



MOOSE POPULATION DYNAMICS DURING 20 YEARS OF DECLINING HARVEST IN BRITISH COLUMBIA

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ABSTRACT: Licenced harvest of moose (*Alces alces*) in British Columbia, Canada declined by approximately half over the 20-year period from 1996–2015. To better understand changes in moose populations coinciding with this period of declining harvest, we modelled population dynamics within 31 Game Management Zones (GMZs). We used aerial survey data (180 density and 159 composition surveys) combined with licenced harvest to develop 4 competing statistical models to assess population dynamics based on constant parameters and temporal trends in calf:cow ratios at 6 months, juvenile survival from 6–18 months, or cow survival. The models indicated that moose populations declined ($\lambda < 1$) in 7 GMZs (23%) from 1996–2005 and in 22 GMZs (71%) from 2006–2015. Over the 20-year period, the best model was fit with declining trends in calf:cow ratios in 8 GMZs, declining juvenile survival in 6 GMZs, and declining cow survival in 8 GMZs. Population growth rate was slightly reduced in those GMZs where licenced antlerless (cow and calf) hunting occurred but was not considered the primary factor causing population decline. Total licenced bull harvest influenced bull:cow ratios that were significantly lower in 2006–2015 ($\bar{x} = 37:100$) than 1995–2005 ($\bar{x} = 48:100$); significant predictive relationships existed between harvest rates and bull:cow ratios. Provincial moose numbers and harvest were highly correlated ($r = 0.81$) suggesting that declining harvest was a reaction to declining population trends. We found that the provincial moose population increased 6% from 1996–2005, subsequently declined 32% from 2006–2015, and declined 29% overall during the 20-year study period.

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Moose (*Alces alces*) remain an important hunted species throughout their circumpolar range (Telfer 1984, Kelsall 1987,

Karns 2007, Boman et al. 2011), but concern exists about declining populations in parts of North America (Lenarz et al. 2009, Decesare

et al. 2014, Timmermann and Rodgers 2017). Moose populations are vulnerable to factors such as predation and hunting, both of which can be influenced by human-induced landscape change (Murray et al. 2006, Brown 2011). Moose co-exist with predators throughout most of their range in Canada and Alaska, and in areas where predators are lightly hunted, moose density is typically low (<400 moose/1000 km²), and male (hereafter bull)—only hunting may be the only viable harvest option (Gasaway et al. 1992, Boertje et al. 1996). In these systems moose populations may fluctuate over time and decline in the absence of hunting (Gasaway et al. 1983).

A recent assessment of the provincial moose population and licenced harvest trends in British Columbia (BC) documented that licenced harvest declined by approximately half over a 20-year period from 1995–2014 as regional population declines of ~50–70% occurred in the central interior (Kuzyk 2016). These declines occurred concurrently with a mountain pine beetle (*Dendroctonus ponderosae*) outbreak and associated salvage logging and road building, which presumably facilitated predator and hunter access to moose (Ritchie 2008). In 2013, the province initiated research to determine factors leading to the population declines in the central interior. Because the declines occurred over a relatively short period of 20 years, it was assumed that female moose (hereafter cow) survival was the most influential population parameter in the decline (Kuzyk and Heard 2014). These declines continue to create concern among stakeholders and First Nations who have requested more refined information about provincial moose population and harvest trends to help inform management decisions (Gorley 2016).

To provide a consistent and objective assessment of relationships between moose

population dynamics and declining harvest levels (Kuzyk 2016), we followed an approach similar to that of Hatter (1999) who assessed moose population trends in relation to harvest strategies in 19 Game Management Zones (GMZs) in northern and central BC from 1994–1996. GMZs generally share similar ecological characteristics and hunter harvest patterns providing a suitable geographic unit for managing moose hunting. All GMZs are amalgamations of 1–13 Wildlife Management Units (WMUs) which is the geographic area used to collect hunting information. We expanded Hatter’s (1999) approach and included all GMZs ($n = 31$) with licenced moose hunting seasons and survey data over a 20-year period (1996–2015). Our objectives were to: 1) evaluate competing models of moose population dynamics in each GMZ to determine which parameters (i.e., calf:cow ratio at 6 months, juvenile survival from 6–18 months, or cow survival) best predicted moose population trend, 2) assess the density, composition, and trend of moose populations based on the best model over the 20-year period within each GMZ, and 3) evaluate the influence of licenced moose hunting based on the best model within each GMZ.

STUDY AREA

We assessed moose population dynamics and licenced harvest in 31 GMZs where moose hunting is authorized in BC (Fig. 1). These areas are ecologically diverse (Meidinger and Pojar 1991) with moose occupying landscapes of differing topography and vegetation including northern boreal forests, dry interior forests of the central plateau, and some mountainous habitats (Eastman and Ritcey 1987, Kuzyk et al. 2016). A mountain pine beetle outbreak beginning in the early 1990s occurred over much of the central interior of the province leaving large amounts of dead pine, which



Fig. 1. Game Management Zones (n = 31) with licenced moose hunting from 1996-2015 in British Columbia, Canada.

led to increased salvage logging and road building (Alfaro et al. 2015). The increased number of roads and cutblocks were thought to facilitate hunter and predator access to moose (Ritchie 2008, Kuzyk and Heard 2014). Moose co-exist with wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and black bears (*U. americanus*) throughout most of their BC range and overlap with cougars (*Felis concolor*) in the central and southern areas (Spalding and Lesowski 1971, Mowat et al. 2013, Kuzyk and Hatter 2014). A diversity of ungulates including mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), bison (*Bison bison*), and caribou (*Rangifer tarandus*) also occur here (Shackleton 1999). Licenced hunting seasons for bulls occurred in all GMZs having a

range of season dates between August 15 and November 30. Bull hunting was regulated with general open seasons with or without antler restrictions, limited-entry seasons (i.e., hunters must draw an appropriate authorization) with no antler restrictions, or a combination of general open and limited entry seasons. Hunting seasons for cows and calves were mostly limited-entry hunts in 7 GMZs between October 1 and December 10 over most of the 20-year period; general open seasons for calves existed in a few select areas.

