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Sex and age-specific differences in the performance of harvest indices as proxies of population abundance under selective harvesting

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Harvest indices are commonly used as proxies to direct population monitoring but sources of variability, including harvest effort and factors influencing detectability of animals to hunters, are rarely considered. Harvest indices may further be influenced by selective harvesting with regulatory differences in harvest effort across sex and age-classes. To evaluate how sex and age-specific harvests vary as proxies of abundance under selective harvesting, we assessed harvest–abundance relationships (H–A) for moose *Alces alces* bulls, cows and calves across 58 wildlife management units (WMUs) in Ontario, Canada. Selective harvesting in our study area resulted in more regulated harvest of bulls and cows than calves. We therefore predicted more proportional H–A for calves than bulls and cows, with variability in H–A influenced by harvest effort, in addition to weather and landscape features that may influence moose detectability to hunters. In contrast to our expectation, we found that H–A was more proportional for adult moose than calves. Additionally, we found harvest was proportionally highest for bulls, despite greater harvest effort for calves. A positive effect of harvest effort on harvest as moose abundance increased helped to explain proportional H–A for adult moose. However, the effect of harvest effort on harvest was curvilinear at high effort levels, indicating that harvest will underestimate abundance when effort by hunters is high. Additionally, we found evidence of lower harvest in relation to abundance in WMUs with higher levels of recent disturbance from wildfire burns and clear-cuts. We demonstrate that the relationship between harvest and abundance can vary across selectively harvested sex and age-classes, while variability in H–A can be attributed to spatial variability in harvest effort and the landscape. We caution that sources of variability in H–A, both across and among sex and age-classes, should not be ignored when using harvest indices, especially for selectively harvested species.

Keywords: *Alces alces*, harvest effort, hunting, moose, population monitoring, wildlife management, detectability, landscape

Indices of population abundance are commonly relied on in wildlife management to replace or supplement direct population monitoring (Rönnegård et al. 2008, Månsson et al. 2011, Stephens et al. 2015). Indices are typically derived from information that are cheaper and less laborious to collect compared to field-based methods that directly count animals on the landscape (e.g. aerial surveys), particularly to monitor species that are widely distributed at low densities and in remote settings (Morellet et al. 2007, Kindberg et al. 2009). There has been a wide range of applications of indices in wildlife management, including to understand population structure (sex or age-ratios), spatial distribution, habitat occupancy and to track changes in population abundance (Morellet et al. 2007, Stephens et al. 2015). Despite their convenience, the suitability of indices to inform management decisions is often questioned (Anderson 2001, Stephens et al. 2015). Of particular concern is the level of uncertainty and bias that may accumulate through indirect sampling of the population (Anderson 2001, Morellet et al. 2007, Stephens et al. 2015). Sources of uncertainty and bias typically include variable sampling effort and detectability in different environments, which introduces non-biological variability and may impact accurate tracking of the biological parameter of interest (Anderson 2001, Morellet et al. 2007). Although not always a trivial task, accounting for sources of non-biological variability, along with appropriate interpretation, can result in successful characterization of indices across space and time for use in population monitoring (Morellet et al. 2007, Stephens et al. 2015).

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For harvested species, a common and indirect method of monitoring is the collection of harvest data. Assessment of harvest is an attractive approach to population monitoring for wildlife managers, as harvest data are relatively cost-effective and easy to obtain in comparison to direct monitoring approaches such as aerial surveys (Månsson et al. 2011, Boyce et al. 2012). The number of individuals of a species harvested is assumed to reflect population abundance and may be used to assess population structure (i.e. sex and age-ratios), and track spatial distribution and/or change through time (Cattadori et al. 2003, Boyce et al. 2012). A common method used to validate indices is their proportionality with abundance (Kindberg et al. 2009, Kahlert et al. 2015). While a proportional relationship between population abundance (or density) and harvest has been reported for several species including game birds (Cattadori et al. 2003) and Cervids (Ueno et al. 2014), other studies have found poor linear correspondence for a range of species (Choate et al. 2006, Pettorelli et al. 2007, Imperio et al. 2010, Willebrand et al. 2011, DeCesare et al. 2016). Non-linear relationships between harvest and abundance may arise because of variability in factors associated with harvest success (e.g. harvest effort), as well as factors such as levels of detectability on the landscape (Schmidt et al. 2005, Willebrand et al. 2011, Ueno et al. 2014). Such discrepancies suggest that a better understanding of harvest–abundance relationships is required to determine whether harvest indices can be used as reliable proxies of population abundance.

A main driver and source of variability in harvest is harvest effort by hunters (Willebrand et al. 2011, Kahlert et al. 2015). Harvest effort can reflect the number of tags allocated by managers (i.e. quotas) or directly reflect the number of hunters and time spent hunting, depending on the harvest system in place (Fryxell et al. 2010, Kahlert et al. 2015). When harvest effort is regulated by managers using tags, harvest may reflect management objectives and tradeoffs that do not exclusively rely on population abundance (Robinson et al. 2016). Tag-regulated harvest effort may therefore introduce variability in how well harvest reflects abundance. The effects of harvest effort on harvest may also differ between sex and age-classes within a species due to selective harvesting. For example, males are often targeted for many deer species and hunters are more likely to continue hunting until they are successful (Fryxell et al. 1988, Solberg et al. 2000, Bhandari et al. 2006), while harvest of females and young may experience less harvest effort and total harvest. To prevent overharvest of certain sex and/or age-classes, managers will often restrict harvest by limiting hunting tags (i.e. quotas) for classes that may experience higher harvest effort. Accounting for sex and age-specific differences in how harvest is managed is rarely considered in the assessment of harvest as a proxy of abundance but may be critical in understanding harvest–abundance relationships. Variable harvest effort across sex and age-classes may be of particular concern if harvest is used to compare trends across classes or infer sex and/or age-specific parameters that assume an equal proportion of the population has been sampled, such as recruitment and/or sex ratios.

