APPLICATION OF POPULATION VIABILITY THEORY TO MOOSE IN MAINLAND NOVA SCOTIA

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ABSTRACT: Populations of moose (*Alces alces americana*) in mainland Nova Scotia, Canada, have been reduced to approximately 1,000 individuals fragmented into a number of isolated populations. Although the data required for a comprehensive population viability assessment (PVA) are not currently available, there are some general rules concerning minimum viable population (MVP) size that may be applied for a preliminary assessment. Genetic evidence suggests that, in general, a genetically effective population (N_e) of 50 individuals is required for short-term persistence and 500 to 5,000 individuals are required for long-term survival. Census population size (N) is generally larger than N_e, and a 10:1 relationship between N and N_e has been roughly established in moose populations elsewhere. Given this relationship, $N = 5{,}000$ individuals may be required for long-term viability. Based on current home range size (30-55 km^2) and population density (0.05/km^2), the minimum critical area required by a population of this size is estimated to be approximately 100,000-200,000 km^2. Strategies for moose conservation and forest management should concentrate on (1) conducting genetic, population, and habitat analyses to increase understanding of population viability and limiting factors; (2) reestablishing connectedness among discrete populations to form a viable metapopulation; (3) protecting/enhancing habitat to meet the critical requirements of a viable population; and (4) increasing carrying capacity of available habitat to support a greater population density.

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Prior to European colonization, moose were widely distributed and abundant throughout mainland Nova Scotia (Pulsifer and Nette 1995). However, only a few small and isolated populations currently remain (Fig. 1) and little is known about their status. There are approximately 500 individuals in the Cobequid Highlands, 300 in the southwestern portion of the province, and scattered pockets elsewhere (A.L. Nette, Nova Scotia Department of Natural Resources, personal communication). Because the total population is ≤ 1,000 individuals, moose are considered to be at risk of extirpation in mainland Nova Scotia (CESCC 2001). Because small and isolated populations are more likely to become extinct than large populations (Diamond 1976, Terborgh and Winter 1980, Shaffer 1981, Henriksen 1997), it is important to address the viability of these moose populations.

POPULATION VIABILITY

A viable population is one that will continue to exist and to function naturally so that, over the long term, reproductive rates remain higher than or equal to rates of loss (Salwasser et al. 1984, Newmark 1985). The minimum viable population (MVP) is the population size below which the probability of extinction is unacceptably high,

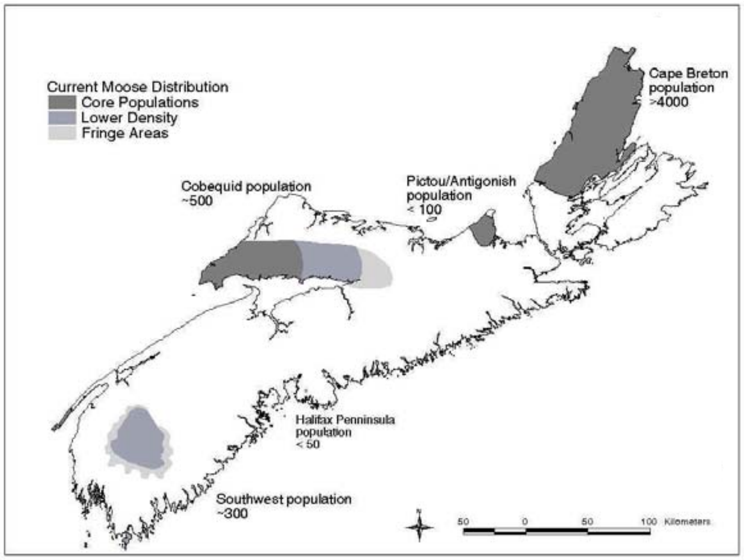

Fig. 1. Current distribution of moose in Nova Scotia [figure adapted from Snaith and Beazley (2002)].

but at or above which the probability of extinction is reduced to an acceptable level over a given period of time (Shaffer 1981, Samson 1983, Lehmkhul 1984, Gilpin and Soulé 1986, Lacy 1993/94, Henriksen 1997). Population viability requires maintenance of enough individuals to form an effective breeding population. Extinction, demographic, environmental, and spatial factors are among the factors that influence population viability.

