DEMOGRAPHY AND SUSTAINABLE HARVEST RATES OF LOW-DENSITY MOOSE IN NORTHERN BRITISH COLUMBIA

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ABSTRACT: Numerous moose (*Alces alces*) populations throughout Alaska, Yukon, and the Northwest Territories occur at low-density, a condition that often persists for decades and is referred to as a low-density equilibrium (LDE). The demographic conditions for these populations include low-density (≤ 0.4 moose/km^2), low annual recruitment of calves (~ 0.25 calves/cow), and static population growth ($\lambda \sim 1.00$). I used data from aerial surveys and hunter harvest surveys to assess if these conditions applied to 4 moose populations in northern British Columbia, Canada over a 20-year period from 1996/97–2015/16. All populations exhibited low-density, low recruitment, and static growth suggesting that moose in this part of the province exist within a LDE state. Harvest and moose densities were positively related. Harvest rates from survey data ranged from 2.4–3.2% of the total population and 6.1–10.5% of the bull population. A stochastic model was used to estimate sustainable harvest rates defined as rates where the harvest risk was ≤ 10% probability that the post-hunt bull:cow ratio dropped below a given adult sex ratio threshold after 50 years of harvest. Sustainable harvest rates averaged ≤ 2.4% of the total population or ≤ 8.4% of the bull population with 0.50 bulls/cow as the threshold, ≤ 3.2% of the population or ≤ 13.0% of bulls with 0.40 bulls/cow as the threshold, and ≤ 4.1% of the population or ≤ 20.4% of bulls with 0.30 bulls/cow as the threshold. Modelling indicated that even small changes in harvest rates could greatly affect the probability of bull:cow ratios dropping below adult sex ratio thresholds. Research focussed on specific factors contributing to low moose density and increased population survey effort should improve estimates of sustainable harvest rates and management of moose in northern British Columbia.

ALCES VOL. 58: 101–112 (2022)

Key words: adult sex ratio threshold, *Alces alces*, bull:cow ratio, calf recruitment, demography, low-density equilibrium, moose, predation, sustainable harvest rate

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Numerous moose (*Alces alces*) populations throughout Alaska, Yukon, and the Northwest Territories occur at low-density (≤ 0.4 moose/km^2) in a state often referred to as a low-density equilibrium (LDE) or low-density dynamic equilibrium (LDDE), that may persist for decades (Bergerud 1992, Gasaway et al. 1992, Stenhouse et al. 1995, Lake et al. 2013, Joly 2017). In this state, body condition, productivity, and survival of adult moose are relatively high and sufficient to allow population growth. However, the population does not increase because wolf (*Canis lupus*) and bear (*Ursus* spp.) predation limit calf recruitment. Harvest is typically restricted to bull-only to prevent further decline in these predator-prey systems (Gasaway et al. 1992). Bergerud (1992) hypothesized that for each low-density population there is also a stabilizing recruitment of calves (*Rs*) where the growth rate is static. In unhunted or lightly hunted moose populations *Rs* ~ 0.25 calves/cow (Bergerud 1992, Bergerud and Elliott 1998). Messier (1994) modelled moose-wolf interactions over a broad spectrum of moose densities in North America and predicted that moose would stabilize at ~ 2.0 moose/km^2 in the absence of predation and at ~ 1.3 moose/km^2 in the presence of wolves. However, if moose productivity was diminished through deteriorating habitat quality or bear predation on calves, then a LDE (0.2–0.4 moose/km^2) was predicted. These demographic conditions for LDE populations have received general support from additional reviews on the effects of predation on moose numbers (Van Ballenberghe and Ballard 1994, Ballard and Van Ballenberghe 1997, Van Ballenberghe and Ballard 1997).

Hatter (1999) reviewed moose harvest management in central and northern British Columbia and suggested that the demography of 4 northern moose populations adjacent to Yukon and the Northwest Territories may exist in a LDE state, and that sustainable harvest rates may be substantially lower than in higher density populations in central British Columbia. The objectives of this analysis were to: 1) assess if the demographic conditions for LDE populations (i.e., low-density [≤ 0.4 moose/km2], low calf recruitment [R ~ 0.25 calves/cow], and static population growth [λ ~ 1.0)]) applied to these 4 populations from 1996/97–2015/16; 2) estimate average harvest rates for each population based on survey and harvest densities during this 20-year period; and 3) determine sustainable harvest rates for moose existing in a LDE state based on a stochastic demographic model.

