Conservation of erupting ungulate populations on islands – a comment*

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Abstract: A generalised model for herbivores experiencing abundant forage over time is that their numbers erupt and then decline. This model has been applied to fluctuations in caribou (*Rangifer tarandus*) populations especially those on islands. Since this generalised model for erupting herbivores was first proposed, two assumptions have slipped in (1) that an erupting population will crash; and (2) that the crash will be density-dependent. The problem with the assumptions is that, without testing, they can lead to inappropriate management such as culls. The first assumption arises from uncritical use of earlier accounts and the second assumption from not discriminating between the effects of environmental variation from the effects of the high herbivore numbers on forage availability (density-dependence). Often typical density-dependent effects such as lowered initial reproduction, reduced early survival of calves, and subsequent calf, yearling and juvenile survival are used to justify the contention that there are too many herbivores. But such reasoning is flawed unless cause/effect relationships are established and the role of environmental variation is evaluated. We argue that it is overly simplistic to believe that every population's subsequent performance and fate will follow a singular pattern with only one paramount factor driving and ultimately dictating an inevitable outcome. The relative importance of unpredictable abiotic factors in influencing and causing variation in the response of ungulate populations should be investigated, no matter whether those factors are sporadic or periodic.

Key words: crashes *vs.* declines, herbivore populations, management *vs.* myths, *Rangifer tarandus*.

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Introduction

The primary goal of wildlife management when it involves subsistence users is for sustainable annual yield of animals over the greatest possible continual period of time (*cf.* Leopold, 1948). With this goal in mind, managers and many biologists give a great deal of thought to extremes in population size--too few or too many animals. The consequences of too few animals for the desired levels of sustained annual harvest is relatively straightforward. On the other hand, many managers and biologists believe that it is a self-evident truth that "too many" animals is an equally serious problem, which must be dealt with in a timely manner. The long-term outcome of high animal densities remains essentially untested and thus questionable. It remains unproven that excep-

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tionally high mean densities of ungulates in a closed population will always lead to deterioration of their range. Further, it is also unproven that this condition would necessarily cause a meaningful and lasting reduction in the 'carrying capacity' of that range and a subsequent marked reduction in ungulate numbers. The probability that events involving abiotic environmental factor(s) may control a population before any density-dependent condition comes into play at a biologically meaningful level cannot be discounted out of hand. Given our current knowledge, it is just as likely that any preemptive action taken to reduce the number of ungulates in a population may not achieve the desired long-term results: more animals for a greater period of time. Based on this belief, we offer the following discourse in the hope that we can stimulate renewed debate and foster new ideas or at least firm up old ones.

Management of caribou or reindeer (*Rangifer tarandus* ssp.) especially on islands often involves two unfounded assumptions: first that a population will erupt and then crash; and second, that the crash will be density-dependent. The assumption that an erupting population crashes was not part of the original model for erupting populations of large mammalian herbivores (Riney, 1964; Caughley, 1970). The original model described the population dynamics of large herbivores colonising an area with abundant forage: the Himalayan thar (*Hemitragus jemlahicus*) a mountain goat introduced to the Southern Alps of New Zealand's South Island in 1904. Those colonising thar underwent an eruptive fluctuation which was "... a steady rise in numbers over at least two generations followed by a marked decline." (Caughley, 1970: 53). Caughley (1970) did not mention the term 'crash.' Herein, we arbitrarily define a crash as at least a 30% decrease in the estimated population size in 1 year. Although the trajectory of an increasing population is obviously restricted to the species' maximum rate of increase, the trajectory of a declining population has no such constraints.

The second assumption is that when an erupting herbivore population crashes, the crash is density-dependent or amplified by density-dependence. We comment on these two assumptions because they can lead to the presumption that to forestall a crash, we should reduce the herbivore's numbers by large-scale removals (translocation or cull). We do agree with the need for animal removals on some occasions, but we disagree with them when they are offered as a solution to a problem that is assumed rather than based on a careful examination of all pertinent data.