Effective Population Size

The effective population *(N_e)* is that portion of the actual or census population (*N*) that represents a genetically ideal population (Brussard 1985, Samson et al. 1985). In a genetically ideal population, all individuals are breeding adults, individuals mate at random, generations do not overlap, sex ratio is equal, reproductive success does not vary among individuals, there is no migration, mutation, or selection, and all individuals contribute equally to the genetic variation of the next generation. Formally defined, N_e is the size of a genetically ideal population that has the same rate of inbreeding or loss of genetic diversity through genetic drift as the real population being considered (Franklin 1980, Brussard 1985, Reed et al. 1986).

N_e is almost always smaller than the actual population size (*N*) due to demographic and genetic factors that represent a departure from the genetically ideal population, such as the presence of non-breeding individuals (Brussard 1985, Newmark 1985, Samson et al.1985, Henriksen 1997). Empirical determination of N_e is difficult and data-intensive because sex ratio, age structure, reproductive behaviour, variability in reproductive success, dispersal patterns, and population fluctuations must be known (Soulé 1980, Brussard 1985, Nunney and Elam 1994).

Very few studies have attempted to quantify the relationship of *N* to N_e for moose. Using a computer simulation model to predict N_e under a variety of harvest management options, Ryman et al. (1981) estimated that, for moose, N_e was approximately 5% to 20% of actual population size. Arsenault (2000) theoretically determined that, based on local average population structure, N_e was 8.5% of N. Taken together, these studies suggest that a 10:1 relationship between N and N_e may be conservatively applied as a preliminary general rule for moose populations.

Extinction Factors

A population's ability to survive depends on three characteristics: resilience, fitness, and adaptability (Soulé 1980, Salwasser et al. 1984, Brussard 1985, Reed et al. 1986). Resilience is the short-term ability of a population to persist, despite normal reproductive fluctuations. Fitness is the ability to cope with prevailing environmental conditions, and depends on the retention of sufficient genetic variability to avoid inbreeding depression and genetic drift over the short- to mid-term (decades). Adaptability is necessary for the long-term persistence of a population and involves the ability to evolve. The capacity to adjust to environmental change depends on the maintenance of enough genetic variability to accommodate the evolutionary process of natural selection and to respond to a variety of demographic, environmental, genetic, and spatial extinction factors (Terborgh and Winter 1980, Shaffer 1981, Brussard 1985, Newmark 1985, Samson et al. 1985, Gilpin and Soulé 1986).

Demographic factors.—Demographic stochasticity refers to random fluctuations in population parameters, such as birth-rate or mortality, which influence the probability of extinction over time (Shaffer 1981, Samson 1983, Brussard 1985, Theberge 1993). Stochastic variations of population processes are more likely to lead to extinction in small populations because the effects of random fluctuations are amplified (Shaffer 1981, Samson 1983, Brussard 1985, Boyce 1992, Theberge 1993, Henriksen 1997). Small populations are also prone to the Allee effect (Allee 1931), whereby very low populations experience decreasing reproductive rates (Henriksen 1997, Reed et al. 1998). Although little information is available regarding the population structure among mainland Nova Scotia moose, demographic factors may be important considerations due to the small and fragmented nature of the populations that currently persist at very low densities [approx. 0.05/km^2 (Pulsifer and Nette 1995)].