In addition to harvest effort, variables influencing detectability of animals to hunters, and therefore, number of animals harvested, may help explain the relationship between harvest and abundance. For example, weather (e.g. average temperature and precipitation), as well as landscape features (e.g. proportion of suitable habitat), may affect both animal and hunter activity directly, influencing the likelihood of hunters successfully harvesting an animal (Schmidt et al. 2005, Lebel et al. 2012, Kahlert et al. 2015). Higher density of road access to huntable areas may also improve encounter rates of animals to hunters, and therefore, the number of animals that are harvested (Rempel et al. 1997, Schmidt et al. 2005). Sex and age-specific differences in preference to certain habitat types or weather conditions within a species are also possible and can consequently influence harvest sex and age-ratios (Solberg et al. 2000, Bunnefeld et al. 2009). Harvest indices are often employed uniformly across management areas, yet these variables may vary from year to year and among management areas, further complicating the relationship between harvest indices and population abundance.

In this study, we evaluated the use of sex and age-specific harvest as a proxy of population abundance for moose *Alces alces* across 58 wildlife management units (WMUs) in Ontario, Canada. Moose is a large mammal species that is widely distributed across North America and is typically found at low densities (Timmermann and Rodgers 2005). Although moose are directly monitored in Ontario using aerial surveys, their large distribution permits that only a small fraction of WMUs inhabited by moose are sampled each year, leaving gaps in monitoring information. Moose harvest by resident hunters is used to fill information gaps between years and to detect changes in population abundance among WMUs. Harvest indices used to supplement moose monitoring are not corrected for potential sources of non-biological variability (e.g. harvest effort) to ensure proportionally between harvest and abundance. Harvest is additionally used in the province to inform management decisions regarding moose harvest regulations (i.e. tags and season length). Since 1980, the province has adapted a selective harvesting system with restrictions on number of tags available for adult moose (particularly for cows) while permitting higher harvest of calves. Sex and age-specific difference in harvest–abundance relationships should therefore be expected but are not considered when relying on harvest indices as proxies of abundance. In our study, we assessed sex and age-specific differences in harvest–abundance relationships (hereafter referred to as H–A) for moose bulls, cows and calves. Specifically, we expected less restricted calf harvest to result in abundance explaining a greater proportion of variation in harvest (higher r^2) for calves than for bulls and cows. We further expected that less restricted calf harvest would result in proportionally higher rate of change in calf harvest in relation to abundance (higher slope of regression line), compared to bull and cow harvest. We further assessed whether harvest effort, as well as the confounding effects of weather, including temperature and precipitation during the hunting season, and landscape features, including forest type, forest disturbance and road access, could account for additional unexplained variation in sex and age-specific H–A.

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Methods

Study area

The study area extended across continuous moose range in Ontario, Canada and was located predominately in the Boreal Shield ecozone, extending into the Hudson Bay Lowlands ecozone in the north-east of the province (Fig. 1). The Boreal Shield is dominated by the Boreal forest region in the north and Great Lakes St-Lawrence forest region in the south, while the Hudson Bay Lowlands are made up of a mixture of boreal forest and extensive wetlands (Rowe 1972). Temperatures across Ontario can vary based on the season and region and ranged on average from −13°C in winter to 13°C in summer (Girardin and Mudelsee 2008). Forestry practices have been increasing across the Boreal Shield since the 1950s, with clear-cuts being the most common silviculture system (Perera and Baldwin 2000). Wildfire burns are also common across the Boreal Shield but are variable in frequency and severity due to active fire suppression and/or forestry practices (Girardin and Mudelsee 2008).

Moose range in Ontario overlaps with three other ungulate species, including: white-tailed deer *Odocoileus virginianus*, boreal woodland caribou *Rangifer tarandus caribou* and elk *Cervus canadensis*. Primary predators are shared by all ungulate species in the province and include wolves *Canis lupus*, coyotes *Canis latrans* and black bears *Ursus americanus*.

Ontario is divided into wildlife management units (WMUs) that facilitate the monitoring and management of wildlife, primarily of harvested species. Our study included 58 WMUs that overlap moose range in the province, spanning an area of 564 989 km² (Fig. 1). WMUs ranged in size from 842 to 40 657 km² and were selected based on the availability of both harvest records and moose aerial inventory data for the same year.

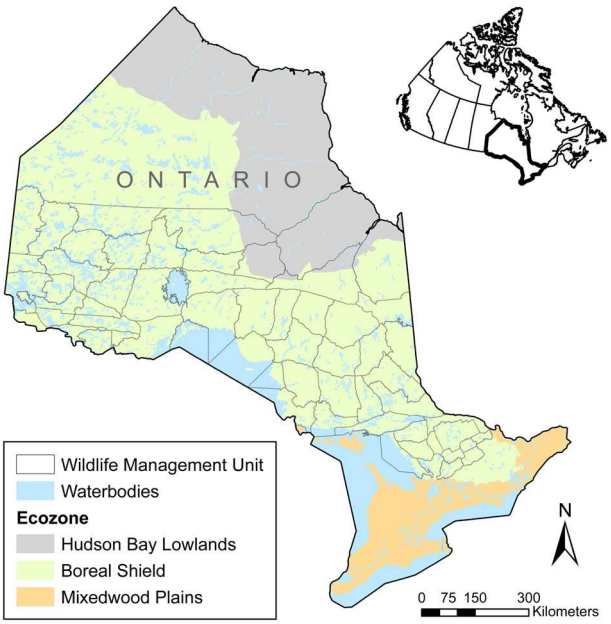

Figure 1. Map outlining the wildlife management units in Ontario, Canada included in the study.