STUDY AREA

The study area included Game Management Zones (GMZ) 6f, 6e, 7Pd, and 7Pe in northern British Columbia, Canada (Fig. 1). GMZs are amalgamations of adjacent Wildlife Management Units which share similar ecological characteristics and hunter harvest patterns, and thus provide a suitable framework for assessing moose demography and harvest rates over large geographical areas (Hatter 1999, Kuzyk et al. 2018). GMZs 6f, 6e, 7Pd, and 7Pe comprised 29,256 km^2, 44,587 km^2, 38,330 km^2, and 61,204 km^2 of habitable moose range, respectively. Six moose ecotypes have been identified in British Columbia based on ecological, climatic, and physiographic differences in their habitats (Eastman and Ritcey 1987). The Boreal Upland ecotype occupies GMZs 6f, 6e, and 7Pd while the

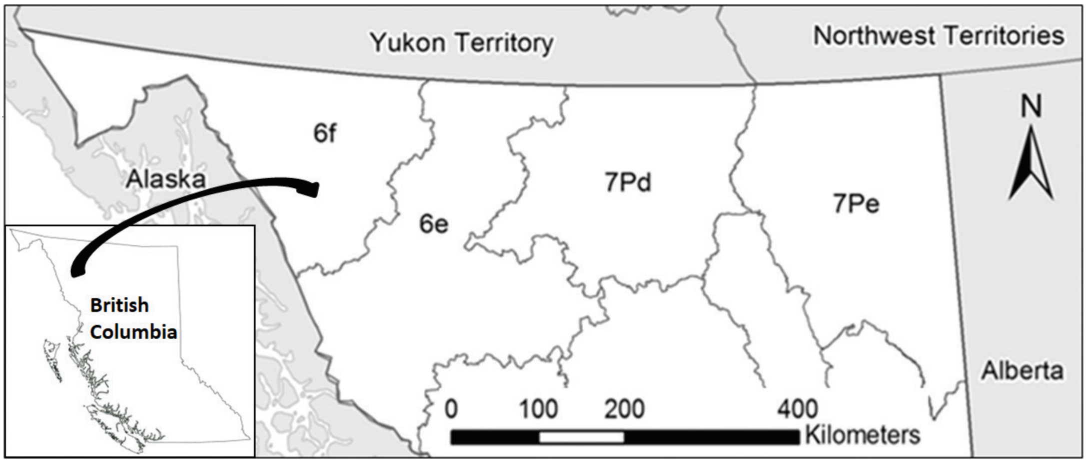

Fig. 1. Location of Game Management Zones 6f, 6e, 7Pd, and 7Pe in northern British Columbia.

Boreal Lowland ecotype occupies GMZ 7Pe. The Boreal Upland ecotype primarily occurs within the Boreal Black and White Spruce, the Subalpine Spruce-Willow-Birch, and the Alpine Tundra biogeoclimatic zones. GMZ 7Pe is comparatively homogeneous and the Boreal Lowland ecotype almost exclusively occupies the Boreal White and Black Spruce biogeoclimatic zone. In general, moose habitat quality is higher in the Spruce-Willow-Birch zone of GMZs 6f, 6e, and 7Pd and lowest in the Boreal Black and White Spruce zone in GMZ 7Pe. The climate for all 4 GMZs is characterized by long, cold winters and cool, short summers.

Moose co-exist with wolves, grizzly bears (*U. arctos*), and black bears (*U. americanus*) in all 4 GMZs. Wolf density ranged between 5–15 wolves/1000 km^2 with lower densities in GMZ 7Pe (BC FLNRO 2014, Serrouya et al. 2015). Grizzly bear density ranged from 10–30 bears/1000 km^2 in GMZs 6f, 6e, and 7Pd with ≤ 10 bears/1000 km^2 in GMZ 7Pe (BC FLNRO 2020). Black bears occur at unknown density in all 4 GMZs. Caribou (*Rangifer tarandus*) occur throughout much of the study area, with mountain goats (*Oreamnos americanus*) and thinhorn sheep (*Ovis dalli*) in mountainous regions. Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*) are moderately abundant in the extreme southern portion of GMZ 7Pe, and either absent or occur at very low to low density elsewhere. Small numbers of reintroduced bison (*Bison bison*) occupy portions of GMZs 7d and 7e.

Licensed hunting seasons were restricted to bull-only (bag limit of 1 moose/hunter) in all GMZs with season dates generally between 15 August and 30 November. Bull hunting was primarily regulated by general open seasons although limited-entry seasons with no antler restrictions, or a combination of general open and limited entry seasons occurred in some areas (Kuzyk et al. 2018). Only bulls with spike or fork antlers and bulls with tri-palm antlers could be harvested during September – October from 1996–2002 in GMZs 7Pd and 7Pe. After 2002, bulls with at least 10 points on one antler could also be harvested. Indigenous people also harvest moose at unknown levels throughout the 4 GMZs. Harvest is generally tied to access from roads and waterways, and although considerable road access exists within GMZ 7Pe, it is limited elsewhere.