METHODS

Moose density and composition

Two winter aerial survey methods were used to collect reliable population information following provincial standards (RISC 2002).

Density surveys collected a combination of population size, density, and composition (i.e., bull:cow and calf:cow ratios) information, whereas composition surveys gathered only bull:cow and calf:cow ratios. Density surveys were typically conducted in 5–7 consecutive days in December–March using stratified random blocks that could be remeasured to detect population trends 5–7 years later (Gasaway et al. 1986). Certain surveys were modified to include habitat-based stratification (Heard et al. 2008), and distance sampling surveys were used in more open habitats (Peters et al. 2014); all survey types produced comparable density estimates. A sightability correction factor developed in central BC (Quayle et al. 2001) was used to account for detection probability. These surveys followed established standards for accuracy and precision (90% CI) with allowable error from ± 15 –25% of the estimated population size (RISC 2002).

Composition surveys were conducted over 1–3 days in early winter (December–January) prior to typical antler drop. These surveys provided bull:cow and calf:cow ratios which were used as a general index of population trend to gauge progress towards harvest management objectives. Frequency of surveys varied among GMZs due to population objectives, and financial and logistical constraints. There were a total of 180 density surveys (GMZ range = 1–15) and 159 composition surveys (GMZ range = 1–24) used in our analysis. Over the 20-year period, the average number of density and composition surveys per GMZ was 5.8 (min = 1, max = 15) and 5.1 (min = 0, max = 24), respectively.

Licensed harvest

Licensed resident harvest was estimated annually from 1996–2015 with a provincial hunter survey generating data from mail-out questionnaires sent to a random sample of

moose hunters. These estimates (95% CI) were produced from an annual average of 15,477 questionnaires with an average response rate of 68%. Reporting of non-resident licensed harvest was mandatory and obtained from guide declarations. We used both resident and non-resident harvest in the models, but only used resident kill per unit effort (KPUE; resident kill/100 resident hunter days) as an indicator of population trend. We recognized that success rates differed between resident and non-resident hunters, and that the overwhelming majority of moose hunters were residents.

Unlicensed hunter harvest, which we defined as moose legally harvested by First Nations and moose harvested illegally, was not quantified as an annual harvest statistic due to the limited availability of these data. Unlicensed harvest mortality was incorporated in estimates of annual non-hunting survival rates derived from radio-collared moose (Kuzyk et al. 2016), and was assumed as a constant proportion of annual mortality.

Modelling approach

Our models provided a reasonable trade-off between what can be measured practically by biologists and what is needed to help predict moose population trends and responses to harvest management strategies (Hatter 1999). The intent was to utilize a statistically rigorous and objective modelling approach while maintaining a relatively easy-to-implement procedure for constructing population models from multiple types of population data. Because we wanted to make comparisons among GMZs, it was important that the standardized approach and assumptions were consistent among models. We used models built in Microsoft EXCEL® and model fitting was accomplished using EXCEL's built-in optimizer function, SOLVER.

We constructed discrete-time, stage-structured population models for each of the 31 GMZs. Our model and model-fitting approach followed White and Lubow (2002), where the focus was on building a series of simple candidate models and selecting the most parsimonious model (i.e., the model that best fits the data with the fewest number of estimated parameters) using Akaike Information Criteria (AIC) (Burnham and Anderson 2002). An exception was that we included resident KPUE as a trend index. Although KPUE was available for all GMZs and was consistently collected over the 20-year study period, we did not use KPUE in GMZs 3b, 3c, 8a, and 8b because the trends in KPUE were inconsistent with the trends from periodic population estimates. For all other GMZs, we fit the KPUE index to the model using procedures described by Hatter (1998) and Haddon (2001).

The data for each GMZ typically included estimates of absolute abundance in winter, which were extrapolated from density surveys, winter age and sex ratios (i.e., bull:cow and calf:cow ratios), KPUE, and the annual harvest (bulls, cows, and calves). The key parameters estimated by the model included: R , the recruitment rate or the calf:cow ratio when calves were ~6 months old which we define as the calf:cow ratio at 6 months; S_p , the calf survival rate from 6–18 months which we define as juvenile survival from 6–18 months; and S_r , the annual cow (>18 months) survival rate excluding licenced hunting which we define as cow survival. We used cow survival rates estimated from radio-collared cows from 5 study areas, and juvenile survival rates from 2 of these areas (Kuzyk et al. 2016). Survival rates were available for a 2-year period in 5 study areas corresponding to GMZs 7Ob, 7Oc, 6c, 5d, and 3c; we used the documented survival rate from the corresponding study area for these GMZs each year. For the

remaining GMZs, we used the average of the 5 study areas for each year. The juvenile survival rates were obtained from GMZ 7Ob and 7Oc in 2016. The estimates were based on the change in calf:cow ratios between early winter and late winter surveys, and included an adjustment for adult cow survival between these 2 time periods (Skalski et al. 2005). All field-based estimates except harvest level included the standard error (SE). We fixed 3 model parameters at values reported in the literature: wounding loss equaled 15% of licenced hunting (Gasaway et al. 1983, Boer and Keppie 1988, Fryxell et al. 1988), calf sex ratio was 50:50 (Ballard et al. 1991, Boer 1992), and the natural adult bull survival rate was 96% of the cow survival rate (Peterson 1977).