Environmental factors.— Environmental factors which affect population demographics include characteristics of the physical environment, populations of other species, and human activity. Deterministic, or long-term systemic factors, such as habitat destruction, climate change, and environmental variation through time and space create variation in habitat carrying capacity and thereby influence population size, persistence, and probability of extinction (Shaffer 1981, Samson 1983, Salwasser et al. 1984, Samson et al. 1985, Lacy 1993/94, Theberge 1993, Henriksen 1997). Environmental stochasticity refers to random environmental events that affect all individuals in a population (Shaffer 1981, Samson 1983, Brussard 1985, Samson et al. 1985, Gilpin and Soulé 1986, Mangel and Tier 1993, Henriksen 1997). For example, randomly fluctuating food availability, climatic conditions, competition, disease, predation, or hunting can lead to population-wide changes in mortality or reproductive success. In situations where environmental stochasticity is frequent or severe, only large populations will have reasonable probabilities of survival.

The Nova Scotia moose herd has been reduced due to a number of environmental factors including habitat reduction and fragmentation; hunting and poaching; interspecific competition with white-tailed deer (*Odocoileus virginianus*); black bear (*Ursus americanus*) predation; and disease caused by environmental contamination, brainworm (*Parelaphostrongylus* *tenuis*), and the winter tick (*Dermacentor albipictus*) (Dodds 1963, Pulsifer and Nette 1995, Snaith and Beazley 2004). Because the remnant populations are small, isolated, and restricted to small fragments of suitable habitat, they are increasingly at risk of extirpation due to environmental fluctuations. Moose are near the southern limit of their range in mainland Nova Scotia, and are potentially subject to further stress resulting from climate change (Peters and Darling 1985, Snaith and Beazley 2004).

Genetics.— Genetic variation is the key to population fitness, adaptability, and survival. In small populations, genetic drift and inbreeding reduce genetic variability and increase the probability of extinction (Franklin 1980, Soulé 1980, Shaffer 1981, Lehmkhul 1984, Salwasser et al. 1984, Newmark 1985, Samson et al. 1985, Gregorius 1991, Boyce 1992). Inbreeding depression is caused by the expression of deleterious genes and is associated with reduced fitness and reproductive success. Genetic drift refers to the random loss of heterozygosity (genetic variation) and can contribute to inbreeding depression, especially in chronically small populations.

Founder populations constrained to small numbers for short periods of time may not suffer the negative consequences of genetic drift and inbreeding depression provided that the population can subsequently expand in a relatively short period of time (Franklin 1980, Soulé 1980, Lehmkhul 1984). A population bottleneck will only have negative consequences if heterozygosity is lost, deleterious genes become fixed, and the population loses its ability to expand (Franklin 1980, Soulé 1980, Lehmkhul 1984). Some species, such as the northern elephant seal (*Mirounga angustirostris*) (Lehmkhul 1984), seem well adapted to low levels of genetic variation but may be susceptible to environmental fluctuations due to low adaptive potential (Soulé 1980, Lehmkhul 1984). The importance of genetic variation within natural populations is supported by genetic evidence indicating a positive relationship between heterozygosity and fitness (Soulé 1980). To maintain long-term viability, a population should be large enough to retain genetic variability and adaptability.

The population density and distribution of moose populations in mainland Nova Scotia have been significantly reduced from historic levels (Pulsifer and Nette 1995). Nonetheless, moose populations are adapted to maintaining low densities in sub-optimal habitat, and their reproductive potential may allow rapid population expansion when good habitat becomes available (Geist 1974, Timmermann and McNicol 1988). In a number of cases, where suitable habitat was readily available, moose populations have grown from very small founder populations into large, widely distributed populations (Kelsall 1987, Pulsifer 1995, Basquille and Thompson 1997, Wangersky 2000). Genetic evidence from Newfoundland and Cape Breton indicated that heterozygosity was reduced by 14% to 30% due to founder events (Broders et al.1999). Although there have been no known negative phenotypic consequences, and the populations evidently maintain enough genetic variability to persist for the short term, long-term viability may be compromised by limited adaptive potential due to this observed reduction in genetic variability (Broders et al. 1999). Similarly, genetic evidence indicated low heterozygosity among a Swedish moose population that suffered a bottleneck event but was subsequently able to expand rapidly (Ryman et al. 1977).