METHODS

Moose and Hunter Harvest Surveys

Moose were counted in helicopter surveys in each GMZ, generally in mid-December through late February in suitable weather and snow conditions. Stratified random block or distance sampling survey methods were used to enumerate bulls (1+ year-old males), cows (1+ year-old females), and calves (Kuzyk et al. 2018); unclassified animals were typically ≤5% of total count. The survey areas were assumed representative of moose density and composition within a GMZ. Although herd composition counts were also conducted periodically, they were deemed less reliable and not used in this analysis. A total of 20 surveys were used to estimate density, and bull:cow and calf:cow ratios from 1996/97–2015/16 in the 4 GMZs.

Annual hunter surveys were used to estimate the licensed resident harvest, number of hunters, and hunter days from 1996–2015. Annual mail questionnaires were sent to 15,477 (average) provincial hunters chosen randomly, with an average response rate of 68% (Kuzyk et al. 2018). Reporting of non-resident licenced harvest was mandatory and obtained from guide declarations.

Moose Demography

Moose within each GMZ were assumed to comprise a discrete population (Hatter 1999, Kuzyk et al. 2018). I used the resident licensed kills/100 hunter days of effort (KPUE) as an annual population index for each GMZ, and estimated the growth rate (λ) by regressing ln(KPUE) against year from 1996–2015 where $\lambda = e^r$ and r is the exponential rate of growth. The 95% CIs were estimated by bootstrapping with 2000 samples (Haddon 2001). I considered the population to be stable if the 95% CIs for λ included 1.00. I determined the average winter moose density, calf:cow ratio and bull:cow ratio for each GMZ from 1996/97–2015/16 by weighting each estimate by the size of the survey area. This assumed larger survey areas provided a more accurate estimate of the population parameters at the GMZ level, that the population was stable, and that each survey area was randomly placed within the GMZ. I used 2000 bootstrap samples to estimate 95% CIs on the weighted (by area) estimates of the population ratios and moose density. Harvest density was calculated as the bull harvest/1000 km^2 of moose range within each GMZ and the 95% CIs with 2000 bootstrap samples. Harvest rates were calculated for each GMZ as (bull harvest/1000 km^2)/(moose/km^2 ×1000) for the population harvest rate and (bull harvest/1000 km^2)/(bulls/km^2 ×1000) for the bull harvest rate.

Sustainable Harvest Rates

Sustainable harvests were characterized as those where the post-hunt bull:cow ratio remained above a specified adult sex ratio threshold. I considered 3 ratio thresholds: 0.3, 0.4, and 0.5 bull:cow. I used these thresholds as both 0.3 and 0.5 bull:cow ratios are used as management targets in British Columbia (BC MOE 2010), and 0.4 is used in Yukon (Czetwertynski 2015). I assessed the licensed harvest only (bulls), and did (could) not consider the Indigenous harvest as it was unknown.

I estimated harvest sustainability with a demographic model parameterized on the average density and population composition from moose winter surveys of the 4 GMZs; density dependence was not modelled. Nutritional density dependence affecting population performance was unlikely due to the low moose density, and inadequate information existed to model density dependence of mortality due to predation. The modelled post-hunt population (N) was partitioned into bulls (B), cows (C), and calves (Ca) as follows:

$$N_{t+1} = B_{t+1} + C_{t+1}\ Ca_{t+1} \qquad (1)$$

where:

$$B_{t+1} = B_t Sm_t + 0.5(Ca_t Sj_t) - (Mh_t N_t) \qquad (2)$$

or

$$B_{t+1} = B_t Sm_t + 0.5(Ca_t Sj_t) - (Mh_t B_t) \qquad (3)$$

$$C_{t+1} = C_t Sf_t + 0.5(Ca_t Sj_t) \qquad (4)$$

$$Ca_{t+1} = C_t+_1 \times R_{pst,t+1} \qquad (5)$$

where t was year, Sm was the annual bull survival rate, Sf was the annual cow survival rate, Sj was the annual calf survival rate (i.e., from post-hunt or 0.5 years-of-age to the next post-hunt period or 1.5 years-of-age), R_{pst} was the post-hunt recruitment rate (i.e., the average calf:cow ratio from moose density surveys of the 4 GMZs), and Mh was the harvest rate. The post-hunt calf sex ratio was assumed to be 1:1 (Ballard et al. 1991, Boer 1992). Sf was set to 0.89 which was the average survival rate from 5 cow mortality studies within low-density moose populations ($Sf = 0.91$, Larsen et al. 1989; $Sf = 0.91$, Gasaway et al. 1992; $Sf = 0.88$, Stenhouse et al. 1995; $Sf = 0.88$, Bertram and Vivian 2002; $Sf = 0.90$, Joly et al. 2017). Previous studies of naturally fluctuating moose populations reported adult sex ratios near parity, suggesting that *Sm* and *Sf* are equal or 1:1 (Timmerman 1992). Conversely, the annual survival rate of bulls was lower than cows in the unhunted moose population on Isle Royale (Peterson 1977), with the average adult sex ratio of 0.8 bull:cow on the island from 1950–1981 (Page 1992). I therefore modelled 3 bull survival rates corresponding to unhunted adult sex ratios: 1.0, 0.9, and 0.8 bull:cow. The annual calf survival rate was determined by iteratively adjusting *Sj* until the modelled population achieved a stable age distribution with $\lambda = 1.0$. I used this value of *Sj* in the model projections as I was interested in sustainable harvest rates for stable, low-density moose populations.

Bergerud (1992) considered moose calves at 6–9 months of age to be fully recruited, or that calves and cows have similar winter survival rates. However, several studies found that winter survival rates of calves are lower than cows (Ballard et al. 1991, Joly et al. 2017, Kuzyk et al. 2019), suggesting that recruitment should be measured when calves are 1 year-of-age (Hatter 2020). I determined the annual recruitment rate (R) from R_{pst} and the ratio of the winter calf (Sj_w) and cow (Sf_w) survival rates where:

$$R = R_{pst} \times Sj_w/Sf_w \qquad (6)$$

(Hatter 2020). Mortality of cows was assumed negligible from calving to the post-hunt period (i.e., $Sf_w = Sf$). Similarly, mortality from 1 year-of-age to the post-hunt period was assumed negligible (i.e., $Sj_w = Sj$). *Rs* was equal to *R* when $\lambda = 1.0$.

Harvest rates were applied to either the total population (bull harvest/post-hunt population, Eq. 2) or the bull population (bull harvest/post-hunt bulls, Eq. 3) because both metrics are commonly used by moose managers in British Columbia (Kuzyk et al. 2018). I considered harvest rates up to 6% of the total population and up to 25% of the bull population.

I made the demographic model stochastic to assess harvest risk (i.e., the probability that the harvest rate was not sustainable) by including the SE for each parameter based on estimates of the coefficient of variation (CV). I set CV(*Sj*) = 0.15 (Ballard et al. 1991) and CV(*Sf*) = 0.017 from the 5 cow mortality studies. The CV for the winter calf:cow ratio was calculated from survey estimates in the 4 GMZs. The CV for implementation uncertainty (i.e., annual variation in harvest rates) was set to 19% to match annual changes in reported harvests for each of the 4 GMZs during 1996–2015. The CV for survey uncertainty of the population size and bull:cow ratios was set to the survey standard by Gasaway et al. (1986) where a CV of 15.2% equals + 25% of the true value 90% of the time. For the survival rates, I portioned the total variance for *Sj*, *Sf*, and *Sm* into $SE_{environmental}$ and $SE_{sampling}$ by assuming 50% of the variance was due to environmental uncertainty and 50% was sampling error. Finally, I generated correlated random winter survival rates (Burgman et al. 1993) with $r = 0.75$ for bulls and cows, $r = 0.5$ for cows and calves, and $r = 0.5$ for bulls and calves. All random variables were drawn from a normal distribution.

I conducted 2000 Monte Carlo simulations of the model for each bull survival rate and harvest rate during a 50-year period. I chose 50 years because mean annual bull:cow ratios changed very little after that. Survey uncertainty was incorporated into the initial simulation year. The harvest rate was considered sustainable if the percentage of the simulations that resulted in final (year 50) bull:cow ratios below the adult sex ratio threshold was ≤ 10%. Simulations were performed with the Microsoft Excel add-in program PopTools 3.2 (Hood 2011).