We built 4 competing models for each GMZ ($n = 124$) and considered each as a potential hypothesis driving population dynamics. Model 1 held all 3 parameters constant; i.e., calf recruitment, juvenile survival from 6–18 months, and cow survival. The other 3 models included a single parameter as a linear trend while holding the other 2 constant (Table 1). For each model we calculated the corrected AIC_c for a small sample in order to determine the best model for each GMZ and AIC weight (w_i) (Burnham and Anderson 2002).

Changes in moose population dynamics over 4 time periods (1996–2015, 1996–2005, 2006–2015, 2011–2015) were evaluated. We chose 1996–2015 as a long-term (20 year) overview as it corresponded to the earlier moose population assessment (Kuzyk 2016) and when provincial survey methods became standardized. The period of 1996–2005 corresponded to when the provincial harvest was relatively stable, and the 2006–2015 period corresponded to when annual harvests declined by 37%. The 2011–2015 period corresponded to when additional harvest restrictions were imposed for numerous

Table 1. Sequence of models fit to moose population survey and harvest data for using parameters of calf:cow ratios at 6 months (R), juvenile survival from 6–18 months (S_j), or cow survival (S_F) in each of 31 Game Management Zones in British Columbia, Canada.

Model	Calf:cow ratio (R)	Juvenile survival (S_j)	Cow survival (S_F)	Model structure
1	Constant	Constant	Constant	$R_t = R$ $S_{j,t} = S_j$ $S_{F,t} = S_F$
2	Linear trend	Constant	Constant	$R_t = R_{intercept} + R_{slope} \cdot (Year_t - Year_0)$ $S_{j,t} = S_j$ $S_{F,t} = S_F$
3	Constant	Linear trend	Constant	$R_t = R$ $S_{j,t} = S_{j,intercept} + S_{j,slope} \cdot (Year_t - Year_0)$ $S_{F,t} = S_F$
4	Constant	Constant	Linear trend	$R_t = R$ $S_{j,t} = S_j$ $S_{F,t} = S_{F,intercept} + S_{F,slope} \cdot (Year_t - Year_0)$

GMZs due to increasing concerns about declining moose densities (Kuzyk and Heard 2014, Kuzyk 2016). Annual population estimates were summed across all GMZs to provide the provincial estimates from 1996–2015.

We used the best fit model estimates of post-hunt females (cows and calves) to assess the influence of cow and calf hunting on moose population growth. We calculated both the potential rate of population change without female hunting (λ_p) and the actual rate of change with female hunting (λ_h). A λ_p value >1 indicated potential growth and thus some opportunity for cow harvest, and a value <1 implied that licenced cow harvest had some negative influence on population growth.

We used the modelled estimates of the post-hunt adult ratios to assess the influence of bull hunting on bull:cow ratios. It is unknown what adult sex ratio ensures that cows are synchronously bred to avoid impeding population growth (Timmermann 1992). Ministry policy is to maintain post-hunt, bull:cow ratios ≥ 30 bulls:100 cows in areas with densities > 200 moose/1000 km², and 50 bulls:100 cows in areas with <200 moose/1000 km² (BC MOE 2010).

RESULTS

Best models

Model 1 was the best model (i.e., lowest AIC_c) in 7 (23%) GMZs, Model 2 in 12 (39%) GMZs, Model 3 in 2 (6%) GMZs, and Model 4 in 10 (32%) GMZs (Table 2). Model 1 had substantial support (i.e., $\Delta AIC_c < 2$) in 12 GMZs (39%), Model 2 in 16 GMZs (52%), Model 3 in 6 GMZs (19%), and Model 4 in 14 GMZs (45%). Models 2 and 4 had very strong support in 10 GMZs, each with a relative AIC weight of 1 in 5 GMZs. Twenty GMZs had a single top model with strong support (i.e., $\Delta AIC_c < 2$), 5 GMZs had 2 models, and 6 GMZs had 3 models (Table 2).

Population dynamics

We calculated the average (1996–2015) moose density, population composition, key population parameters, and rate of change by GMZ for the best fitting models, and the average rate of population change (λ) in 1996–2005, 2006–2015, and 2011–2015 (Table 2). The rate of population change varied spatially between 1996–2005 and 2006–2015 (Fig. 2). Population density in 1996–2015 varied from 6 (GMZ 4Wb) to 1078 (GMZ 7Ob), averaging 334 moose/1000 km² (SD = 271) across

Table 2. The average moose density, population composition, key population parameter estimates, and rate of change based on the best models (lowest AIC_c) in 31 Game Management Zones from 1996–2015 in British Columbia, Canada. The average rate of change is shown for 1996–2015, 1996–2005, 2006–2015, and 2011–2015, and 2011–2015; those in gray have $\lambda < 1$.