Moose population abundance

Year-specific estimates of moose population abundance were derived from aerial surveys conducted by the Ontario Ministry of Natural Resources and Forestry (MNRF) between the years 2000 and 2015. Aerial surveys were conducted every 3–5 years in each WMU during the winter following the annual moose hunting season and used plot-based stratified random sampling or, in some northern WMUs with low moose density, systematic transects. With respect to plot-based surveys, each WMU was divided into a grid of 25 km² plots and a stratified random sample of plots was flown with a helicopter to record all moose observations by sex and age-class (bull, cow or calf). Moose numbers were projected for the entire WMU by the MNRF based on observed counts within each stratified plot (McLaren 2006). Observation error that may result from variation in moose detectability (e.g. vegetative cover and observer experience) was not accounted for in projected counts, therefore, measures of moose population abundance are likely under-represented for each WMU (Crête et al. 1986, McLaren 2006). Effort to maintain consistency in the proportion of the population surveyed was achieved by flying surveys under a set of guidelines (e.g. under conditions that will improve moose visibility to observers) and during the same time each year (McLaren 2006).

Harvest indices

The hunting season for moose in Ontario took place from September to December, with dates and season length varying slightly among WMUs and by firearm type (gun or archery). Bull and cow harvest were regulated through a lottery-based moose validation tag draw with bull and cow tag numbers varying according to management decisions and moose population objectives specific to each WMU. Calf tags were available for purchase to all licensed hunters, with a limit of one calf tag per hunter, across most WMUs. Four WMUs in our study area had restricted calf harvest since 2004 with tags issued based on a validation tag draw. Mailed-out postcard surveys were used to collect harvest information from a random sample of hunters each year. Harvest reporting was voluntary across the province during our study period except in WMUs where calf harvest was restricted. Harvest information collected from hunters included number of bulls, cows or calves killed and harvest effort (number of hunters and days spent hunting). Our analysis included moose harvest records from 1999 to 2014, starting in the year that information on harvest effort began to be collected by the province. Due to non-mandatory reporting by hunters across most WMUs during the period of our study, raw harvest-records likely under-represented harvest by hunters. To account for variable reporting, we used projected rather than raw harvest in our analysis. Projected harvest for each WMU and year was provided by the MNRF and was calculated as the proportion of hunters with a tag that successfully harvested a moose divided by the return rate of postcard surveys for a given WMU and year.

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Predictors of harvest–abundance relationships

To explore variability in harvest not accounted for by abundance, we assessed the effects of harvest effort, as well as the confounding effects of weather and landscape features on H–A. We used number of hunters to represent harvest effort because this metric was correlated ($r > 0.65$) with both days spent hunting and tags allocated (for bulls and cows) or sold (for calves). To assess how the effect of harvest effort may vary based on population abundance, we evaluated the interacting effect between harvest effort and population abundance on sex and age-specific harvest. We expected harvest effort to have a higher effect on harvest when population abundance was high, as higher population abundance should increase the encounter rates of moose by hunters (Schmidt et al. 2005, Willebrand et al. 2011, Ueno et al. 2014). Further, weather and landscape variables were predicted to influence hunter success in encountering and harvesting a moose, and therefore, how well harvest linearly reflected abundance. At the WMU scale in our analysis, we expected similar factors to influence detectability of moose to hunters across sex and age-classes.

Weather variables considered to impact moose harvest included averaged maximum monthly temperature (°C) and average precipitation (mm) during the hunting season (Table 1). While temperatures are typically mild during the moose hunting season (on average between 15 and −5°C), warmer temperatures in the fall have been found to result in an increased use of densely forested areas for thermal cover and increasing nocturnal activity by moose (Dussault et al. 2004). Higher temperatures during the hunting season may therefore result in lower detectability of moose to hunters and lower harvest rates. Similarly, precipitation or snow depth may limit daily movement of moose (Lowe et al. 2010) as well as hunters, which may result in reduced harvest. Maximum monthly temperatures were averaged over the months overlapping the hunting season (between September and December) for each WMU and year included in the study. Similarly, monthly precipitation was averaged over the hunting season (between September and December) for each WMU and year. Weather data was extracted for each WMU/year from monthly, spatially continuous grids composed by Natural Resources Canada (McKenney et al. 2006, 2007).

Landscape variables considered to impact moose harvest included: proportion of roads, dense forest cover, sparse forest cover, mixed-deciduous forest cover and disturbances including wildfire burns and clear-cuts (Table 1). Moose prefer mixed-deciduous forest cover (Dussault et al. 2006, Brown 2011) and forest disturbances, such as wildfire burns and forestry clear-cuts, where forest regeneration provides forage opportunities (Dussault et al. 2006). Moose, particularly cows, may also avoid recent (< 10 year) forest disturbances such as clear-cuts and wildfire burns, as these areas likely offer poor forage opportunity and low cover from predators (Maier et al. 2005, Dussault et al. 2006). Forested areas that provide adequate cover from predators have similarly been found to be selected by moose, especially cows with calves (Kunkel and Pletscher 2000, Dussault et al. 2005), with avoidance of open areas with sparse cover during the day (Bjørneraas et al. 2011). Likely in consequence, harvest success may also increase in sparser forested areas near forest disturbances where hunters have greater visibility (Brinkman et al. 2009, Lebel et al. 2012). Additionally, roads have also been associated with higher moose density at larger spatial scales (Brown 2011, Beyer et al. 2013) and they provide access to moose habitat for hunters, which may result in increased harvest (Rempel et al. 1997, Schmidt et al. 2005).