RESULTS

Moose Demography

Six moose surveys ranging from 1943–7766 km^2, 7 surveys ranging from 1533–7319

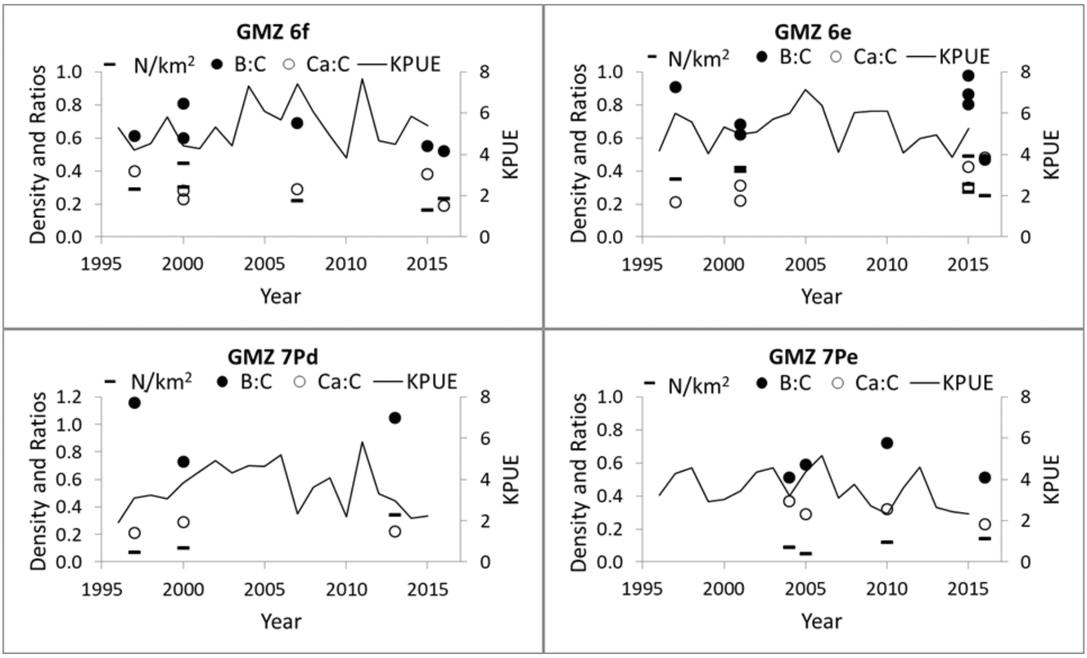

Fig. 2. Survey and harvest parameters for Game Management Zones 6f, 6e, 7Pd, and 7Pe from 1996/97–2015/16. N/km^2 = moose/km^2, B:C = bull:cow ratio, Ca:C = calf:cow ratio, and KPUE = resident kill per 100 resident hunter days.

km^2, 3 surveys ranging from 5675–8917 km^2, and 4 surveys ranging from 11,022–34,260 km^2 were conducted in GMZ 6f, GMZ 6e, GMZ 7Pd, and GMZ 7Pe, respectively, in 1996/97–2015/16 (Fig. 2). Moose population growth rate based on KPUE was approximately stable in the 4 GMZs over the 20-year period (Table 1). Although GMZ 7Pe had a slightly declining growth rate (λ = 0.98), the 95% CIs included λ =1.00. Further, no decline occurred in the density estimates in GMZ 7Pe from the 4 moose surveys conducted in 2004–2016, and calf:cow ratios were among the highest in the 4 GMZs (Table 1).

The average moose density was 0.27/km^2, 0.36/km^2, 0.16/ km^2, and 0.09/km^2 in GMZ 6f, GMZ 6e, GMZ 7Pd, and GMZ 7Pe, respectively. The winter calf:cow ratio ranged from 0.24 (GMZ 7Pd) to 0.32 (GMZ 7Pe), averaging 0.28 (Table 1); the CV was 0.27 from the 20 moose surveys in the 4 GMZs. The bull:cow ratio ranged from 0.58 (GMZ 7Pe) to 0.97 (GMZ 7Pd), averaging 0.75 across the 4 GMZs (Table 1). Assuming a stable population (λ = 1.0), 0.28 calf:cow ratio in early winter, a density of 0.22 moose/km^2, and a cow winter survival rate of 89%, the modelled winter calf survival rate was 79% and stabilizing recruitment (*Rs*) was 0.25 calves/cow. *R* for each moose population, after adjustment for winter survival rates of cows and calves, was 0.25 (GMZ 6f), 0.26 (GMZ 6e), 0.21 (GMZ 7Pd), and 0.28 (GMZ 7Pe).

Harvest density based on hunter survey data was lowest in GMZ 7Pe (3.0/1000 km^2) and highest in GMZ 6e (8.5/1000 km^2) (Table 1). Population harvest rates from moose and hunter survey data were 2.5% (GMZ 6f), 2.4% (GMZ 6e), 2.9% (GMZ 7Pd),

Table 1. Demographic status of low-density moose populations within 4 Game Management Zones (GMZs) located in northern British Columbia, 1996/97–2015/16. Moose/km^2 and sex/age composition are from moose density surveys during winter. Growth rate and harvest are from hunter harvest surveys. Numbers in brackets are 95% CIs.