GMZ	Models ^{1,2} with $\Delta AIC_c < 2$	AIC weight $(w_i)^3$	Density /1000 km ²	Sex/Age Ratios		Key Population Parameters ⁴				Rate of Change (λ) ⁵			
				B:100 C	Ca:100 C	R	S _j	S _f	1996–2015	1996–2005	2006–2015	2011–2015	
3b	1, 2, 4	0.43	242	18	34	34	89	89	1.03	1.04	1.03	1.05	
3c	1, 3	0.57	209	29	37	37	68	89	1.01	1.01	1.02	1.02	
3d	2	1.00	161	69	47	15–79	81	81	0.97	1.03	0.91	0.87	
4Ea	2	1.00	204	46	30	6–53	90	92	1.02	1.07	0.97	0.94	
4Eb	2	1.00	128	40	27	7–48	90	91	1.02	1.07	0.97	0.94	
4Ec	1	0.60	94	60	27	27	86	86	0.96	0.95	0.97	0.98	
4Wa	2, 1	0.61	85	55	49	23–75	90	90	1.10	1.17	1.04	1.02	
4Wb	4	0.99	6	49	30	30	81–90	81–99	0.99	1.01	0.97	0.95	
5a	2, 1	0.55	264	38	28	19–36	90	90	0.99	0.99	0.99	0.98	
5b	1, 2, 4	0.41	535	28	34	34	84	84	0.98	0.98	0.98	0.99	
5c	4, 2, 1	0.47	352	34	40	40	79–84	79–84	0.98	0.96	1.00	1.01	
5d	2	1.00	224	38	35	25–45	84	84	0.99	1.01	0.96	0.95	
6b	2	1.00	92	56	46	33–60	79	79	0.98	1.01	0.95	0.93	
6c	4	1.00	526	35	37	37	77–89	77–89	0.98	1.02	0.95	0.92	
6d	4	0.96	361	47	46	46	25	86–97	0.97	0.99	0.95	0.93	
6e	4	1.00	305	58	36	36	81–90	81–91	1.01	1.03	0.99	0.98	
6f	2, 4, 1	0.51	511	56	31	27–35	69	90	1.00	1.01	1.00	0.99	
70a	2	0.68	225	43	25	6–45	90	94	0.98	1.00	0.96	0.95	
70b	4	1.00	1078	35	32	32	64	81–96	0.97	1.00	0.94	0.92	
70c	4, 3	0.57	954	43	25	25	59	85–99	0.98	1.00	0.95	0.94	
70d	3, 4, 2	0.46	568	49	35	35	50–86	86	0.98	1.00	0.96	0.95	
70e	4	0.99	215	49	25	25	79–90	79–99	1.00	1.04	0.96	0.93	
7Pa	4	1.00	574	42	30	30	74–90	74–96	0.98	1.05	0.92	0.88	
7Pb	4	1.00	572	32	34	34	73–88	73–93	0.97	1.03	0.92	0.88	
7Pc	2	0.79	903	28	17	13–22	89	89	0.96	0.98	0.95	0.94	
7Pd	2, 3	0.71	316	49	25	15–34	87	87	0.98	1.01	0.95	0.93	

(Continued)

Table 2. (Continued)

GMZ	Models ^{1,2} with $\Delta AIC_c < 2$	AIC weight $(w_i)^3$	Density /1000 km ²		Sex/Age Ratios		Key Population Parameters ⁴			Rate of Change (λ) ⁵		
			B/100 C	Ca/100 C	R	S_j	S_f	1996–2015	1996–2005	2006–2015	2011–2015	
7Pe	2, 1, 3	0.38	57	29	22-36	86	86	0.98	1.00	0.96	0.95	
8a	1	0.87	38	43	43	90	92	1.09	1.07	1.13	1.12	
8b	1	0.62	35	35	35	87	87	1.01	0.99	1.02	1.02	
8c	3	0.74	42	48	48	26-90	95	1.07	1.12	1.03	1.02	
8d	1	0.64	30	45	45	83	83	1.02	1.02	1.02	1.02	

¹ Model 1. Calf:cow ratio at 6 months (R), juvenile (S_j) and cow survival (S_f) rates are constant.

Model 2. Linear trend in calf:cow ratio at 6 months. Juvenile and cow survival rates are constant.

Model 3. Linear trend in juvenile survival rate. Calf:cow ratio at 6 months and cow survival rates are constant.

Model 4. Linear trend in cow survival rate. Calf:cow ratio at 6 months and juvenile survival rates are constant.

² Models listed starting with lowest ΔAIC_c value.

³ AIC relative weight of best fitting model.

⁴ R = Recruitment rate (calves:100 cows), S_j = % calf survival rate (6 - 18 mths), S_f = % cow survival rate (>18 mths).

⁵ Rate of change (λ) by time period. $\lambda < 1.0$ are highlighted in grey.

all GMZs. The adult bull:cow ratio in 1996–2015 varied from 18:100 (GMZ 3b) to 69:100 (GMZ 3d), averaging 42:100 (SD = 12) across all GMZs. Bull:cow ratios were significantly lower (paired t test: $t = 4.48$, $df = 30$, $P < 0.001$) in 2006–2015 ($\bar{x} = 37:100$, SD = 12.3) than in 1996–2005 ($\bar{x} = 48:100$, SD = 15.3). Calf:cow ratios varied from 17:100 (GMZ 7Pc) to 49:100 (GMZ 4Wa), averaging 34:100 (SD = 8.0) across all GMZs. Across the 20-year period, calf:cow ratios at 6 months declined in 12 GMZs (39%), juvenile survival from 6–18 months declined in 9 GMZs (29%), and cow survival declined in 10 GMZs (32%). No GMZ experienced an increase in calf:cow ratio, juvenile survival, or annual survival of cows. The annual rate of population change (λ) varied from 0.96 (GMZ 7Pc) to 1.10 (GMZ 4Wa) from 1996–2015; λ was ≥ 1 in 24 GMZs (77%) from 1996–2005, but only ≥ 9 in GMZs (29%) from 2006–2015 ($\chi^2 = 12.7$, $df = 1$, $P < 0.001$). Only 8 GMZs (3b, 3c, 4Wa, 5c, 8a, 8b, 8c, and 8d) had an average $\lambda > 1$ in the most recent 5-year period (2011–2015).

The highest modelled population estimate across the province occurred in 2002 (258,532) and the lowest in 2015 (169,752) (Fig. 3). Percent change within the 4-time periods was: -29% from 1996–2015 ($\lambda = 0.98$), 6.4% from 1996–2005 ($\lambda = 1.01$), -32% from 2006–2015 ($\lambda = 0.96$), and -20% from 2011–2015 ($\lambda = 0.95$). There was a strong correlation between the decline in the population estimate and licenced harvest ($r = 0.81$, $P < 0.001$).

