growth. If it did, then virtually every *R. tarandus* population in the world would have to be considered in a continual state of extreme nutritional stress! Also, if the theoretical maximum annual rate of population increase was realized in 1944–46, as previously discussed, there would have been no depression in the average annual rate of population growth for the 17 years from 1946 to 1963. The 28% per year population growth rate, occurring after serious reduction of the lichens, still approaches the suggested realized maximum rate of $r \approx 0.30$ for North American caribou (Bergerud, 1978).

Similar to the reindeer on St. Matthew Island, the reindeer introduced on St. Paul Island increased rapidly over nearly 3 decades (27 yr) at about one-half the annual rate of increase of reindeer on St. Matthew Island: i.e., $\lambda = 1.18$ *versus* $\lambda = 1.32$, respectively. After the peak in 1938, their temporal patterns of decline differed markedly from the St. Matthew Island population, but the end result was essentially the same (Fig. 1B). The St. Paul reindeer herd declined during a 12-year period nearly to extirpation in 1950 (Scheffer, 1951). They then experienced a population recovery over the next 12 years and suffered a crash of about 40% in winter 1962–63 at only about one-third of the overall density they were at in the first year of decline in 1938–39 (Swanson & Barker, 1992: Fig. 6). When the reindeer were at their highest mean density of 19.1 • km$^{-2}$ in 1938, they declined < 7% in one year. Then in 1939, when at 17.8 • km$^{-2}$, they declined 36% in 1 year. Yet, 7 years later, in 1947, three consecutive years occurred with major crashes, with the reindeer population falling at 68% per year from a mean density of only 2.2 • km$^{-2}$ to < 0.1 • km$^{-2}$.

The reindeer decline on St. Paul Island, unlike the one on St. Matthew Island, appears to have followed the pattern of decline that was hypothesized by Caughley (1970) for irrupting ungulate populations. However, we believe, as did Gunn *et al.* (2003), that the last 3 years of the first overall decline (1938–50) do not appear to be a solely density-dependent relationship—the 68% average annual rate of decrease suggests that unfavorable weather was driving the decline at that time. Most likely the decline was accelerated and deepened by compaction of the snow cover by strong winds and the presence of different mechanisms of widespread or even range-wide icing on, in, or under the snow pack caused by winter rain events and thaw-freeze periods. These have been reported previously for St. Paul Island and other islands in the region (e.g., Scheffer, 1951; Bos, 1967; Lent, 1999); also for Svalbard reindeer, *R. t. platyrhynchus* (e.g., Reimers, 1977, 1982, 1983); and for Peary caribou, *R. t. pearyi* (e.g., Parker *et al.*, 1975; Miller *et al.*, 1977; Miller & Gunn, 2003a, b) and elsewhere.

Although winter 1963–64 was reported as one of "extreme cold" for St. Matthew Island (Klein, 1968) and reiterated by Leader-Williams (1988), what is considered "extreme cold" is relative to the geographical location under consideration. Weather records from St. Paul Island indicate considerable fluctuations in temperature above and below 0 °C during the 1963–64 winter. The coldest month on St. Paul Island was February 1964 with a monthly average minimum of -12.7 °C and a monthly average maximum of -5.7 °C. By contrast, the monthly average minimum and maximum temperatures for February 1964 in the central Canadian Arctic Archi-

pelago (Resolute Airport: Climate Archives of Canada) were -38.1 °C and -31.3 °C or about 25 °C colder than on St. Paul Island. Only three monthly average maximum temperatures fell below the freezing point on St. Paul Island in winter 1963–64 (Jan, -0.6 °C; Feb, -5.7 °C; and Mar, -2.8 °C) (http://www.wrcc.dri.edu/summary/lcdak.html). No one knows whether there was extensive icing compounding the severity of the snow pack on St. Matthew Island in winter 1963–64—and no one ever will. Freezing rain events could have occurred under the temperature regime recorded in any month of the 1963–64 winter on St. Paul Island, and by inference on St. Matthew Island. Thus, the probable role of icing cannot be ruled out and should not be ignored, as it can be an important factor in the life equation of any *R. tarandus* population living on islands with low-growth tundra forms of forage plants (e.g., Miller *et al.*, 1977, 1982).

*Comparison to Canadian High Arctic Islands*
The reindeer situation on St. Matthew Island is not directly comparable to the Peary caribou situation on the Canadian High Arctic Islands because the High Arctic has a more unpredictably severe climate and the islands are linked by sea ice for 9–10 months of the year. Peary caribou can disperse in response to environmental conditions or migrate seasonally between or among islands (e.g., Miller, 1990; Miller *et al.*, this proceedings). Also of importance, Peary caribou live with a larger grazer, the muskox (*Ovibos moschatus*) and their major predator, the wolf (*Canis lupus*).