This commentary first offers an explanation for how these two assumptions for density-dependent crashes became incorporated in the erupting herbivore model and the consequences for management. Secondly, we propose that the erupting populations are a special case of a more general relationship between herbivores and their forage. We then argue that the ecologically sound conservation of herbivores (specifically caribou) depends on our developing a functional understanding of the role that environmental variation plays in herbivore-forage relationships.

The Erupting Population Model for Herbivores

Riney (1964) suggested that either established or introduced ungulates, when experiencing an abundance of food over time, erupt in a single oscillation. Caughley (1970) tested the validity of Riney's idea using thar introduced to New Zealand and graphically summarised his findings in his now classical 1970 paper. The thar populations went through increase, stabilisation and decrease phases with concomitant changes in adult female fecundity, juvenile survival, and fat reserves. A decrease in forage indexed by grass tussock size paralleled the thar population's stabilisation and decline.

The assumption that erupting populations crash is neither stated nor implied in the 'Riney-Caughley model.' As Caughley (1970) illustrated, the decline in thar density and other population parameters were shown as occurring over nearly a decade: a prolonged trajectory that he did not consider as a 'crash'. He reported that the decline was density-dependent: demographic rates declined as densities increased. He believed it was the rise in deaths and not fecundity changes that triggered the decline.

Yet, if most of us were to sketch the trajectory of an eruptive population, we would show an asymmetrical curve with a long period of increase followed by a rapid decrease usually described as a crash. The critical question becomes why or how this rapid decrease phase became perceived not just as a marked decline but also as a precipitous crash? A possible explanation is the axiom that a picture is worth a thousand words. Caughley (1970) reviewed the story of the Kaibab northern plateau deer herd and he graphically reconstructed the anecdotal evidence. His three graphs (Caughley, 1970: Fig. 1: 54-55) clearly shows an asymmetrical sequence of events-a relatively prolonged period with a high rate of increase followed by a relatively brief and sharp decline. When the text and figure captions are read, the reader should realise just what a speculative curve it is. However, such is the power of a clear figure: most of us remember the form of a graphical illustration better than its shaky basis in reality. Ironically and in contrast to

Caughley's (1970) Kaibab deer illustration, his graph of the introduced thar data is small, crowded and complex–thus it is much less memorable.

Two years before Caughley's (1970) paper, Klein (1968) produced his often referred to paper on the St. Matthew Island reindeer crash, a small island (332 km^2) in the north-central Bering Sea. In that paper, Klein (1968) also illustrated a similar asymmetrical pattern of a long period of increase and a sharp decline. Like the graphs for the Kaibab deer, the graph for the reindeer leaves a vivid and memorable impression.

We collectively may have locked our minds onto and generalised from those two clear graphical representations of the Kaibab deer and St. Matthew Island reindeer that erupting populations do not just decline--that is, the decline is so rapid as to be a crash. Two other related factors may have reinforced the impressions left by those graphs. First is the lack of information. Caughley (1970) commented that there was more information on the increasing phase than the decline of the thar and that holds as true today for other species, including the reindeer on St. Matthew Island. We know surprisingly little about population declines: they often go undetected or they are not detected until well underway. Also, if detected, it may be after the event is over. Most importantly the cause(s) of a decline often go undetermined or unrecorded, whether dispersal, shifts in age specific fecundity, mortality, or some combination of these. The decline phase of fluctuations is a continuum in rapidity and severity extending from minor losses, subtle and gradual (often imperceptible) to severe and rapid declines (crashes). A parallel is that year-to-year fluctuations in environmental conditions are not distinct from "catastrophes" which are large infrequent environmental perturbations. The scaling rules governing the trend of persistence on population size do not differ between year-to-year environmental fluctuations and catastrophes (Lande, 1993).

Reindeer numbers have crashed at least nine times on the seven Alaskan islands for which there is enough information to graph population trends for the introduced reindeer (Swanson & Barker, 1992). At least five of those crashes were during severe winters. For the four other crashes, it is unclear if they occurred during winter or what environmental circumstance brought on the crash. Thus even for the more conspicuous case of crashes, we are often handicapped as investigation into die-offs is often incomplete: carcasses are counted and sometimes necropsied but discrimination between ultimate and proximate cause(s) is often not explored. One exception is the description of a widespread drought in Australia. Some 40% of kangaroos (*Macropus* spp.) died mostly in 3 months (Caughley *et al.*, 1985). The death rate did not correlate with density, leading Caughley *et al.* (1985) to conclude that "Apparently the speed with which the drought intensified, muffled or overrode any effect of grazing on the rate at which the plant biomass declined."