Licenced hunting

The average annual licenced harvest during 1996–2015 varied from 18 (GMZ 8c) to 1490 moose per GMZ (GMZ 7Ob; Table 3). Harvest composition was predominantly bulls in all GMZs, with the antlerless harvest >10% of the total harvest in 8 GMZs: 3b (12%), 3c (15%), 3d (10%), 4Wb (31%), 7Oa (32%),

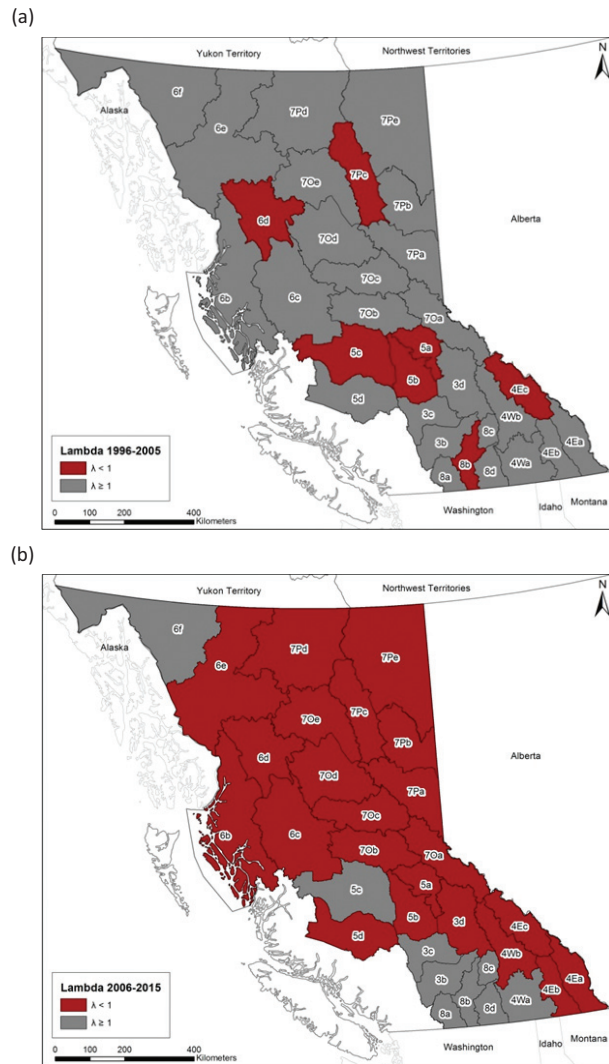


Fig. 2. Population rate of change (λ) in 31 Game Management Zones having licenced moose hunting seasons from 1996–2005 (a.) and 2006–2015 (b.); λ values < 1 are highlighted in burgundy and values ≥ 1 in gray. (Footnote: λ for GMZ 8b was 0.993 from 1996–2005 and 1.024 from 2006–2015. GMZ 5c was 0.961 from 1996–2005 and 1.000 from 2006–2015).

7Ob (41%), 7Oc (32%), and 7Od (27%). The harvest rate of bulls relative to the population (bull harvest/pre-hunt population) averaged 5% (range = 2–12%), and the proportional bull harvest rate (bull harvest/pre-hunt bulls) averaged 17% (range = 5–36%). In comparison, the proportional cow (range = 1–3% of cows) and calf harvest rates (range = 1–9% of calves) were low.

Antlerless hunting generally had minimal influence on population growth rate. During 1996–2015, the average λ_p for GMZs 3b, 3d, 7Ob, and 7Oc was 1.00; λ_h was slightly lower in these and other units (0.97 in 7Ob and 0.99 in 3b, 3c, and 7Oc). When the 1996–2005 growth rate estimates were compared to those in 2006–2015, both λ_p and λ_h were > 1 in 1996–2005, and < 1 in

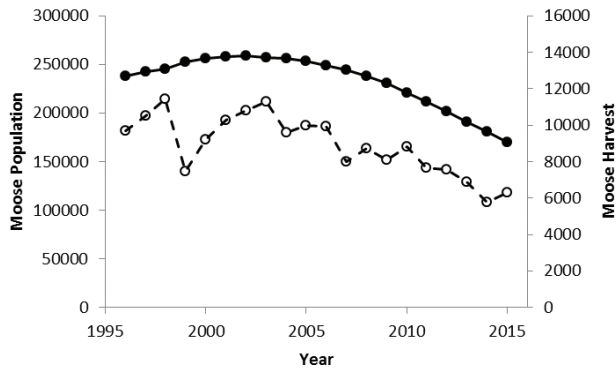


Fig. 3. Trend in modelled population size of moose (solid circles) and the licensed hunter harvest (open circles) from 1996–2015 in British Columbia, Canada.

2006–2015, with the exception of GMZ 3b where $\lambda_p = 1.00$ and $\lambda_h = 0.99$. Antlerless harvest may have reduced population growth rate somewhat during both time periods in certain GMZs, but was not a primary influence in the overall decline of cows during 2006–2015.

Modelled adult sex ratios averaged 43 bulls:100 cows during 1996–2015, 49 bulls:100 cows from 1996–2005, 37 bulls:100 cows from 2006–2015, and 35 bulls:100 cows from 2011–2015. Adult sex ratios were <30 bulls:100 cows in 4 GMZs from 1996–2015, 3 GMZs from 1996–2005, 11 GMZs from 2006–2015, and 13 GMZs from 2011–2015 (χ^2 [1996–2005, 2006–2015] = 4.5, $P = 0.034$). Bull harvest rate ($R^2 = 0.82$, $P < 0.001$; Fig. 4) and moose harvest rate ($R^2 = 0.70$, $P < 0.001$; Fig. 5) were strong predictors of the bull:cow ratio (i.e., # post-hunt bulls:100 cows). A ratio of 30 bulls:100 cows was achieved at a population harvest rate of 6% and bull harvest rate of 23%.