GMZ	Moose/km^2	Bulls/Cow	Calves/Cow	Growth rate (λ)	Harvest/1000 km^2
6f	0.27	0.65	0.28	1.01	6.5
	(0.20–0.35)	(0.57–0.74)	(0.24–0.34)	(0.99–1.02)	(6.1–7.0)
6e	0.36	0.81	0.29	1.00	8.5
	(0.29–0.43)	(0.69–0.90)	(0.24–0.35)	(0.98–1.01)	(7.9–9.1)
7Pd	0.16	0.96	0.24	0.99	4.5
	(0.07–0.34)	(0.73–1.16)	(0.21–0.29)	(0.97–1.02)	(4.2–4.7)
7Pe	0.09	0.58	0.32	0.98	3.0
	(0.06–0.12)	(0.51–0.69)	(0.25–0.36)	(0.97–1.00)	(2.6–3.4)
$\bar{x}$	0.22	0.75	0.28	1.00	5.6
SD	0.12	0.17	0.03	0.01	2.4

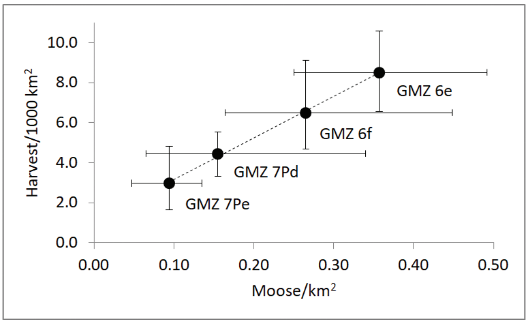

Fig. 3. Relationship between average surveyed hunter kill density (harvest/1000 km^2) and average surveyed moose density (moose/km^2) in four Game Management Zones in northern British Columbia, 1996/97–2015/16. Error bars display minimum and maximum values.

and 3.2% (7Pe); bull harvest rates were 7.3% (GMZ 6f), 6.1% (GMZ 6e), 6.7% (GMZ 7Pd), and 10.5% (GMZ 7Pe). The average harvest and moose density were highly correlated among GMZs ($r = 1.00$, $P = 0.001$, Fig. 3), but harvest rate and bull:cow ratio were not (population harvest rate: $r = -0.18$, $P = 0.82$; bull harvest rate: $r = -0.75$, $P = 0.25$).

Sustainable Harvest Rates

Sustainable harvest rates were affected by different bull survival rates, with lower survival rates associated with reduced harvests (Table 2). Population harvest rate up to 2.0% of the modelled post-hunt moose population posed little risk of reducing the bull:cow ratio below threshold values (Table 2a). Sustainable population harvest rates, averaged across the 3 estimates of *Sm*, were ≤2.4% with the 0.5 bull:cow ratio threshold, ≤3.2% with the 0.40 threshold, and ≤4.1% with the 0.30 threshold. The average population harvest rate was 2.8% based on survey data which was the upper limit of sustainability for the 0.5 bulls/cow threshold. However, the bull:cow ratios from winter moose surveys were ≥0.5, suggesting that the modelling results are conservative.

Simulated bull harvest rates up to 7% of the modelled post-hunt bull population presented little risk of lowering adult sex ratios below bull:cow thresholds (Table 2b). Sustainable bull harvest rates averaged ≤8.4% with the 0.5 bull:cow threshold, ≤13.0% with the 0.40 threshold, and ≤20.4% with the 0.30 threshold. The

Table 2. Sustainable harvest rates (*Mh*) where bull survival rates (*Sm*) are 0.890 (unhunted sex ratio = 1.0 bull/cow), 0.878 (unhunted sex ratio = 0.9 bulls/cow), and 0.862 (unhunted sex ratio = 0.8 bulls/cow).

a. Harvest rate applied to total population (*Mh* = bull harvest/post-hunt population)

Threshold value	*Sm* = 0.890	*Sm* = 0.878	*Sm* = 0.862
0.3 bulls/cow	*Mh* ≤ 4.4%	*Mh* ≤ 4.1%	*Mh* ≤ 3.8%
0.4 bulls/cow	*Mh* ≤ 3.6%	*Mh* ≤ 3.1%	*Mh* ≤ 2.8%
0.5 bulls/cow	*Mh* ≤ 2.8%	*Mh* ≤ 2.4%	*Mh* ≤ 2.0%

b. Harvest rate applied to bull population (*Mh* = bull harvest/post-hunt bulls)

Threshold value	*Sm* = 0.890	*Sm* = 0.878	*Sm* = 0.862
0.3 bulls/cow	*Mh* ≤ 21.6%	*Mh* ≤ 20.6%	*Mh* ≤ 19.1%
0.4 bulls/cow	*Mh* ≤ 14.2%	*Mh* ≤ 13.2%	*Mh* ≤ 11.5%
0.5 bulls/cow	*Mh* ≤ 9.6%	*Mh* ≤ 8.4%	*Mh* ≤ 7.0%

average bull harvest rate based on survey data was 7.7% which was within the range of modelled sustainable rates for the 0.5 bull:cow threshold.