A consequence of not having information about declines and crashes is that it demands that their causes be deduced by conjecture. This situation becomes even more complex because more than one factor may initiate or accelerate the decline. For example, the reindeer crash on St. Matthew Island had a separate cause which changed what otherwise might have been a prolonged decline of an erupted population (as on St. Paul Island, discussed below) rather than a 1-2 year crash. Two separate events may have happened simultaneously-but only one, severe weather, was necessary to cause the crash compared to a decline.

The second assumption that came to be incorporated into the 'Riney-Caughley' erupting herbivore model is that a crash is density-dependent. The original model did, of course, have a density-dependent decline phase, at least its initiation did. To assume that a crash will be density-dependent seems, at first, to be reasonable. Again, with St. Matthew Island reindeer, Klein (1968) appeared to give credence to the idea that a severe winter's effect was density-dependent based on high reindeer densities and depleted lichen stands-but he did not demonstrate competition for forage. The role of other factors beside forage competition in reducing body weight and juvenile survival preceding the crash were not ruled out. A run of unfavourable weather could have the same effect as too many animals. The evidence for forage shortage depended mostly on observations that reindeer had eaten and trampled the lichens. Sedges and grasses had replaced the lichens. But now we have more evidence that caribou are plastic in their foraging and that lichens are not essential winter forage (discussed further in Section 2). In other words, the assumption of density dependence was reasonable but it was not rigorously tested.

A contrast to the rapid crash of reindeer on St. Matthew Island comes from the earlier introduction of reindeer to St. Paul Island (ca. 400 km NE from St. Matthew Island) (Figs. 1, 2). The pattern of decline on St. Matthew and St. Paul was outstandingly different. In 1911, 25 reindeer were introduced to St. Paul Island; they increased to 2046 animals or 19.1 reindeer • km^{-2} by 1938; then declined to only 8 animals in 1950 (Fig. 1: Scheffer, 1951). Consideration solely of the relative number of reindeer on each island at the start of their respective decline period can be some-