DISCUSSION

We found that moose populations were declining ($\lambda < 1$) in 23% of the GMZs from 1996–2005, and in most (71%) GMZs from 2006–2015. While cow survival was declining in certain GMZs, variation (decline) in

the calf:cow ratio at 6 months and juvenile survival from 6–18 months was extensive and likely added to population decline in areas where cow survival was constant (Gaillard et al. 1998). The variation and decline measured in both parameters were consistent with previous studies indicating that their temporal variation is more common than in cow survival (Gaillard et al. 2000, Eberhardt 2002). Further, they may be more influential in local population change (Monteith et al. 2014), especially in variable seasonal environments (Raithel et al. 2007, Hurley et al. 2014). Others conclude that population growth rate is most influenced by calf and juvenile survival in predator-limited populations, especially in summer (Ballard et al. 1991) due to high calf predation by wolves, grizzly bears, and black bears (Gasaway et al. 1992, Boertje et al. 1996, Hayes et al. 2003), and presumably certain regions of BC are similar. Nutritionally-compromised cows also experience reduced pregnancy rate and calf survival (Murray et al. 2006, Schwartz 2007), both of which negatively influence recruitment and population growth rate.

Predation is considered the major factor influencing cow survival in parts of Canada and Alaska (Hauge and Keith 1981, Mytton

Table 3. Summary of average harvest parameters based on the best models (lowest AIC_c), and assessment of hunting influence (λ_p, λ_h , and bull:cow ratio) in 31 Game Management Zones from 1996–2015 in British Columbia, Canada.

GMZ	Models ^{1,2} with $\Delta AIC_c < 2$	AIC weight (w_i) ³	% Harvest Composition						% Harvest Rate			Rate of Change ⁴					Bulls:100 Cows ⁵				
			Total Harvest		Bulls		Cows		Bulls	Cows	Calves	Total	λ_p	λ_h	1996–2015	1996–2005	2006–2015	2011–2015			
			Bulls	Cows	Calves	Bulls	Cows	Calves	Bulls	Cows	Calves	Total	λ_p	λ_h	1996–2015	1996–2005	2006–2015	2011–2015			
3b	1, 2, 4	0.43	191	88	9	3	36	1	1	1	7	1.03	1.02	18	18	19	23				
3c	1, 3	0.57	137	85	12	3	26	1	1	1	6	1.03	1.02	29	36	21	21				
3d	2	1.00	97	89	8	2	11	1	0	0	4	1.00	0.99	69	87	51	45				
4Ea	2	1.00	104	98	1	0	18	0	0	0	5	1.05	1.05	46	63	29	21				
4Eb	2	1.00	38	97	1	2	16	0	1	1	4	1.03	1.03	40	44	35	28				
4Ec	1	0.60	24	95	5	0	9	0	0	0	3	0.97	0.97	60	72	47	46				
4Wa	2, 1	0.61	23	100	0	0	14	0	0	0	4	1.11	1.11	55	65	44	43				
4Wb	4	0.99	75	69	24	7	18	3	3	3	7	1.04	1.00	49	67	31	29				
5a	2, 1	0.55	137	93	7	0	24	1	0	0	6	1.02	1.02	38	54	23	21				
5b	1, 2, 4	0.41	433	99	1	0	25	0	0	0	6	0.98	0.98	28	29	27	26				
5c	4, 2, 1	0.47	519	99	0	1	22	0	0	0	5	0.98	0.98	34	33	36	37				
5d	2	1.00	160	100	0	0	18	0	0	0	5	0.99	0.99	38	37	38	36				
6b	2	1.00	110	99	1	0	11	0	0	0	3	0.98	0.97	56	53	60	60				
6c	4	1.00	1001	97	2	1	21	0	0	0	5	0.99	0.99	35	36	35	34				
6d	4	0.96	86	99	1	0	6	0	0	0	1	0.98	0.98	47	54	40	38				
6e	4	1.00	380	100	0	0	10	0	0	0	3	1.02	1.02	58	63	52	52				
6f	2, 4, 1	0.51	191	100	0	0	5	0	0	0	2	1.00	1.00	56	56	56	56				
70a	2	0.68	261	68	21	11	24	3	6	6	9	1.06	1.02	43	64	22	18				
70b	4	1.00	1490	58	15	26	17	2	9	7	7	1.00	0.97	35	37	33	32				
70c	4, 3	0.57	809	68	15	17	11	1	5	4	4	1.00	0.99	43	53	34	32				
70d	3, 4, 2	0.46	424	73	16	11	10	1	2	4	4	0.99	0.98	49	50	48	46				
70e	4	0.99	101	100	0	0	10	0	0	0	3	1.00	1.00	49	53	45	46				
7Pa	4	1.00	372	100	0	0	12	0	0	0	3	0.98	0.98	42	40	43	42				
7Pb	4	1.00	798	95	1	3	22	0	1	6	6	0.98	0.97	32	32	31	30				
7Pc	2	0.79	361	100	0	0	14	0	0	0	3	0.96	0.96	28	27	29	28				
7Pd	2, 3	0.71	172	100	0	0	6	0	0	0	2	0.97	0.97	49	45	53	51				
7Pe	2, 1, 3	0.38	184	99	0	0	6	0	0	0	2	0.98	0.98	57	56	57	56				

(Continued)

Table 3. (Continued)

GMZ	Models ^{1,2} with $\Delta AIC_c < 2$	AIC weight (w_i) ³	Total Harvest	% Harvest Composition			% Harvest Rate			Rate of Change ⁴		Bulls:100 Cows ⁵				
				Bulls	Cows	Calves	Bulls	Cows	Calves	Total	λ_p	λ_h	1996–2015	2006–2015	2011–2015	
8a	1	0.87	38	99	0	1	40	0	0	12	1.11	1.11	38	53	24	25
8b	1	0.62	86	97	3	0	26	0	0	6	1.03	1.02	35	47	24	25
8c	3	0.74	18	97	3	0	17	0	0	4	1.09	1.09	42	56	28	22
8d	1	0.64	41	99	1	1	28	0	0	6	1.02	1.02	30	33	27	28

¹ Model 1. Calf:cow ratio at 6 months (R_6), juvenile (S_j) and cow survival (S_p) rates are constant.

