WINTER HABITAT USE OF MOOSE IN CAPE BRETON, NOVA SCOTIA

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ABSTRACT: Aerial survey data collected between 2001 and 2020 were used to assess winter habitat use by moose (*Alces alces*) in the Greater Highland Ecosystem of Cape Breton, Nova Scotia. These data were analyzed using generalized additive mixed models that explored the influence of habitat variables. We compared abundance estimates developed directly from the surveys to those estimated from habitat use. Moose generally occupied the same general area throughout the study despite a marked population decline. Moose favoured areas comprised of greater proportions of coniferous forest showing preference for younger forest, and moose meadows, areas of predominantly coniferous forest but with abnormal or retarded regeneration due to high moose herbivory. Moose occupied areas farther away from roads inferring that moose preferred areas with younger plant forage and lower human access. The use of long-term survey data coupled with related habitat use relationships provided a useful approach to assess temporal tends in abundance and habitat use of moose in Cape Breton.

A fundamental objective of wildlife management is to maintain healthy sustainable wildlife populations (Fryxell et al. 2014). Monitoring population-wide demographics such as abundance and vital rates is one effective approach for managing populations (Williams 2011, Boyce et al. 2012, Fryxell et al. 2014). Another important strategy is to anticipate effects of management actions on wildlife populations by understanding wildlife-habitat relationships in the context of environmental change (Krausman 1999, Hebblewhite and Merrill 2008). In this study, our primary objective was to assess moose (*Alces alces*) habitat use in the Greater Highland Ecosystem of Cape Breton, Nova Scotia using 20 years of aerial survey data.

Aerial surveys are commonly used to assess large mammal populations active during winter (Gasaway et al. 1986, Kantar and Cumberland 2013). This approach has been used in many jurisdictions, including Nova Scotia, to assess changes in moose populations and to inform management decisions (Snaith et al. 2002, Van Beest et al. 2012, Andreozzi et al. 2016). Moose, like other mammals, show seasonal patterns of habitat use (Schwartz and Franzmann 1998, Manly et al. 2002, Van Beest et al. 2012). Therefore, by noting spatial variation in the abundance of moose observed during aerial surveys, we can infer habitat preferences across the landscape (Manly et al. 2002, Van Beest et al. 2012, Andreozzi et al. 2016). However, one must also account for how easily animals are detected during surveys, or their sightability. If not corrected for, sightability can bias survey results (Anderson and Lindzey 1996).

In Cape Breton, moose habitat selection is predominantly shaped by a history of

spruce budworm (*Choristoneura fumiferana*) infestations with the last major outbreak in the late 1970s (Bridgland et al. 2007, Smith et al. 2015). As a result, Cape Breton has experienced significant change in habitat composition and forest age structure in recent decades, providing a unique opportunity to examine habitat use by moose in response to this forest heterogeneity. Further, because road density varies greatly across the Cape Breton landscape, we also examined its potential influence on habitat use. We predicted that moose should be attracted to younger softwood forests and avoid areas nearer roads (Schwartz and Franzmann 1998, Manly et al. 2002, Van Beest et al. 2012).

STUDY AREA

In Cape Breton, moose were abundant prior to European arrival. However, subsequent change in land use (i.e., habitat) and hunting pressure caused population decline that continued until the early 1900s when moose were virtually extirpated from the region (Pulsifer and Nette 1995, Davis and Browne 1996). In 1947 and 1948, Parks Canada reintroduced moose to the Cape Breton Highlands National Park (CBHNP) by translocating 18 moose from Elk Island National Park in Alberta (Davis and Browne 1996). This reintroduction was successful and moose gradually spread across the region, and by the mid-1980s the population was approximately 4000 animals (Pulsifer and Nette 1995). In the mid-1970s, a major spruce budworm outbreak caused extensive tree mortality spurring an abundance of new tree growth (Bridgland et al. 2007, Smith et al. 2015). Taking advantage of this abundant food source, the population rapidly grew in the late-1990s until 2004 when it peaked at just over 8000 animals (Bridgland et al. 2007, Smith et al. 2015). The population

gradually declined to ~ 4500 in 2015 and roughly halved again to 2300 animals by 2020 (Smith et al. 2015, Nova Scotia Lands and Forestry 2020a).