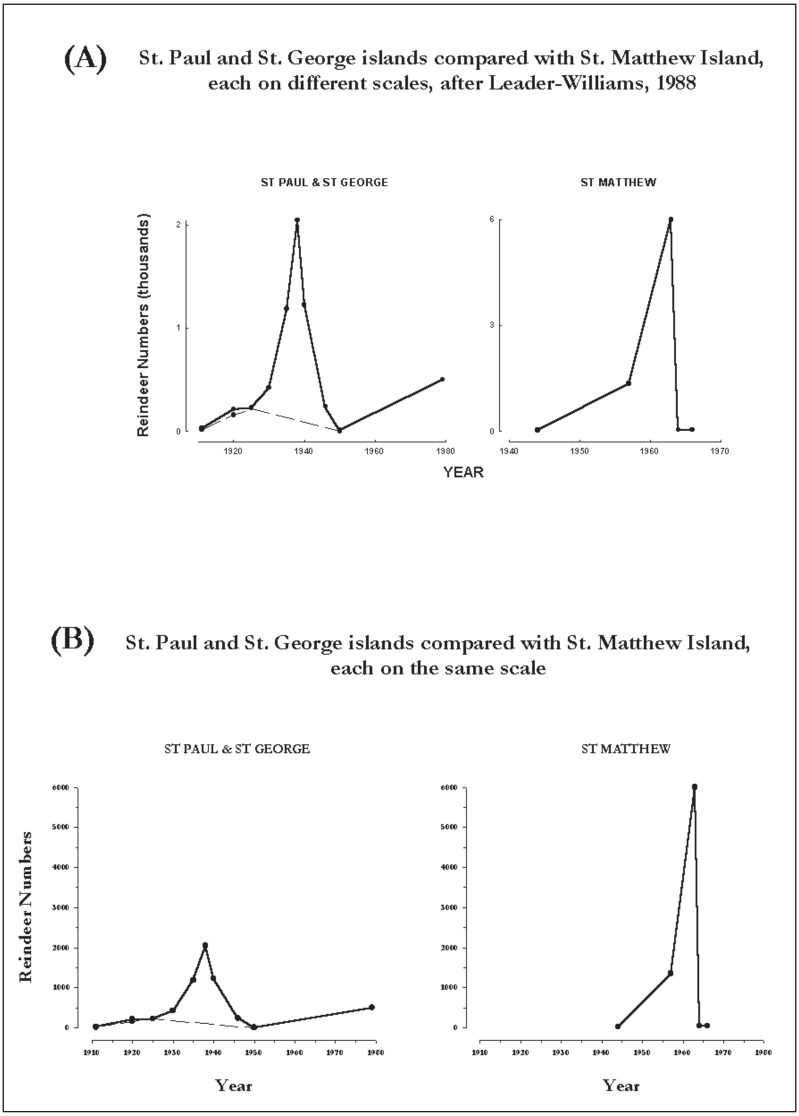

Fig. 1. (A) An example from Leader-Williams (1988) of three data sets in two graphs that are visually distorted in their presentation by the use of different scales presented on axes of equal length, (B) the same three data sets presented in the same graphs but with equal scales to more clearly show the distinctions among the three.

what misleading in terms of the possible pressures exerted on each range (6000, St. Matthew Island *vs.* 2046, St. Paul Island). Examining mean densities for reindeer on St. Matthew Island *vs.* those on St. Paul Island during their respective crash and decline helps to clarify this point (18.1 reindeer • km^{-2} *vs.* 19.1 reindeer • km^{-2}, Fig. 2). The maximum mean density of reindeer on St. Paul Island slightly exceeded that on St. Matthew Island, and in this respect, the magnitude of the subsequent decline on each island was essentially the same (Fig. 2). However, the St. Paul Island reindeer population took 12 yr to decline to a remnant population; whereas, the St. Matthew Island reindeer population supposedly crashed to that level in only 1 yr or possibly 2 yr at the most (Fig. 2). The pattern of annual die-offs on St. Paul Island during the 12-yr period was highly variable and appeared to follow no set pattern of density-dependence. In the first year of the 12-yr decline (1938-39), the St. Paul reindeer population was at 19.1 reindeer • km^2 but declined only <7%. Then, in 1939-40, when at 17.8 reindeer • km^{-2}, it fell a further 36%. In the third year (1940-41), however, when at 11.5 reindeer • km^{-2}, it declined only 4%. No data were obtained during the War Years but 6 yr later in 1947 the estimated 250 reindeer indicated that the population had to have declined at an average annual rate of about 23% (from 11.0 to 2.3 reindeer • km^{-2}). Then, for unknown reasons, for the last 3 yr, 1948-50, when at only 1.1 to <0.1 reindeer • km^{-2}, the population plummeted at an average annual rate of 68%. The level of annual mortality did not consistently correlate with the then prevailing annual density of reindeer on St. Paul Island. Only one annual crash occurred while the reindeer were at a high mean density. In contrast, three consecutive annual crashes occurred at the end of the overall period of decline–in years when the reindeer were at low to exceptionally low mean densities.

Thus, on a proportional basis, the St. Paul Island reindeer population experienced greater annual losses at low densities that it did at high densities and the annual severity fluctuated back and forth markedly.