Model 2. Linear trend in calf:cow ratio at 6 months. Juvenile and cow survival rates are constant.

Model 3. Linear trend in juvenile survival rate. Calf:cow ratio at 6 months and cow survival rates are constant.

Model 4. Linear trend in cow survival rate. Calf:cow ratio at 6 months and juvenile survival rates are constant.

² Models listed starting with lowest ΔAIC_c .

³ AIC relative weight of best fitting model.

⁴ λ_p = potential annual growth rate of females without hunting, λ_h = annual growth rate of females with hunting. $\lambda < 1$ is highlighted in grey.

⁵ Bull:cow ratios by time period. Adult:sex ratios < 30 bulls:100 cows are highlighted in grey.

and Keith 1981, Larsen et al. 1989, Ballard et al. 1991, Gasaway et al. 1992). Given that a third of GMZs had declining cow survival, particularly in remote areas of northern BC, these areas probably reflect a natural predator-prey system with minimal human influence (Ballard et al. 1991). In such systems, the main cause of cow mortality is generally wolf predation (Hauge and Keith 1981, Ballard et al. 1991) with less predation by grizzly bears (Boertje et al. 1988). A current study with radio-collared cows in central BC is evaluating a landscape change hypothesis that assumes cow survival has a greater proportional effect on population growth rates than calf survival (Kuzyk and Heard 2014). In that study, annual cow survival rate ranges from 86–92% (Kuzyk et al. 2016) and is within the expected range of stable populations (Bangs et al. 1989, Ballard et al. 1991, Bertram and Vivion 2002), and exceeds rates measured in the Northwest Territories (85%; Stenhouse et al. 1995) and northern Alberta (75–77%; Hauge and Keith 1981). The primary causes of mortality (as of Kuzyk et al. 2016) were predation (43%), health-related (28%), and unlicensed hunting (16%).

We found proportionally steeper population declines in the last 5 years (2011–2015) when 45% of populations were in >20% decline compared to 29% of populations declining $\leq 20\%$ previously. These accelerated declines are consistent with other studies in which ungulate species globally have declined ($\leq 23\%$) in the past 40 years (Di Marco et al. 2014). For example, recent declines have been reported for mule deer (Lendrum et al. 2013) and pronghorn antelope (*Antilocapra americana*) in North America (Christie et al. 2015), ungulates in Africa (Western et al. 2009), and saiga antelope (*Saiga tatarica*) among other species in the Soviet Union (Milner-Gulland et al. 2001). The level of decline in our study was likely influenced by the rate of early calf

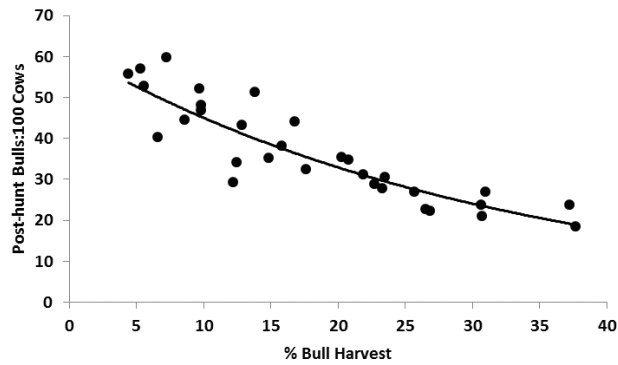


Fig. 4. Predictions of the post-hunt, bull:cow ratio based on the modelled bull harvest rate from 31 Game Management Zones in British Columbia, Canada; $\hat{y} = 61.595e^{-0.031x}$ where \hat{y} is the post-hunt bull:100 cows ratio, and x is the bull harvest rate (bull harvest/pre-hunt bull population).

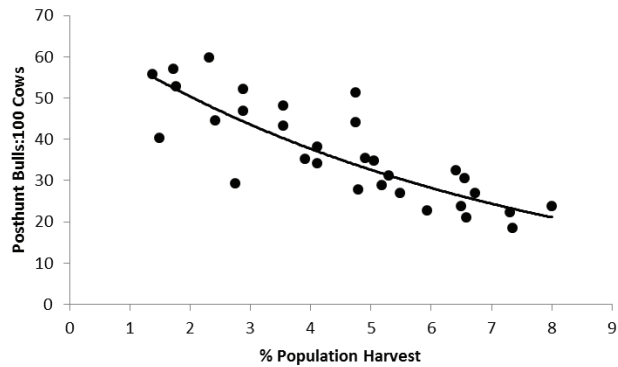


Fig. 5. Predictions of the post-hunt, bull:cow ratio based on the modelled population harvest rate from 31 Game Management Zones in British Columbia, Canada; $\hat{y} = 67.339e^{-0.145x}$ where \hat{y} is the post-hunt bull:100 cows ratio, and x is the population harvest rate (bull harvest/pre-hunt population of bulls, cows, and calves).

survival which is directly related to the level of predation (Larsen et al. 1989, Bertram and Vivion 2002, Patterson et al. 2013). Presumably, stochastic environmental events during the 20-year period added to the variability of reproductive rates and juvenile and adult survival rates (Sæther 1997, Gaillard et al. 2000), and that decline in individual GMZs reflected the combined influence of these parameters and local anthropogenic disturbances (Brown 2011).