We generated landscape variables using the Ontario land cover classification (Anonymous 2004), which was updated with annual forest harvest and wildfire layers available from the MNRF to integrate year-specific landscape changes. We derived landscape variables from raster layers as a percent area covered for each WMU based on year included in the study. We conducted all spatial analysis involving covariate data extraction using ArcMap ver. 10.2.2 (ESRI 2014).

Statistical analysis

We evaluated the linear relationship between annual moose harvest and aerial survey-based moose abundance using linear mixed-effect models (LMER) in R package *lme4* version 1.1-21 (Bates et al. 2015). Due to multiple years of sampling within WMUs, both random effects of WMU (to accounting for spatial variability) and year (to account for temporal variability) were included in each model. To address anticipated differences in H–A across sex and age-classes, we initially evaluated how abundance explained variation in harvest for

Table 1. Model variables predicted to influence the linear relationship between moose harvest and abundance. Means, standard error (± SE) and range of values for each variable are based on all Wildlife Management Units (WMUs) and years included in the study (n = 216).

Predictor set	Variable	Description	Mean	± SE	Range
Abundance	Bull abundance	number of bull moose	487	23	22–1560
	Cow abundance	number of cow moose	871	43	30–3095
	Calf abundance	number of calf moose	261	13	10–1086
Harvest effort	Bull hunters	number of bull hunters	201	17	9–1332
	Cow hunters	number of cow hunters	85	9	1–1197
	Calf hunters	number of calf hunters	1083	63	8–4323
Weather	Temperature	average maximum temperature (°C) during the hunting season	10.1	0.157	15–2
	Precipitation	average precipitation (mm) during hunting season	88.3	2.8	25–224
Landscape	Dense	% continuous forest canopy	0.19	0.005	0.02–0.41
	Sparse	% patchy or sparse forest canopy	0.13	0.005	0.03–0.31
	Mixed-deciduous	% mixed deciduous forest	0.11	0.004	0.02–0.30
	Disturbance	% < 10-year-old forest clear-cuts and burns	0.12	0.004	0.01–0.31
	Roads	% major roads and development (including forestry roads)	0.005	0.0003	0–0.02

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bulls, cows and calves combined. An interaction term for sex and age-class (bull, cow or calf) was included to assess whether there was a significant difference in how abundance explained variation in harvest among sex and age classes. We then modelled bull, cow and calf H–A separately to further assess sex and age-specific differences in linear model fit. We used the fit of the regression line (r^2) to evaluate how well abundance explained variation in harvest and the slope of the regression line to evaluate proportional rate of change in harvest in relation to abundance.

We further assessed whether variability in harvest that was not attributed to abundance could be explained by harvest effort and weather and landscape variables using generalized additive models (GAMs, R package *mgcv* ver. 1.8-28, Wood 2011). We fit smoothing curves to predictor variables to assess non-linear relationships with harvest using thin plate regression splines and limited degrees of freedom (df) to 3 for each predictor variable to avoid model overfitting. Assessing non-linear relationships permitted us to characterize deviations from linear H–A. Nine candidate models were assessed for each sex and age-class that evaluated the role of population abundance, harvest effort, weather, landscape features and their combinations in affecting harvest. Abundance was retained in each candidate model to assess the additive effects of each variable on harvest. We additionally tested the significance of an interaction term between harvest effort and abundance for each sex and age-class by fitting a tensor product-based smooth function for interactions to the predictors. A random effect of WMU and year was included in each model set. All predictor variables were standardized with a mean 0 before analysis and evaluated for collinearity to prevent correlated variables ($r > 0.7$; Dormann et al. 2013) from being included in the same model. GAMs were fit with a Gaussian distribution and identity link and heteroscedasticity was addressed by square-root transforming response variables after adding 0.5 to each value to account for 0s in the data (Zuur et al. 2007). Model residuals were further assessed to ensure that they were normally distributed following the transformation of response variables. During model evaluation, smooth functions were removed from predictor variables if df was equal to 1. Candidate models were compared to identify the most parsimonious model using Akaike's weights based on maximum likelihood (w_i) and difference in Akaike's information criterion (ΔAIC) (Burnham and Anderson 2002). The proportion of null model deviance explained (total sum of squares equivalent) was also evaluated for each model (Zuur et al. 2007, Wood 2011). Final model selection for bulls, cows and calves was based on model fit determined by w_i and ΔAIC (Zuur et al. 2009). If $\Delta AIC \leq 2$ for two or more models, the final model was chosen based on w_i and preference was given to the model with a lower number of predictor variables. Model coefficient estimation was conducted using restricted maximum likelihood (REML). The importance of each predictor variable and its effect on sex and age-specific H–A was further assessed by plotting component smooth functions and linear term effects for all significant ($p < 0.05$, based on Wald test) predictors in each final model (Wood 2011). Plotted GAM curves provided a visual representation of individual predictor variable effects and potential thresholds in smoothed terms based on confidence intervals (Zuur et al. 2009). All statistical analyses were conducted using R software ver. 3.5.3 (<www.r-project.org>).