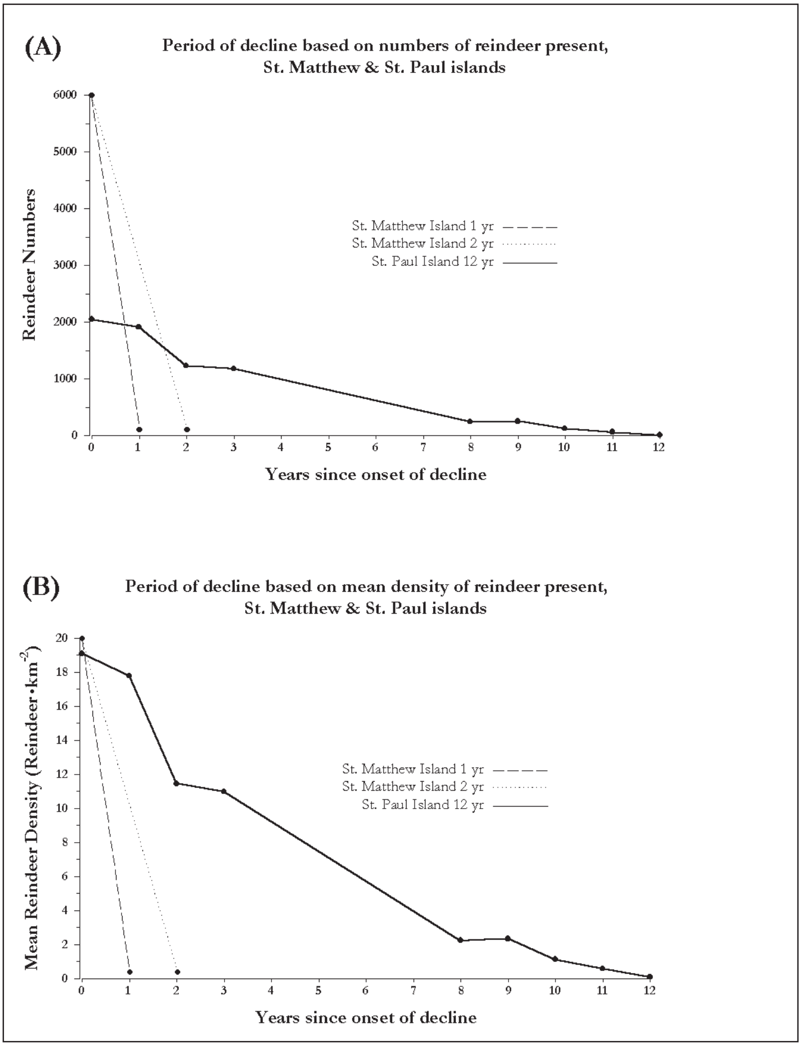

Fig. 2. Comparison of the period of decline for the reindeer population on St. Matthew and St. Paul islands (A) by number of reindeer present on each island and (B) by mean density of reindeer present on each island.

The pattern and duration of the 12-yr decline period suggests that abiotic factors (*i.e.*, snow and, more likely, ice: see Scheffer, 1951) were affecting the relative availability of forage, which perpetuated the continual decline even at low reindeer densities. It appears that die-offs in only 4 of the 12 yr were severe enough to be correctly labeled crashes and, most importantly, the 3 most severe crashes occurred when the reindeer were at their lowest mean densities during the 12 yr. Also, that the overall decline stagnated for at least 2 yr immediately prior to the last 3 yr of the greatest annual rates of decline adds considerable complexity to evaluating the period of reindeer die-offs on St. Paul Island. This is particularly true when attempting to compare the decline of the reindeer population on St. Paul Island to the very different abrupt crash of the reindeer population on St. Matthew Island.

Leader-Williams (1988: 28; Fig. 2.6), in his book on the introduction of reindeer to South Georgia, compared the declines of reindeer populations on Alaskan islands. His illustration creates a misleading visual impression similarity in the growth and decline periods for reindeer populations on St. Matthew and St Paul islands. In reality, the entire period of growth for the reindeer population on St. Paul Island was 42% longer than for reindeer population on St. Matthew Island (1911-38 *vs.* 1944-63). Most importantly, the average annual rate of population increase was 83% greater on St. Matthew Island than on St. Paul Island (λ=1.324 *vs.* λ=1.177). Seemingly, this visual shortcoming in Leader-Williams' (1988) comparison results from his effort to present both curves at different scales so that they could be formatted at about equal sizes in the side-by-side illustration (*e.g.*, Fig. 1A, herein). The reader should note in the direct comparison made by Leader-Williams (1988: 28; Fig. 2.6) that 1.27 cm on the horizontal axis for the St. Paul (and St. George) reindeer population, equals 20 yr, while for St. Matthew Island, 1.27 cm equals only 10 yr–a 100% difference in scale. At the same time, 1.90 cm on the vertical axis equals 1000 reindeer for St. Paul Island and 3000 reindeer for St. Matthew Island–a 300% or 3-fold difference in scale. These marked differences in scale could leave the impression that both declines were precipitous crashes that followed the same pattern and a similar duration (Fig. 1A). Not so, in fact the slope (intensity) of each decline was meaningfully different and that point is made clear when illustrated using the same scale for both populations for the number of reindeer in each population (Fig. 1B). This condition is particularly evident when the respective number of reindeer present and the mean densities of reindeer in each population during each overall period of decline are depicted both at the same scale and ratio of 'x' to 'y' axes (Fig. 2A, 2B).