Moose on Cape Breton Island are almost exclusively found in one region, the Greater Highland Ecosystem (GHE), with limited migration, immigration, and emigration. The GHE makes up the northwestern third of Cape Breton Island (Fig. 1) and is bordered by the Gulf of Saint Lawrence to the west where the land rises rapidly from the ocean to a height of 500 m. The land forms a large plateau that slopes eastward and northward toward the Atlantic Ocean. South of the CBNHP, there is an extensive road network built in the 1980s in conjunction with increased logging. The area has a maritime climate with average winter and summer
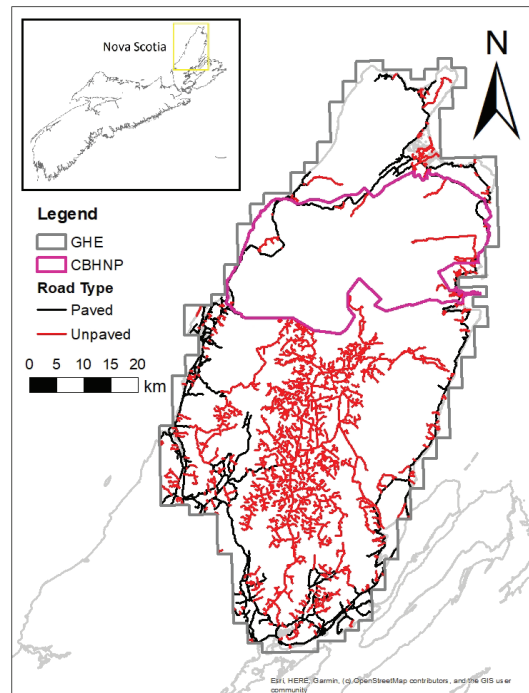

Fig. 1. Map of Nova Scotia's Greater Highland Ecosystem (GHE). The map also shows the location of Cape Breton Highlands National Park (CBHNP) and paved and unpaved roads.

temperatures of −5 and 18°C, respectively. Annual precipitation averages 1053 mm of rainfall and 337 cm of snowfall (Environment Canada 2020).

The GHE has 3 major land types: boreal forest, Acadian forest, and taiga (Smith et al. 2015) which are characterized by a mixture of forest types and ages over recent decades (Table 1). Following disturbance events, boreal succession typically starts with rapid growth of trees in the understory favouring faster growing shade-intolerant species such as white birch (*Betula papyrifera*). These shade intolerant species are eventually overtaken by slower growing shade tolerant conifer species (MacLean and Ostaff 1989, Smith et al. 2010). However, herbivores can affect this successional pattern through their foraging activity, most typically by over-browsing preferred plants (McLaren et al. 2004, Smith et al. 2010). Moose in many areas of the GHE consume nearly all conifer trees before they can grow large

enough to escape herbivory. The resultant forest is characterized by open savannahs dominated by remnant white birch, alder (*Alnus spp.*), black spruce (*Picea mariana*), and herbaceous growth (Smith et al. 2010, 2015), hereafter termed "moose meadows" that are mostly located on the western side of the CBHNP.

METHODS
Aerial Survey

Data were collected as part of 10 aerial surveys conducted over a 20-year period (2001, 2002, 2004, 2006, 2008, 2011, 2013, 2015, 2019, 2020). These helicopter surveys were conducted by 4 personnel: 2 back-seat observers, 1 front-seat recorder, and the pilot. All surveys were completed in 1–2 days during the first week of March and conducted in conditions of adequate visibility and minimal precipitation. Effort was made to maximize sightability of moose by flying at low speed (< 130 km/h) and altitude (< 100 m above ground), and only recording animals within 150 m of either side of the helicopter (Gasaway et al. 1986). This work was completed as part of an effort by Nova Scotia Lands and Forestry to monitor moose in the area and done in partnership with Parks Canada, the Unama'ki Institute of Natural Resources, and the Confederacy of Mainland Mi'kmaq.

To survey the area, we divided the GHE into 893 equal-sized survey blocks that were 2 min of longitude (~ 2.5 km) × 1 min of latitude (~1.9 km) large, or ~ 4.7 km². Data were collected on an east-west transect flight flown over the midline of each block; transect lines were 1 min of latitude apart (~ 1.9 km). Observations (sightings) of moose were made within 150 m of the helicopter covering 1/6 of the block area; the number of moose observed per transect was recorded. A total of 8674 transects were flown over the 20-year study period.