Results

Relationship between harvest indices and abundance

We used 216 WMU-year samples that had both moose harvest and aerial survey data available. Return rates of harvest reports from hunters averaged 60% across WMUs and years. Fill rates of adult tags (total moose killed/total tags issued) were low across WMU-years at 35% on average for bulls and 30% for cows. Harvest success rates (total moose killed/total number of hunters) averaged 40% for bulls, 41% for cows and 3.5% for calves.

Linear regression revealed a significant interaction between moose abundance and sex/age-class (analysis of variance F value = 37.8, $p < 0.0001$), so we subsequently ran separate H–A models for bulls, cows and calves. Regression analysis revealed that a linear model relating abundance to harvest had an explained deviance of $r^2 = 0.79$ for bulls, $r^2 = 0.68$ for cows and $r^2 = 0.51$ for calves when variation among WMUs and years was accounted for. Regression coefficients, indicating the rate at which harvest increased in proportion to abundance, were highest for the bull H–A model (slope = 0.07, SE = 0.01, df = 209.1, t = 6.5, $p < 0.0001$), followed by the calf H–A model (slope = 0.06, SE = 0.01, df = 194.2, t = 4.8, $p < 0.0001$) and lastly the cow H–A model (slope = 0.02, standard error = 0.003, df = 118.6, t = 8.2, $p < 0.0001$) (Fig. 2). When the relationship between harvest and abundance was evaluated with splines, a non-linear relationship performed better than linear (df > 1) for cow H–A ($r^2 = 0.80$, F = 37.8, smoothed df = 1.56, $p < 0.0001$) and calf H–A ($r^2 = 0.61$, F = 22.8, smoothed df = 1.96, $p < 0.0001$), but linear model best described bull H–A ($r^2 = 0.88$, F = 24.2, smoothed df = 1, $p < 0.0001$).

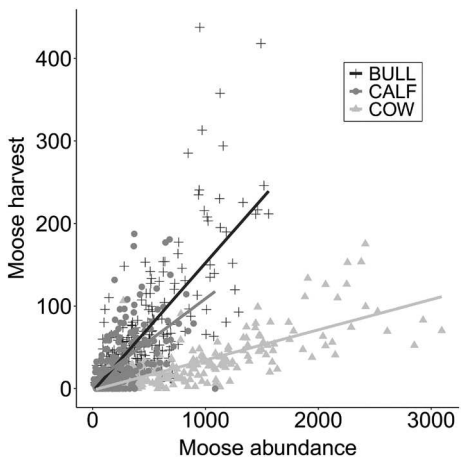

Figure 2. Linear relationship between moose harvest and abundance for bulls, cows and calves. The slope of each regression line was significantly different from zero ($p < 0.0001$).

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Variables influencing harvest–abundance relationships

Harvest effort explained the greatest proportion of null model deviance for bull and cow harvest, while abundance explained the greatest proportion of null model deviance for calf harvest (Table 2). Additive effects of harvest effort and abundance did not greatly improve deviance explained for any sex or age-class model, however, the interaction between harvest effort and abundance did improve model fit in all cases. Final models selected for bulls, cows and calves included the main effects of harvest effort and abundance, their interaction and landscape predictors (Table 2, 3). Inclusion of weather predictors in final models did not improve model deviance explained, and although ΔAIC was < 1 in the calf model that included weather predictors (Table 2), w_i was higher for the model that excluded weather, therefore, the most parsimonious of the two models was chosen. There was no collinearity among variables included in each model set (harvest effort, abundance and landscape) (Supplementary material Appendix 1 Table A1), permitting the inclusion of predictor variables in final models for each sex and age-class.

In final models, bull and calf abundance had a linear effect on respective harvest, while the effect of cow abundance on harvest was positive and curvilinear at high abundance levels (Table 3, Fig. 3). Calves showed the widest range of harvest for a given abundance (Fig. 3). Harvest effort had an approximately quadratic relationship with harvest for bulls, cows and calves that either plateaued or decreased at high levels of harvest effort (Fig. 3). Calves showed the widest range of harvest for a given level of harvest effort, while the relationship was approximately linear for adult moose at lower levels of harvest effort (Fig. 3). A significant interaction effect between abundance and effort on harvest revealed that bull and cow harvest increased linearly with abundance as harvest effort increased, but the effect was curvilinear when harvest effort was high (Table 3, Supplementary material Appendix 1 Fig. A1). Alternatively, harvest effort did not increase linearly with abundance for calves, resulting in higher calf harvest at high abundance and low effort levels, followed by approximately mid-abundance and high effort levels (Supplementary material Appendix 1 Fig. A1). Both bull and cow harvest were also high at high abundance and low effort levels. Cow harvest was additionally high at approximately mid-levels of harvest effort and low levels of abundance (Supplementary material Appendix 1 Fig. A1).

Habitat variables showed a range of importance in explaining variation in harvest based on F-values, but only forest disturbance (representing < 10 year old forestry clearcuts and burns) was significant ($p \leq 0.05$) for each sex and age-class (Table 3). Based on GAM response curves, the relationship between forest disturbance and harvest was curvilinear and a negative effect was significant (confident intervals non-overlapping zero) at approximately ≥ 25% WMU area disturbed for bulls, ≥ 20% WMU area disturbed for cows and ≥ 18% WMU area disturbed for calves (Fig. 3).