However, the most detailed examples of a low-density Peary caribou population experiencing winter–spring crashes come from the Bathurst Island complex (Fig. 1C). The single-year crashes that occurred in 4 out of 24 years between 1973 and 1997 among Peary caribou on the western Queen Elizabeth Islands of the Canadian High Arctic conclusively show that a high animal density is not mandatory for population crashes (Parker *et al.*, 1975; Miller *et al.*, 1977; Miller, 1998; Gunn & Dragon, 2002; Gunn *et al.*, 2003; Miller & Gunn, 2003a, b). Such major crashes could occur even at exceptionally low caribou densities. Bathurst Island at 16 042 km² and Melville Island at 42 149 km² are 48 and 127 times as large as St. Matthew Island (332 km²). On Bathurst Island, Peary caribou crashed by 68% in 1973–74 from 0.04 caribou • km⁻²; by 30% in 1994–95 from 0.18 caribou • km⁻²; by 78% in 1995–96 from 0.11 caribou • km⁻²; and by 83% in 1996–97 from an exceptionally low 0.03 caribou • km⁻². On Melville Island, Peary caribou crashed by 51% in 1973–74 from 0.81 caribou • km⁻² and crashed by 30% in 1996–97 from an exceptionally low 0.02 caribou • km⁻² (Miller *et al.*, 1977; Miller, 1998; Gunn & Dragon, 2002).

Thus, prolonged extremely unfavorable snow and ice conditions caused crash events in low-density populations of Peary caribou that were capable of travel on the sea ice to escape from individual islands in a region of 100 000 km² or beyond. It is noteworthy that muskoxen at low densities and on different diets from Peary caribou also experienced crashes in similar proportions during the same years on the same ranges (Miller *et al.*, 1977; Miller, 1998; Thomas *et al.*, 1999; Gunn & Dragon, 2002). Also, like other stochastic events, crashes can occur in consecutive years, with three consecutive years of crashes documented on the south-central Queen Elizabeth Islands (Fig. 1C: see also Fig. 3 of Miller & Gunn, 2003a). As a result, the Peary caribou population in the Bathurst Island complex plummeted an estimated 97% between winter 1994–95 and summer 1997. In each year, the apparent single cause of each crash was snow and ice conditions that were exceptionally severe and prolonged.

*Ecological implications of cause versus effect (response)*
In order to advance our ecological understanding of a crash event, it is necessary that we comprehend why the crash occurred. Thus, it is all-important to first clearly identify the fundamental cause of the crash. In the absence of a sudden island-wide massive loss of vegetation and in the absence of predators, competitors, contagious disease or heavy parasite burdens, only weather in the form of deep snow, densely compacted snow, snow compounded by extensive icing, or thick island-wide icing can cause such a single-year cataclysmic crash event. Total snowfall on St. Paul Island in 1963–64 was 2.6 m. If a similar, or even a considerably lesser, amount fell on St. Matthew Island and persisted throughout the winter, the depth of the snow cover alone would have caused the island-wide starvation and the death of 99% of the St. Matthew Island reindeer population in winter 1963–64.

Although the high density of reindeer on St. Matthew Island in summer 1963 meant that there were many reindeer present, density-dependent effects cannot necessarily be inferred. It is our contention that the reindeer crash on St. Matthew Island would have happened even if the reindeer were at a much lower density. The magnitude of the crash is mostly related to the duration of exposure to severe abiotic factor(s) and not to the density of animals present per se (e.g., Behnke, 2000). In a parallel situation, Stimmelmayr (1994) reported a reindeer die-off on Hagemeister Island (east of St. Matthew Island) in 1991–92 during a winter with deep snow and con-

cluded that, despite a poor winter lichen range, there was no conclusive evidence that the herd had experienced effects of density-dependent food limitation. Scheffer (1951) had previously commented on the importance of icing during wintertime on St. Paul Island, as had Palmer for subarctic Alaskan islands in general (*in* Scheffer, 1951; Palmer, 1929).

The lichen mat component of the forage supply available to the reindeer on St. Matthew Island was reduced to a mere remnant of its pristine abundance by summer 1963. Although the loss of lichens did not bode well for the future growth of the reindeer population, there was no evidence that it seriously influenced the population's performance, which was still exceptionally high. Klein (1968: 361) reported that the removal of lichens allowed sedges, grasses, and some forbs to increase in abundance and although willows were being used heavily by 1963, they had decreased only 4% from their 1957 level. He noted from Palmer (1929) that reindeer on ranges where lichens are depleted graze heavily on grasses and sedges during winter. Scheffer (1951) noted that on St. Paul Island, after a marked reduction in lichens, reindeer fed heavily in winter on the abundant sea grass (*Elymus*). Scheffer (1951: 359) reported "The availability of this grass, rather than the amount, is the critical factor." Also, L. J. Palmer (*in* Scheffer, 1951: 359) "cautioned that 'because of winter rains... herds may suffer great losses through starvation, since the animals cannot paw through hard crust to get food'."

It is possible that the reindeer entered the 1963–64 winter in "relatively poor condition" as a result of competition for high quality forage in summer 1963, but that is only supposition. Importantly, a 'relatively poor condition' does not necessarily equate with a potentially lethal condition, and the proportions of calves and yearlings in the 1963–64 die-off population were both high. Not only were initial calf production and early survival of calves in 1962 and 1963 favorable, the overwinter survival of 1962 calves to yearlings in 1963 also must have been at least average, if not higher, based on the 1966 skeletal sample of the 1963–64 die-off population.