Harvest risk rose sharply as the modelled harvest rates were increased. For example, a population harvest rate of 2.5% had a 0% probability of reducing the bull:cow ratio below 0.5 bulls/cow, whereas a harvest rate of 3.5% had a 95% probability (Fig. 4). Similarly, a bull harvest rate of 8% had a 0% chance of reducing the adult sex ratio below 0.5 bull:cow, but a 12% harvest had an 81% chance (Fig. 5).

DISCUSSION

Moose from all 4 GMZs in northern British Columbia met the demographic conditions for LDE populations. All populations were at low density (≤0.4 moose/km^2) and their long-term (20 year) population growth rate was static ($\lambda \sim 1.0$). Across the GMZs, surveys indicated that the winter calf:cow ratio averaged 0.28, the modelled winter calf

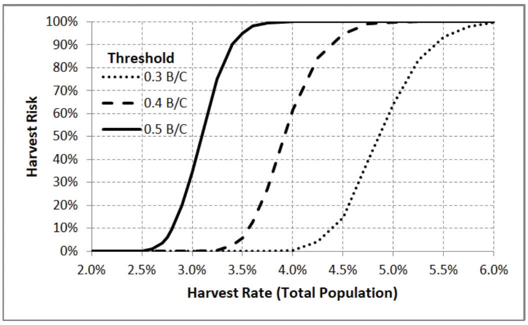

Fig. 4. Relationship between harvest risk and total population harvest rate for post-hunt adult sex ratio thresholds of 0.30, 0.40, and 0.50 bulls/cow. The harvest risk is the estimated probability that a specified harvest rate will result in a bull:cow ratio (B/C) below the adult sex ratio threshold. The adult bull survival rate was 0.890.

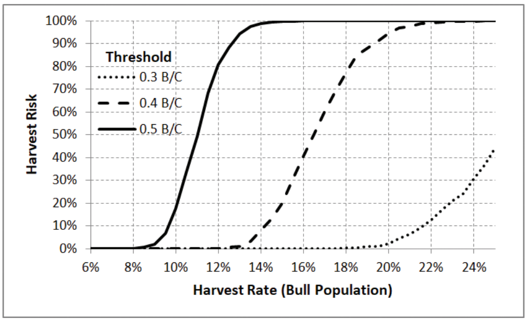

Fig. 5. Relationship between harvest risk and bull population harvest rate for post-hunt adult sex ratio thresholds of 0.30, 0.40, and 0.50 bulls/cow. The harvest risk is the estimated probability that a specified harvest rate will result in a bull:cow ratio (B/C) below the adult sex ratio threshold. The adult bull survival rate was 0.890.

survival was 78%, and annual calf recruitment averaged 0.25 calves/cow.

Bergerud (1992) hypothesized that the mechanism for a LDE in a moose population is density-dependent wolf predation on calves, augmented by density-independent bear predation on neonates; food was not considered to be a limiting factor. Joly et al. (2017), however, studied a low-density (0.06–0.12 moose/km^2) population in north-central Alaska and found that productivity was significantly lower in areas with less high-quality habitat, indicating that forage resources/nutrition could be a contributing factor in a LDE population. They suggested that the relative roles of predation on young calves, winter weather, and nutritional constraints likely interact to maintain low moose density. Much of the moose range in GMZ 7Pe consists of low to moderate habitat capability (Thiessen 2010), suggesting that habitat quality may be a local limiting factor in this population. Alternatively, the lower moose density in GMZ 7Pe may reflect a lack of suitable habitat for moose to space-out and avoid predation (Bergerud 1992).