Evidence suggests that mainland Nova Scotia moose populations, although significantly reduced, possibly have the potential to expand if enough suitable habitat is restored, and other factors, such as disease or competition, are not limiting the populations.

However, given the lengthy period of population decline and constraint (at current levels for 20 to 70 years), it is possible that genetic drift and inbreeding have led to a decrease in heterozygosity and adaptive potential. Prolonging the small and isolated condition of moose populations in Nova Scotia is likely to further decrease their viability.

Spatial considerations.—Spatial factors, including habitat reduction and fragmentation, influence population structure and size, and may increase vulnerability to extinction by isolating and reducing populations. If total isolation does not occur, habitat fragmentation may force a continuous population to take on the structure of a metapopulation, where several distinct local populations are loosely associated by periodic exchange of individuals (Levins 1970, Wilson 1975, Caughley 1977, Fahrig and Merriam 1994, Fahrig and Grez 1996, Beissinger and Westphal 1998). In this situation, the deleterious effects of inbreeding and genetic drift can be compensated for by the addition of genetic variation from immigrants (one reproductively successful migrant per generation is required to maintain sufficient heterozygosity) while local divergence in response to environmental conditions may still occur (Soulé 1980, Brussard 1985, Reed et al. 1986, Beier 1993). When local populations become completely isolated, migration and gene flow become impossible, the metapopulation structure is lost, and overall N_e is reduced to that of the local populations (Brussard 1985, Gilpin 1991).

Mainland Nova Scotia currently supports scattered moose populations separated by distances of 200 to 300 km, areas of unsuitable habitat, and barriers such as a major highway system (Snaith 2001). As a result, it is unlikely that exchange of individuals occurs at an adequate rate for the herd to be an effective metapopulation (A.L. Nette, Nova Scotia Department of Natural Resources, personal communication). Therefore, for the purposes of viability considerations, each mainland population should be treated as a separate and isolated local population until connectivity, and thus genetic exchange, is reestablished.

POPULATION VIABILITY ANALYSIS

Population viability analysis (PVA) is a comprehensive approach used to determine MVP or to evaluate extinction probabilities (Lehmkhul 1984, Salwasser et al. 1984, Shaffer 1990, Boyce 1992, Lindenmayer et al. 1993, Theberge 1993, Lacy 1993/94, Reed et al. 1998). PVA and MVP estimates can be used to identify threatened populations and to quantitatively identify target population size for conservation efforts. Ideally, PVA is a species- and area-specific assessment that accounts for the demographic and genetic characteristics of the population in question, the quality and quantity of available habitat, and local environmental factors. Empirical evidence, model results, and genetic analyses seem collectively to indicate that for many species an effective population of less than 50 individuals will not persist beyond the short term, that 500 to 5,000 breeding individuals are required to ensure long-term adaptability and persistence, and that habitat considerations are of primary importance in determining the fate of populations (Franklin 1980; Soulé 1980; Shaffer 1981, 1983; Samson 1983; Brussard 1985; Samson et al. 1985; Lande 1987; Berger 1990; Thomas 1990; Henriksen 1997; Belovsky et al. 1999).

ESTIMATING MVP FOR MOOSE IN MAINLAND NOVA SCOTIA

The detailed demographic and genetic data required for a reliable PVA are currently not available for moose in Nova Scotia. However, given the current risk of extirpation, it is important to make some preliminary estimates. Thus, the general findings that an effective population of at least 50 individuals is required for short-term persistence, and 500 for the long-term, was used as a preliminary estimate of MVP (Franklin 1980, Soulé 1980, Shaffer 1981, Brussard 1985, Lande 1987, Berger 1990, Thomas 1990, Henriksen 1997, Beazley 1998). Assuming a 10:1 relationship between N and N_e (Ryman et al. 1981, Arsenault 2000), as previously described, $N_e = 500$ may require $N = 5{,}000$ individuals to ensure long-term persistence, and for short-term viability, $N_e = 50$ may require $N = 500$ individuals.