We believe that the extreme crash experienced by the St. Matthew Island reindeer in 1963–64 was weather-related and not an inevitable consequence of high population density. Regulation of a population through the limitation of its absolute food supply should be measurable by reductions in successful reproduction and rearing of calves and serious reduction in yearling recruitment, and elevated mortality in general (*cf.* Caughley, 1970). There are no quantified population data from Klein (1959, 1968) that support any serious depression in reproduction and

survival between 1957 and 1963. Rather, the data clearly show no meaningful change occurred between 1957 and 1963 or even between 1944 and 1963.

With regards to Riney's (1964) and Caughley's (1970) four hypothetical stages of population change following liberation of herbivores on new ranges, the St. Matthew Island reindeer population had not even reached stage 2 of 'initial stabilization' where the rate of increase would be zero. If the reindeer population on St. Matthew Island had followed the Riney–Caughley model, they would have increased throughout stage 1 and reached a peak density at stage 2, with rates of increase tending to zero; then, becoming negative at stage 3, and subsequently returned to and fluctuating around zero in stage 4. Leader-Williams (1980, 1988) interpreted the St. Matthew Island situation as follows: the reindeer went through stage 1, completely skipped stage 2, bottomed out in an exaggerated stage 3, and then were nearly extirpated and never made it into stage 4. Such extreme variation on the concept of a 4-stage model greatly detracts from the usefulness of its general application. Caughley (1970) apparently recognized this when he concluded that "While the generality of the {4-stage} pattern should not be accepted uncritically, it may be useful as a hypothesis to be tested further." We believe that his emphasis on 'further testing' has been overlooked or at least not actively pursued and examined critically. Most importantly, neither Riney (1964) nor Caughley (1970) ever stated or implied that an irrupting population will inevitably crash (*cf.* Gunn *et al.*, 2003). It appears the boundary separating theory from fact remains blurred in the quest for understanding the population dynamics of *R. tarandus* and the relationship between *R. tarandus* and its environment.

## Conclusions

We do not believe density-dependent food-limitation was the primary factor or even a necessary essential factor in the 1963–64 St. Matthew Island reindeer crash. The population parameters do not substantiate lethal or even advanced severe food limitation prior to the crash. The reindeer population grew at an exceptionally high average annual rate of 32% for all 19 years after introduction and up to the year of the crash. We do not question Klein's (1968) conclusion that the rapidly expanding reindeer population reduced the lichen abundance and we believe that there would have been a future density-dependent response if the severe winter weather of 1963–64 had not prematurely caused the crash. However, there was no evidence in 1963 that such a correction would have occurred soon and especially not in the winter of

1963–64. Even when such a correction happened, it would have taken years of overall decline—not just a matter of months. In addition, the magnitude of any long-term decline would not necessarily approach the size of the 99% single-year crash.

There are no conclusive facts to indicate that the abundance and quality of the absolute food supply, other than lichens, was critically depleted in 1963. Given what we now know about the relationship of reindeer and caribou to their environment, the high density of the reindeer and the serious deterioration of the lichen component of the range in itself is only evidence that the population was already locked into an initial phase of increasing density-dependent forage-limitation with future consequences to come in subsequent years. It does not support the inference that it was in a well-advanced phase and surely not that it was in an imminently lethal and final state. Single-year crashes have to be the result of rapid extremely severe changes in the animals' environment that occur in a matter of weeks or a few months on a regional or an area basis. Perhaps, even only one extremely severe snowstorm, especially one associated with extensive icing, or even a single heavy freezing rain event in early winter could be enough to set up conditions that would reduce the relative availability of the food supply to a point where a late winter–spring die-off or crash would occur as a result.

Our intent is not to universally reject density-dependence effects. We are dealing only with the St. Matthew Island reindeer crash in 1963–64 and our thesis is that density-dependency was not a necessary part of the crash and, in fact, could not have caused such a rapid near-total single-year crash. We believe the more important query is not what dictates the number of animals that will die, but what dictates the number of animals that can possibly survive a crash event. That is, in a situation where a viable escape by dispersal and subsequent return is not possible (or is not freely employed), it is the severity, extent, and duration of the abiotic factors that will dictate how many individuals can survive. Under extreme conditions, it does not matter that the absolute food supply is abundant, when it is nearly all unavailable until snowmelt. When foraging is not energy-efficient or the animal cannot get to the food for an extended period of time, the end result is death by starvation, regardless of the animal's initial nutritional status.

It was the island-wide, prolonged unavailability of forage that the reindeer experienced in winter 1963–64 that dictated the maximum number of animals that could possibly survive the weather event. The all-important point is that it was neither the number nor density of the animals, nor their nutritional state

at the beginning of the die-off period that caused the crash and determined the number of survivors. In winter 1963–64, the record-setting, extremely severe weather created a rare and near total relative unavailability of the food supply across St. Matthew Island. Those lethal conditions persisted and only about 50 reindeer survived. We need to look no further than the record-setting exceptionally severe winter conditions of 1963–64 for the cause of this spectacular single-year population crash.

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