Two important considerations in managing low-density moose populations are to maintain an appropriate bull:cow ratio that provides hunting opportunities for large-antlered bulls and to ensure adequate numbers of bulls are available to locate and breed all receptive cows (Timmermann 1992). Given these considerations, adult sex ratios for low-density populations (≤0.2 moose/km^2) in British Columbia are managed with an objective to maintain a bull:cow ratio ≥0.5, with higher density populations managed with a threshold bull:cow ratio ≥0.3 (BC MOE 2010). In Yukon, low-density moose are managed to maintain an adult bull:cow ratio of at least 0.4 (Czetwertynski 2015), while in parts of Alaska the management objective is a ratio of 0.3 (Young and Boertje 2008). I used a stochastic model to assess harvest risk, or the probability that a specified harvest rate will reduce the bull:cow ratio below the adult sex ratio threshold. I considered the harvest rate as sustainable if the harvest risk was ≤10%. Sustainable harvest rates averaged ≤2.4% of the total population or ≤8.4% of the bull population at the 0.50 bull:cow ratio threshold, ≤3.2% of the population or ≤13.0% of bulls at the 0.40 threshold, and ≤4.1% of the population or ≤20.4% of bulls at the 0.30 threshold. Similarly, a harvest rate of 10% of adult bulls or 2.2–3.3% of the total population was sustainable in low-density Yukon moose populations with a bull:cow ratio objective (threshold) of 0.4 (Czetwertynski 2015).

While the surveyed harvest and moose densities were highly correlated, harvest rates and bull:cow ratios were not. This may indicate that the surveyed bull:cow ratios were not representative of the GMZ, or some compensatory mortality existed in the licensed harvest. In addition, unmeasured variation in the mortality rates of cows could have affected the bull:cow ratio.

I used KPUE to ascertain long-term (20 year) stability of the moose population within each of the 4 GMZs. While several studies have found that KPUE is correlated with moose abundance (Crête et al. 1981, Fryxell et al. 1988), there is potential for error or bias in growth rates measured with KPUE (Fryxell et al. 1988, Bowyer et al. 1999, Hatter 2001, DeCesare et al. 2016). I assumed that the survey areas provided a representative sample of the moose density and bull:cow and calf:cow ratios within each GMZ. Another data concern was that the Indigenous harvest was unknown and not an annual harvest metric (Kuzyk et al. 2018).

I considered 10% as an acceptable, although subjective level of harvest risk. While higher risk levels such as 15% or 20% could have been chosen with greater risk tolerance, sustainable harvest rates would have only increased slightly. For example, selecting a 20% harvest risk versus 10% risk only increased the sustainable population harvest rate from 2.8% to 2.9% for the 0.5 bull:cow ratio threshold with $Sm = 0.870$.

Computation of stabilizing recruitment required an estimate of the winter cow survival rate. I assumed all cow mortality occurred during winter such that the winter survival rate was equal to the annual survival rate. However, studies of low-density moose populations have documented that some cow mortality occurs during summer (Larsen et al. 1989). Calculation of *Rs* would have been improved with a more reliable estimate of the winter cow survival rate.

I did not include density-dependent nutritional effects in the demographic model as moose density in the 4 GMZs ranged from 0.1–0.4 km^2, and thus were well below the habitat carrying capacity of 1.5–2.0 moose/km^2 for North American populations (Bergerud 1992, Messier 1994). Despite this, nutritional influences may have been present within GMZ 7Pe where habitat quality was lower. Inclusion of density dependence in the model would have increased sustainable harvest rates (Caughley 1977).

The stochastic modelling indicated that minor changes in harvest rates could greatly affect the probability of bull:cow ratios dropping below adult sex ratio thresholds, revealing that small changes in harvest management could affect the resulting bull:cow ratios. Sustainable harvest rates were also affected by different bull survival rates with lower survival rates sustaining reduced harvests. I did not model non-stationarity in environmental variation although global warming is expected to be highly influential to ungulate population dynamics in northern latitudes where variation in demographic rates, and thus sustainable harvest rates, are closely aligned to annual cycles in climate and primary productivity (Brown 2011). For these reasons, wildlife managers should be cautious about applying estimates of sustainable harvest rates from this study to other low-density moose populations.

Despite these limitations, I was able to offer support for the LDE hypothesis for all 4 GMZs in northern British Columbia and provide additional insight on sustainable harvest rates for moose within these northern ecosystems. More study is recommended to identify the relative roles of hunting, predators (wolves and bears), habitat quality, and winter weather in maintaining low densities of moose across northern British Columbia. Further understanding of sustainable harvest rates would benefit from additional moose surveys, Indigenous harvest surveys, and studies of moose survival rates.

ACKNOWLEDGEMENTS

M. Bridger, D. Heard, and H. Schindler kindly reviewed an early draft of the manuscript and made numerous helpful and insightful suggestions. The manuscript was also greatly improved by constructive reviews from N. DeCesare and 2 reviewers.

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