Discussion

Whereas the use of harvest indices as proxies of population abundance can offer a convenient alternative to direct monitoring (Morellet et al. 2007, Stephens et al. 2015), sources of variability, particularly across sex and age-classes, are rarely considered. Our findings indicated that harvest–abundance relationships may reflect differences in harvest regulations across sex and age-classes, warranting caution in the use of harvest indices as proxies of abundance for selectively harvested species. In contrast to our prediction, the use of harvest to inform on spatial and temporal variability in abundance across WMU was more justified for harvest of adult moose (i.e. bulls and cows, for which harvest was more tightly managed) than for calves. Linear H–A model fit was similar for bulls and cows, suggesting that harvest restrictions (i.e. limited number of tags) may have contributed to the proportionality found between harvest and abundance for adult moose. A positive interaction between harvest effort and population abundance, regardless of the harvest system in place, is possible if encounter rates of moose by hunters increases proportionally with population abundance (Schmidt et al. 2005, Willebrand et al. 2011, Ueno et al. 2014). We found that an approximately positive linear interaction as harvest effort and abundance increased was most

Table 2. Model comparison with ΔAIC, Akaike weights (w_i) and % deviance explained for each generalized additive model fit using maximum-likelihood and analyzed with a random effect of wildlife management unit and year.

	Bull			Cow			Calf		
Model*	ΔAIC	w_i	Deviance explained (%)	ΔAIC	w_i	Deviance explained (%)	ΔAIC	w_i	Deviance explained (%)
Abundance	196	0	91.3	207	0	84.7	57	0	70
Effort	64	0	94.9	63	0	92.6	49	0	67.7
Weather	185	0	91.9	170	0	88.2	75	0	68.7
Landscape	179	0	92	172	0	87.9	64	0	68.9
Abundance + Effort	54	0	95.1	63	0	92.3	30	0	71
Abundance + Effort + Abundance × Effort	10	0	96.4	6	0	94.5	3	0	75.8
Abundance + Effort + Abundance × Effort + Weather	12	0	96.4	9	0	94.4	4	0	75.8
Abundance + Effort + Abundance × Effort + Landscape	0	1	96.6	0	1	94.6	0	1	75.4
Abundance + Effort + Abundance × Effort + Weather + Landscape	3	0	96.6	3	0	94.6	1	0	75.4

AIC, Akaike's information criterion.
* Interaction term fit using a tensor product-based smooth function.

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Table 3. Generalized additive model (GAM) results for final bull, cow and calf harvest models fit using restricted maximum likelihood. Results include either linear or smooth effect terms for predictor variables in each model. All smoothed predictors were fit using thin plate regression splines and the interaction between harvest effort and abundance was fit using a tensor product-based smooth function.

	Linear terms				Smooth terms		
Variable	Estimate	SE	t-value	p-value	df	F	p-value
Bull							
Intercept	6.34	0.38	16.52	< 0.0001			
Abundance	0.00	0.00	4.19	< 0.0001			
Effort					1.92	82.54	< 0.0001
Dense					1.58	0.49	0.5
Sparse	−0.16	0.17	−0.95	0.3			
Mixed-deciduous					1.77	2.01	0.2
Disturbance					1.83	3.34	0.02
Roads	0.29	0.17	1.67	0.1			
Abundance × Effort					9.44	4.08	< 0.0001
WMU					40.14	4.94	< 0.0001
Year					10.21	3.32	0.01
Cow							
Intercept	5.06	0.17	29.16	< 0.0001			
Abundance					1.89	12.76	< 0.0001
Effort					1.97	66.62	< 0.0001
Dense	−0.08	0.12	−0.67	0.5			
Sparse					1.51	0.34	0.6
Mixed-deciduous	0.08	0.11	0.72	0.5			
Disturbance					1.83	2.74	0.05
Roads					1.70	2.34	0.2
Abundance × Effort					8.94	7.02	< 0.0001
WMU					35.80	2.92	< 0.0001
Year					9.21	2.72	0.002
Calf							
Intercept	3.63	0.36	10.15	< 0.0001			
Abundance	0.01	0.00	4.42	< 0.0001			
Effort					1.94	22.13	< 0.0001
Dense	−0.22	0.20	−1.11	0.3			
Sparse					1.47	0.26	0.6
Mixed-deciduous	−0.30	0.21	−1.40	0.2			
Disturbance					1.78	4.44	0.01
Roads					1.85	3.16	0.08
Abundance × Effort					5.67	6.68	< 0.0001
WMU					25.47	0.97	0.0003
Year					7.18	1.09	0.03

evident for bull harvest. Noise in the interaction between harvest effort and abundance for cows can explain the non-linear H–A identified in the final cow model and reveals that cow harvest was proportionally higher at high cow abundance in response to greater harvest effort. In contrast, the weak proportionality found between harvest and abundance for calves may suggests that harvest effort for calves was not directly reflective of calf abundance. Additionally, we found calf harvest effort did not greatly improve model deviance explained in calf H–A compared to calf abundance alone, despite calf harvest varying widely across abundance levels. We suggest that the number of moose hunters (i.e. harvest effort) was more influenced by the availability of tags for adult moose than the perceived abundance of calf moose in the population.