Currently, the total population of about 1,000 individuals, fragmented among isolated local populations, is likely too small to maintain long-term viability. Whether the current population maintains the ability to expand to the long-term MVP size is unclear. Nevertheless, 5,000 should be the minimum target population size for long-term conservation efforts.

There appear to be enough individuals in Nova Scotia to maintain viability over the short term. The current population in the Cobequid Hills ($N = 500$) should be large enough for short-term persistence. However, because the population has already been restricted to this size for 20 to 70 years (A. L. Nette, Nova Scotia Department of Natural Resources, personal communication), it is unclear how much longer the population level can be maintained, and it is likely that a significant amount of heterozygosity has been lost. For these reasons, and because other local populations do not reach $N_e = 50$ ($N = 500$) on their own, the reestablishment of connectivity among Nova Scotia moose populations is of primary importance over both the short and long term.

MINIMUM CRITICAL AREA

Minimum critical area (MCA) represents the minimum amount of suitable habitat required to support the population and is calculated based on the number of individuals and their area requirements or population density, and must also take into account the spatial distribution of suitable habitat (Soulé 1980, Shaffer 1981, Newmark 1985, Metzgar and Bader 1992, Theberge 1993, Doncaster et al. 1996, Arsenault 2000). MCA for moose in Nova Scotia might be calculated by multiplying population size and the area requirements (home range size) of each individual (Shaffer 1981, Newmark 1985, Theberge 1993, Doncaster et al. 1996, Beazley 1998). However, this method does not account for variation in home range size, overlap among individual ranges, or non-adjacent home ranges. Alternatively, MCA can be calculated based on dispersion by dividing population size by population density (Metzgar and Bader 1992, Theberge 1993, Arsenault 2000). This method accounts for overlap, but does not satisfactorily take into account density variation through space and absolute area requirements.

Because home range sizes, population density, and the degree of overlap among individual home ranges are poorly understood in Nova Scotia, it is not possible to calculate MCA reliably. However, a number of exploratory calculations can be performed using a variety of values for moose-area relationships based on currently available data (Table 1). When average population density estimates for mainland Nova Scotia are used for the calculation, a long-term MVP of 5,000 individuals requires 100,000 km^2 of suitable habitat. When the calculation is based on home range size, the same population requires 212,500 km^2. While the home range calculation is probably an overestimate because overlapping individual ranges are not accounted for, the estimate based on density is likely inaccurate because it assumes moose are continuously

Table 1. Exploratory calculations of minimum critical area (MCA).

Population Size (N)	MCA N x average HR[1]	MCA $N \div$ average density[2]
Short-term MVP		
$N = 500$, $N_e = 50$	21,250 km^2	10,000 km^2
Long-term MVP		
$N = 5000$, $N_e = 500$	212,500 km^2	100,000 km^2

[1] HR = 45 km^2 calculated as mean of HR = 55 km^2 from empirical studies in southwest Nova Scotia (based on figures from D. Brannen, Nova Scotia Department of Natural Resources, personal communication) and HR = 30 km^2 in habitat similar to northeast Nova Scotia (Dunn 1976; Crossley and Gilbert 1983; Crête 1987; Leptich and Gilbert 1989; McNicol 1990).

[2] density = 0.05/ km^2 (mean of 0.01 to 0.09 from Pulsifer and Nette 1995).

and evenly distributed. Actual MCA may be somewhere between these estimates. By the same calculations, the short-term MVP (N = 500) requires 10,000 to 21,250 km^2 of habitat under current conditions.