The evidence for the role of extreme environmental variation in the crashes of caribou elsewhere other than the above Alaskan islands is stronger for Peary caribou (*R. t. pearyi*) and muskox (*Ovibos moschatus*) populations on Canadian High Arctic Islands (*e.g.*, Parker *et al.*, 1975; Miller *et al.*, 1977; Miller, 1998; Gunn & Dragon, 2002; Miller & Gunn, in press). Those crashes coincided with abiotic factors; exceptionally severe snow and ice conditions; and suggest that density-dependence and high animal densities are not prerequisite conditions to a population crash. Some of the most severe crashes occurred at excessively low caribou densities on Bathurst Island, south-central Queen Elizabeth Islands. The evidence for the primary effect of the weather is overwhelming, however, we cannot completely exclude any secondary density-dependent effects caused by intraspecific competition during the temporary period of severe relative forage unavailability caused by the extreme snow and ice conditions.

Ungulates are exposed to an array of biologically and ecologically different environmental conditions which are intrinsic to each region or ecosystem. Therefore, it seems simplistic to believe that every population's subsequent performance and fate will follow a singular pattern with only one paramount factor driving and ultimately dictating an inevitable outcome. The relative importance of unpredictable abiotic factors in influencing and causing intricate variation in the response of ungulate populations should not be ignored by the investigator, no matter whether those factors are sporadic or periodic. The variation in intensity of response can be exhibited in a variety of unfolding patterns and will be subject to both spatial and temporal considerations.

Management Consequences of Changes in the Erupting Herbivore Model

The legacy of St. Matthew Island reindeer (Klein, 1968) and the impressions left by Caughley's (1970) graphs to wildlife managers is that erupting herbivore populations will crash and that the crash will be density-dependent. Wildlife managers tend to judge that crashes are a bad thing and thus should be avoided by drastic density reductions. Such logic is offered to justify the removal or proposed removal of reindeer from Alaskan islands such as Adak (U.S. Department of Interior and State of Alaska, 1994) and Hagemeister (Stimmelmayr, 1994). Other examples in the Canadian Arctic were the justifications offered for increased commercial hunting of caribou reintroduced to Southampton Island (Heard & Ouellet, 1994) and muskoxen on Banks Island (Gunn *et al.*, 1989a, 1991).

Associated with the judgement that managers should intervene to forestall crashes is also the logic to intervene to prevent 'damage' to ranges especially lichen ranges. The rationale for assuming that there were too many reindeer on St. Matthew Island was mainly derived from the grazing and trampling damage to the lichens. At that time, lichens were believed to indicate 'good' winter range although subsequently, Skoog (1968) and Bergerud (1974) suggested that lichens are not essential for caribou winter diet. A recent example comes from Svalbard reindeer *R. t. platyrhynchus* repatriated to a Svalbard Peninsula (Staaland *et al.*, 1991). After 10 years the reindeer had shifted their foraging to more plant communities and a greater intake of mosses. The loss of highly preferred lichens did not affect productivity or survival as both were high. However, more frequently, lichens dominate mainland caribou winter diets and recently, Gaare (1997) has argued that, over the long term, periodic over-grazing of fruticose lichens is necessary to maintain the lichen productivity.