Although harvest effort was not a strong predictor of variability in calf harvest, high harvest effort for calves was evident in H–A model slopes. Calf harvest was found to be proportionally higher in relation to abundance than cow (but not bull) harvest. Selective harvest strategies that permit higher harvest effort on calves assume that the proportion of calves harvested during the harvest season is near or below the proportion susceptible to natural mortality (Boyce et al. 1999). Nonetheless, selective harvesting that restricts harvest effort for adult moose may result in higher calf harvest due to re-directed harvest effort (Sæther et al. 2001). Re-direction in harvest effort from adults to calves in our study system was particularly feasible, as number of calf tags for purchase by resident hunters was unrestricted (except in four WMU). Low proportional cow harvest detected in our study was expected, as cow harvest was maintained at low quotas (except in one WMU) in our study area. Alternatively, the high slope in H–A for bulls may reflect male-biased harvesting where bull hunters may be more willing to continue hunting until successful compared to hunting for cows or calves (Fryxell et al. 1988, Solberg et al. 2000, Bhandari et al. 2006). Additionally, bulls may be more active than cows and calves during the hunting season that overlaps the rut (breeding season), which may result in greater success of bull harvest (Neumann et al. 2009). The varying effects of harvest effort on bull, cow and calf harvest suggest that harvest indices should not be compared across sex or age classes (i.e. to estimate age or sex ratios), which requires that the population has been equally sampled. Ensuring indices

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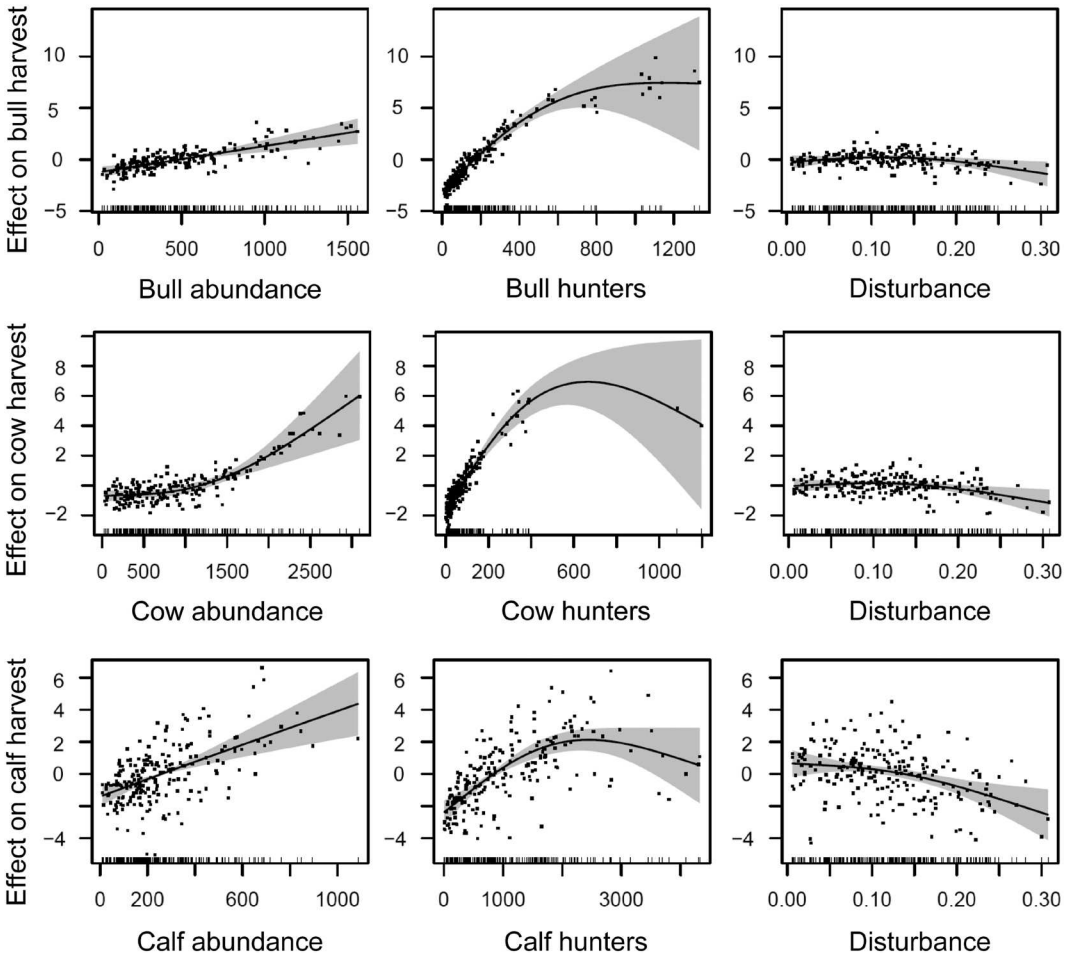

Figure 3. Generalized additive model response curves describing the combined additive effects of abundance (first column), harvest effort represented by number of hunters (second column) and forest disturbance of recent clear-cuts and burns (last column) on bull (top row), cow (middle row) and calf (bottom row) harvest. Each row corresponds to a separate model. Mean response of each variable (solid line) and 95% confidence intervals (gray areas) are indicated and integrate random effects of wildlife management unit and year. Dots indicate residuals of each effect on sex and age-specific harvest. Smooth terms were fit using thin plate regression spline with 3 degrees of freedom. Tick marks on the x-axis of each plot correspond to sample observations.

are reliable is particularly important for managing harvested species, as poorly informed management decisions can lead to the potential over or under-harvest of populations (Fryxell et al. 2010).