A major challenge for wildlife managers is maintaining sustainable harvests of ungulates in systems with multiple factors

influencing population growth (Fryxell et al. 2014), which is especially relevant when populations are declining (Palazy et al. 2012). Moose in BC have high cultural and economic importance, and harvest management objectives are set to ensure that First Nations requirements are addressed, while maintaining diverse opportunities for licenced hunters (BC FLNRO 2015). Licenced antlerless harvest rates were low during the 20-year period, averaging ~1.5% for cows and 3% for calves. These rates were insufficient to initiate population declines, although may have minor additive effect on

populations in decline. Our results are suggestive of areas in Alaska where predator density has been reduced or moose populations are near their nutritional limitations, such that harvest mortality is partially compensatory to natural mortality (Boertje et al. 2007, Boertje et al. 2009). A sustainable harvest in either system can include a combination of bulls, cows, and calves. However, in areas where predation remains high, hunter harvest is often considered additive and restricted to bull-only harvest to avoid further population decline (Van Ballenberghe and Dart 1982, Gasaway et al. 1992, Boertje et al. 1996).

Although a combination of harvest strategies may be required to adapt to variable factors influencing ungulate population growth (Fulton and Huntermark 2004, Stedman et al. 2004), an ongoing challenge is the lack of adequate data to implement and monitor diverse harvest strategies (Bunnefeld et al. 2011), especially with high hunter demand concurrent with declining populations. Ministry policy in BC is to maintain post-hunt, bull:cow ratios ≥ 30 bulls:100 cows in densities >200 moose/1000 km², and 50 bulls:100 cows in densities <200 moose/1000 km² (BC MOE 2010). Although adult sex ratios were > 30 bulls:100 cows in most GMZs, bull:cow ratios were significantly lower during 2006–2015 ($\bar{x} = 37:100$) than 1996–2005 ($\bar{x} = 48:100$); declining recruitment may have been a contributing factor.

We found significant predictive relationships between harvest rates and bull:cow ratios. Although the population harvest rate (bull harvest/pre-hunt population) accounted for 68% of the variance in bull:cow ratios for the time period 2006–2015, it was a poor predictor of adult sex ratios in the other periods. In contrast, the bull harvest rate (bull harvest/pre-hunt bulls) was a good predictor of bull:cow ratios in all time periods.

In 2006–2015 we found that average population harvest rate of 6% and bull harvest rate of 24% resulted in post-hunt, adult sex ratios of 30 bulls:100 cows. In areas with limited survey and monitoring data, our modelling suggests that a maximum population harvest rate of 5% and maximum bull harvest rate of 20% would be sustainable for most populations in BC. These recommendations are similar to those in other northern systems where moose are limited by predation (Hayes et al. 2003). Importantly, calculation of sustainable bull harvest rates must account for bull selectivity in the unlicensed harvest and trends in calf recruitment.

Our assessment provides a more rigorous and refined determination of moose population and licenced harvest trends in BC than previously available at the provincial and regional scales (Hatter 1999, Kuzyk 2016). For example, we found that the provincial moose population declined by 32% ($\lambda = 0.96$) from 2006–2015, which more closely aligns with views expressed by many First Nations and other stakeholders (Gorley 2016, Kuzyk 2016). Further, we determined that the provincial moose population trend and licenced harvest were highly correlated, suggesting that declining harvest was a reaction to the declining population, a conclusion similar to those in certain western United States where harvest and populations have declined in the past 15 years (Decesare et al. 2014, Nadeau et al. 2017, Timmermann and Rodgers 2017).

Despite our efforts to improve understanding of moose population trends by using a statistical model-fitting approach (White and Lubow 2002), we acknowledge that limited survey data in certain GMZs could lead to uncertainty in interpretation and extrapolation of our model results; e.g., 4 GMZs had only a single population estimate and 2 GMZs had only a single year of

sex/age ratio data. Therefore, we used KPUE as a trend index to assist the models in determining population growth rates, especially in certain northern GMZs with limited data. While we acknowledge the limitations of KPUE as a trend index (Crichton 1993, Bowyer et al. 1999, Hatter 2001, DeCesare et al. 2016), particularly in areas with increasing road access, we found similar trends in survey density estimates and KPUE in many GMZs.

Another data concern was that the First Nation's harvest (LeBlanc et al. 2011) was unknown and not quantifiable as an annual harvest statistic. Although field (i.e., radio-telemetry) estimates of cow survival rates have included unlicensed harvest (Kuzyk et al. 2016), sample sizes and distribution of study areas on the provincial landscape were likely insufficient to adequately estimate losses at the provincial scale or account for temporal changes in harvest rate. The amount of unlicensed harvest of bulls and calves is also unknown at the provincial scale, and likely varied spatially and temporally during the 20-year study period. A system of reliably estimating First Nations harvest would benefit provincial and regional moose population modelling by providing a more complete representation of harvest statistics. And, as with most studies, increasing the number and frequency of moose density estimates and composition surveys would also provide more reliable data and population estimates.

Despite these limitations, we were able to assess moose population dynamics and licensed harvest trends over a 20-year period suitable for management purposes. We used science-based and repeatable methods to provide an assessment of provincial and GMZ moose populations, their temporal trends, and predictive relationships useful for developing management strategies. Our approaches and ability to detect

declining population trends will be beneficial when compiling future, broad-scale ungulate population trend assessments.

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