However, the perception that lichens are essential winter forage persists. Range evaluation on several Alaskan islands focused on lichen communities and recommendations were to reduce the reindeer to prevent them dying during winter and to protect the lichens. For example, Swanson & LaPlant (1987) and Swanson & Barker (1992) recommended from a lichen range survey in 1986 that the reindeer be reduced on Hagemeister Island. This was not done and the reindeer continued to increase until the 1991-92 winter when about 300 reindeer starved and died (Stimmelmayr, 1994). But it was mostly adult bulls that died during a winter when snowfall was exceptionally heavy (Stimmelmayr, 1994). Proportionally greater winter and spring mortality among caribou and muskox bulls who apparently have exhausted their body reserves during the rut is known elsewhere (*e.g.*, Leader-Williams, 1988; Gunn *et al.*, 1989b). Productivity and calf survival on Hagemeister Island remained high and the reindeer were in good condition. Despite the lack of evidence for a density-dependent die-off other than reduced lichens (Stimmelmayr, 1994), 750 reindeer were shot and

120 were translocated in November 1992 to allow recovery of the lichen ranges.

The apparent problem of too many animals has confronted wildlife managers elsewhere and lead to similar tactics when calls are made to drastically reduce the herbivore numbers. There are "islands" of another type-those created by national parks and other isolated habitat patches. A review by Caughley, (1981a) found a prevalence of value judgements rather than technical judgements were justifying management actions, which were usually in the form of population reductions (culls). Culls are a common answer to an erupting population which has reached the size where it is considered an 'overpopulation.' The justification for the reduction is, as argued above, based on the assumption that a density-dependent crash will ensue if nothing is done. This prediction goes untested: to quote from Caughley (1981a: 14), "Most treatments of overpopulation are justified by a dire prediction of what might have happened had the treatment been withheld. A more convincing case would be made by demonstrating that the effects of untreated overabundance are irreversible."

The erupting herbivore model as a special case of herbivore dynamics

We collectively may have a bias in seeing the relatively simple case of an island with many herbivores and the threat of their subsequent decline as a specific problem rather than part of a longer-term and more widespread pattern of herbivore-forage relationships. Increasingly, population data and theoretical models argue that large mammalian herbivores rarely attain numerical stability and that fluctuations are to be expected (*e.g.*, Caughley & Gunn, 1993; Behnke, 2000). Extreme fluctuations in abundance of caribou coupled with the unpredictable variability in arctic climate suggest that the Arctic is a 'non-equilibrium system' where "Biotic activity is regulated by a sporadic abiotic variable [or variables]." (Behnke, 2000: 145). This non-equilibrium system seems especially applicable to caribou on the Arctic Islands where productivity and population size will be dictated by abiotic perturbations-caused by annual variation in snow and ice conditions.

The arctic climate is characterised by unpredictable annual variability–*e.g.*, coefficients of variation for annual snowfall are 25-50%. Snowfall is often only indirectly related to snow cover (wind and temperature interact with topography and vegetation) but like snowfall, snow cover is highly variable. Maximum and minimum values for annual maximum snow cover can be ±75% of the mean value (Maxwell, 1980). Correspondingly, the length of the plant growing season and conditions for plant growth can be and often are annually variable at consequential levels.

Fluctuations in caribou and muskox numbers on the Canadian High Arctic Islands encompass annual crashes of 30-90% which are interspersed with variable but usually relatively long periods of recovery (*e.g.*, Parker *et al.*, 1975; Miller *et al.* 1977, Gates *et al.* 1986, Miller 1998, Gunn & Dragon, 2002). The most complete data set is for Bathurst Island. Hundreds of caribou died (nearly 3000 in total) during four winter and spring periods which were four of the five most severe on record (1973-74, 1994-95, 1995-96 and 1996-97). Snowfall was at or approaching twice the long-term average and extensive ice formed over the vegetation as a result of warm temperatures and high winds in both autumn and spring (Miller *et al.*, 1977; Miller, 1998). In the 5th of those 5 years, 1989-90, no increased mortality of 1+ yr-old caribou was detected but the calf crop was still reduced by 40%. Caribou numbers declined from an estimated 3000 in summer 1994 to fewer than 100 animals in summer 1997 (Miller, 1998; Gunn & Dragon, 2002). In each of the four summers before the die-offs began (1991-94), the percentages of calves were consistently high, indicating that the forage supply was adequate for the cows to achieve sufficient body condition to conceive and to successfully produce and rear their calves. Measurements of plant biomass on Bathurst Island in 1998 and empirical data obtained in 15 summers between 1974 and 1998 also provide no evidence of any forage depletion. High rates of death were also recorded for muskoxen across the entire western Queen Elizabeth Islands in 1973-74 and during 1994-97. The islands are linked by sea-ice but only a small proportion of Peary caribou and muskoxen make long-distance movements during times of forage unavailability (summarised in Gunn & Dragon, 2002). Only extreme environmental episodes (such as excessively severe winter and spring weather) could likely cause such a degree of spatially and temporally correlated deaths in two species with markedly different seasonal and annual site-use patterns on the same range.