Our analysis of the interaction effect between harvest effort and abundance revealed that low harvest effort in WMUs with high moose abundance led to a positive effect on bull, cow and calf harvest. This interaction suggests there is high harvest success when moose abundance is high but number of hunters in a WMU is low. Additionally, the curvilinear effect of high harvest effort on H–A for all sex and age-classes suggests that the effect of harvest effort will become saturated (i.e. plateau) at a certain point, making harvest less reliable in WMUs with high harvest effort levels. A saturated effect of harvest effort on harvest was particularly evident for bulls, while the interaction between harvest effort and abundance revealed that harvest was highest just below maximal harvest effort levels. Previous studies have also suggested that harvest effort may not be linearly related to harvest (Schmidt et al. 2005) and will become saturated at high animal densities (Van Deelen and Etter 2003, Kahlert et al. 2015). A potential contributing factor to the saturation of the effect of harvest effort as population abundance increases may be a form of hunter interference, specifically high hunter densities driving animals away from heavily hunted areas (Fryxell et al. 1988). Previous studies have identified that moose will avoid areas where hunter activity is greater during the hunting season (Rempel et al. 1997, Laurian et al. 2008), a pattern also seen for white-tailed deer (Lebel et al. 2012). Evidence of non-linear relationships between harvest and harvest effort has also led to criticism in the use of effort-corrected harvest indices (e.g. kills per hunter-day) that may result in biased estimates of population change (Schmidt et al. 2005, Willebrand et al. 2011, DeCesare et al. 2016). Our results agree with these findings and further provide evidence of variability in how harvest effort will influence harvest–abundance relationships under selective harvesting.

We also found evidence of landscape features influencing bull, cow and calf H–A across WMUs, suggesting that animal behavior and hunter decisions made during the hunting season can also impact the reliability of harvest as a proxy of abundance. Despite forestry activity typically being associated with increased access into wildlife habitat, as well as

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increased visibility for hunters (Rempel et al. 1997, Brinkman et al. 2009, Lebel et al. 2012), our findings indicated that moose harvest was lower in WMUs with a greater proportion of recent clear cuts and burns present. This is likely a result of moose avoiding < 10-year-old forest disturbances that provide poor cover from predators and low forage opportunity (Maier et al. 2005, Dussault et al. 2006). Additionally, hunters may avoid heavily disturbed management units or are generally less successful at harvesting moose in these units. Moose avoiding areas of higher hunter activity may also explain why roads had no effect on H–A. Hunters can choose alternative methods of travel, including boat or off-road vehicle, to access moose habitat (Schmidt et al. 2005), however, hunter access will still be constrained by distance from a road or trail (Lebel et al. 2012). Further, we found no effect of weather (i.e. temperature and precipitation) on moose H–A, corresponding with results by Lebel et al. (2012) who similarly found weather variables did not influence harvest success or detectability of animals to hunters. Because moose hunting occurred during only one climatic season each year, and hunters could choose when during the season to hunt (e.g. during low snow cover), it is likely that variability in weather variables during time spent hunting was minimized or was not detectable within this study.

Evidence of landscape features influencing H–A highlights the importance of accounting for spatial and temporal variability when assessing harvest as an index of abundance, and that accounting for variability in the effect of harvest effort alone may be insufficient. Any source of population monitoring should consider factors that can influence monitoring precision, in addition to accuracy, over time and space to be a reliable index of population change (Anderson 2001, Morellet et al. 2007, Stephens et al. 2015). Mandatory reporting of harvest information may further improve the accuracy of harvest indices and may help future studies reveal additional patterns influencing H–A not detected in this study. It is likely that we did not test all factors that may influence H–A for moose and future studies may expand on this analyses to address other confounding variables, such as the influence of firearm type on harvest success.

Further, while our analyses provided evidence that a general pattern of abundance across space could be detected with harvest, we did not evaluate whether harvest reflected population dynamics (i.e. trends over time). Previous studies have suggested that even when a relationship between harvest and abundance can be identified, harvest may still not be a proper index for assessing population parameters such as WMU specific population trends, recruitment, sex ratios etc. (Ranta et al. 2008, Ueno et al. 2014). Unless proportionality between harvest and abundance over time is validated at the WMU scale, harvest may be best used to supplement monitoring or be integrated as a parameter in models that can provide better estimation of population change (e.g. time-to-event Weibull regression, Schmidt et al. 2005). Also, it is important to note that our results are likely both species and scale dependent, and the influence of different predictors on harvest may vary according to the species and spatial scale (Pettorelli et al. 2007, Imperio et al. 2010). Nonetheless, this study highlights the importance of assessing how well harvest reflects abundance across sex and age-classes that experience different levels of harvest effort.

Conclusion

Here we demonstrate that the relationship between harvest and abundance can vary by sex and age-class within a species in response to selective harvesting. Restricted harvest of adult moose performed better as an index of abundance than the less regulated calf harvest that was prone to higher harvest effort by hunters. Abundance alone explained 79% of variation in harvest for bulls, 68% for cows and 51% for calves. Although there was greater proportionally found between harvest and abundance for adult moose, we identified that harvest is likely to underestimate abundance in WMUs with highest harvest effort. We additionally identified that the relationship between harvest and abundance was not driven by harvest effort alone and can be affected by spatial variability in landscape features that have the potential to influence the detectability of animals to hunters, and consequently, harvest success. We found that harvest is likely to underestimate abundance in WMUs with a higher proportion of recent (< 10 year old) forest disturbances (including clear-cuts and wildfire burns). Whereas harvest effort can be regulated by management, factors influencing success rates by hunters are less easily managed, adding complexity to the application and reliability of harvest as a proxy of abundance. If harvest is used as a proxy to detect change in population abundance, managers should not ignore variability in harvest effort, both across and among sex and age-classes, as well as temporal and spatial variability in the landscape (Bhandari et al. 2006, Kahlert et al. 2015). We caution that harvest may act better as a supplementary index to inform on spatial variability in population abundance rather than as a substitute for direct monitoring approaches for species that experience selective harvesting.

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Supplementary material (available online as Appendix wlb-00629 at <www.wildlifebiology/appendix/wlb-00629>). Appendix 1.

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