The preceding calculations of MCA rely on current home range and density estimates, which are dependent on local habitat quality, carrying capacity and demographic factors. Implicit is the assumption that a larger population will require more area of the same quality than a smaller population. However, the current population density is very low due to a variety of factors including disease, overharvesting, predation, and poor habitat suitability (Dodds 1963, Pulsifer and Nette 1995, Snaith and Beazley 2004, Snaith et al. 2002). If carrying capacity/population density could be increased, then MCA requirements would become smaller.

MANAGEMENT RECOMMENDATIONS

Given current habitat conditions and population densities, these preliminary estimates indicate that a census population of 5,000 moose and 100,000 to 200,000 km^2 of habitat are required for long-term viability. Currently, there are no more than 1,000 moose, and the total land area of mainland Nova Scotia is approximately 45,000 km^2, of which only a small portion is good quality moose habitat (Snaith et al. 2002). Based on these figures, mainland Nova Scotia does not currently support a moose population large enough to persist for the long-term, nor does it contain enough habitat to support such a population in isolation. However, there likely are enough moose to persist for the short term, providing appropriate protection and management actions are taken.

To ensure the persistence of moose in Nova Scotia, short-term conservation efforts should concentrate on the maintenance of sufficient critical habitat (10,000 to 20,000 km^2) of suitable quality to maintain current populations and to prevent further declines. For long-term viability, population size, and thus the extent and/or quality of habitat, must increase. Habitat connectivity must be reestablished among local populations to allow migration and genetic exchange, which will boost the provincial effective population size to that of the metapopulation. Restoration and enhancement of historical connections to populations in New Brunswick may also be required for long-term viability. This strategy will be particularly important if population levels in Nova Scotia cannot reach the target for long-term MVP on their own.

Preliminary habitat suitability analyses indicate that there is little optimal moose habitat in the province, and that road density is an important factor in determining moose location (Snaith et al. 2002). Areas currently occupied by moose populations represent priority areas for protection, along with areas of high suitability and areas with few or no roads. Empirical research is required to refine habitat suitability assessments (Snaith et al. 2002), to establish the carrying capacity of existing habitat, to identify measures that can be used to increase habitat quality, and identify areas with potential for restoration.

In addition to habitat protection and management, mortality factors and population processes unrelated to habitat must also be investigated. Current moose population densities are at an historical low in Nova Scotia and are among the lowest documented worldwide (Pulsifer and Nette 1995, Snaith and Beazley 2004). A wide range of factors has been invoked as the cause for this drastic decline. Research is required to conclusively identify the cause(s) of the decline, to isolate current limiting factors, and to design appropriate strategies for recovery. If factors limiting the population can be controlled, it may be possible to increase moose density within Nova Scotia, thereby reducing the total area required by a viable population.

Given the long period of population decline and restriction, local populations may be at risk of inbreeding depression, genetic drift, or extirpation. Genetic research is required to determine N_e and the level of heterozygosity that remains among local populations. Until habitat connectivity among local populations can be achieved, direct population management such as the translocation of individuals among populations (or from New Brunswick, providing genetic evidence is available suggesting that the populations are of the same stock) may be required. Artificial movement of animals at the rate of one reproductively successful individual per generation should preserve sufficient genetic variability in local populations to maintain genetic fitness and expansion potential (Soulé 1980, Brussard 1985, Reed et al. 1986, Beier 1993). Although this type of management is invasive and expensive, it may prove necessary if adaptability is low among Nova Scotia moose populations.

In summary, strategies for moose conservation and landscape management should concentrate on genetic, population, and habitat analyses; the protection and enhancement of habitat to meet the critical requirements of viable moose populations; and the reestablishment of connectedness among discrete populations. Given that the area required for the long-term persistence of a viable moose population may be greater than the total size of mainland Nova Scotia, and appreciating the variability of habitat suitability across the landscape, these figures suggest that the long-term viability of moose in Nova Scotia will require increased carrying capacity of available habitat, increased population density, and enhanced/restored habitat connectivity to New Brunswick.

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