Caughley & Gunn (1993) concluded "that long-term aperiodic fluctuations characteristic of such systems are ... a mathematical consequence of unpredictable short-term fluctuations in weather." Thus, a major die-off would not be an aberration and the four phases of erupting populations are repeated at varying amplitudes as the population is buffeted by the environment. Therefore, managers of ungulate populations within such systems should have reservations about the classical concepts of 'carrying capacity' and 'sustained yield.'

Still imbedded in herbivore management is, however, the often unspoken notion that fluctuations are an aberration to be avoided, even though variation is the norm. And some wildlife biologists are still recommending culls. For example, "In fact, planned extirpation of some sub-populations on depleted winter ranges could be a management tool allowing the recovery of forage resources and reintroduction of caribou sooner rather than later...." (Ferguson 1996: 251). This proposed management prescription for "planned extirpation" is based on supposition and information from high-density caribou and reindeer populations in other ecosystems. Of particular concern to us, this proposed cull for caribou on arctic islands was recommended without requiring on-site evidence for "depleted winter range" at any scale. And, apparently, without considering the amount of forage that would be required per unit area by 40-50 Peary caribou on islands 15 000 km^2 or more in size or the freedom for possible movement between or among islands for 9-10 months of each year. In addition, the potential prescription is presented without any consideration given to on-site data for the causes of known major die-offs or the measurement of forage biomass after those die-offs (*e.g.*, Miller *et al.*, 1977; Miller, 1998; Thomas *et al.*, 1999; Gunn & Dragon, 2002). In such a non-equilibrium system the guiding principle should be the maintenance of maximal numbers of caribou to promote the maximum number of individuals that would survive an annual die-off episode caused by density-independent abiotic factor(s).

We have three concerns with the suggestion of culls or 'planned extirpations'. Firstly, culls may or may not avert a decline. Culling success will depend on whether or not there is a stochastic event whose effects are severe regardless of the abundance of animals, or otherwise, of the forage. The occurrence of such events will be independent of the state of the population and related to environmental variability (*e.g.*, Caughley & Gunn, 1993; Behnke, 2000).

Secondly, culls, apart from running the risk of being based on faulty assumptions, are in themselves, a major perturbation with ecological consequences often lost in the initial decision to cull. Caughley (1981a) listed six possible ecological mechanisms whereby the herbivore-forage dynamics can be upset, resulting in a less resilient and a more unstable system after drastically reducing a herbivore population. The plants too may respond unpredictably as environmental variability may cause abrupt switches in plant responses to grazing (Noy-Meir 1981). Klein (1987) and Walker (1993) describe grazed vegetation not returning to its relatively pristine state after prolonged grazing by large herbivores even after their subsequent die-off or removal.

Our third concern with culling arctic ungulates is that this is an attempt to regulate caribou and muskox numbers with regard to their absolute forage supply. This approach arises from considering that the arctic is an equilibrium system. We need to recognise the difference in guiding principals between equilibrium and non-equilibrium systems: respectively, reducing animal numbers before a density-dependent event as opposed to maximising numbers before a density-independent event. Therefore, we need to reconsider management interventions, including harvesting strategies, in accordance with the environmental forces controlling a non-equilibrial system. A first step toward understanding relationships in a non-equilibrium system is to determine how annual variation in weather affects forage before we become overly worried about the effects of predation and competitors. Caughley's (1981b: 361) words still ring true–"Until we understand the dynamics of the most simple of natural ecological systems that include animals - a simple herbivore population feeding on a simple supply of vegetation - we are unlikely to get far with a more complicated system that includes predators and competing herbivores. And yet we know very little about the simple system."

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