Table 1. Habitat composition of the Nova Scotia's Greater Highlands Ecosystem in 1999, 2009, and 2020.

Habitat type	% of land cover		
	1999	2009	2020
Non-forest	37.3	28.1	28.1
<25 year conifer	12.0	8.7	2.8
25–40 year conifer	8.9	18.2	5.2
>40 year conifer	3.9	5.4	24.5
Uneven year conifer	4.4	4.6	4.4
<25 year deciduous	0.3	0.1	0.2
25–40 year deciduous	0.8	0.8	0.1
>40 year deciduous	9.2	8.0	8.5
Uneven year deciduous	0.5	1.3	1.3
<25 year mixed wood	2.8	1.2	0.6
25–40 year mixed wood	3.2	5.0	1.0
>40 year mixed wood	10.5	9.9	14.6
Uneven year mixed wood	2.2	5.0	4.8
Moose meadow	3.9	3.9	3.9

To control for sightability, we created a sightability correction factor (SCF) in each survey year. This required flying 6 equidistant, east-west transect lines over 28–44 survey blocks each year, counting all moose observed; lines were spaced 300 m apart. These same areas were re-flown using a more intense survey regime of 12 flights spaced 150 m apart with half the viewing distance. Moose counts from the two surveys were compared to determine if more animals were observed in the more intense survey. These comparisons were averaged to create a SCF in each survey year (Table 2). These same SCFs were used when historical moose abundances were first calculated in the area (Bridgland et al. 2007, Smith et al. 2015, Nova Scotia Lands and Forestry 2020a).

Habitat and Surface Features

Habitat type underlying survey transects was determined using Nova Scotia's 1999, 2009, and 2020 Forest Inventories (Nova Scotia Lands and Forestry 1999, 2009, 2020b). The 1999 and 2009 forest inventories were based on forestry records and

Table 2. Sightability correction factors (SCF) for each year of aerial moose surveys in Nova Scotia. SCF were calculated based on the average difference between two sets of surveys flown over the same areas using different survey intensities.

Year	n	SCF	Variance
2001	36	1.21	0.02
2002	37	1.36	0.05
2004	30	1.12	0.01
2006	37	1.14	0.01
2008	32	1.14	0.01
2011	28	1.30	0.02
2013	36	1.25	0.02
2015	36	1.51	0.05
2019	44	1.48	0.07
2020	38	1.18	0.01

satellite imagery, and the 2020 inventory was based on forestry records and age progression of the 2009 inventory. The 2001–2005 surveys were assessed with the 1999 inventory, the 2006–2014 surveys with the 2009 inventory, and those in 2015–2020 with the 2020 inventory. Habitat types were categorized according to forest type (deciduous, conifer, mixed) and stand age (< 25 years old, 25–40 years old, > 40 years old, and uneven aged) and included an additional forest category for moose meadows. All non-forested habitats were combined into a single category. The forest inventories were also used to calculate the average percent crown closure within each transect. Additionally, provincial road (distinguishing paved and unpaved) and surface water maps were used to assess abiotic habitat characteristics.

Because data collection was restricted to 150 m on either side of transect lines, we created a 150 m buffer from the transect using ArcGIS (version 10.5.1, Environmental Systems Research Institute 2018). We then calculated the percent habitat cover for each habitat type in each transect using the ArcGIS add-in Patch Analyst Version 5.2 (Rempel et al. 2016). To determine the average distance to paved and unpaved roads and surface water features in each transect, we first calculated the Euclidian distance of all these features on the landscape. We then averaged these values in each transect to produce a measure of the distance to these features. We repeated the entire process for each survey block to subsequently use this information to determine the likely abundance and distribution of moose across the landscape.

Statistical Analysis

To determine how site composition affects moose numbers in each transect, we used a generalized additive mixed model (GAMM) with a Poisson distribution using the R package "gamm" (Version 0.2–6, R

Core Team 2019, Wood and Scheipl 2020). A Poisson (P) distribution was chosen over a negative binomial (NB) distribution as it yielded a lower Akaike information criteria (AIC) value when the two were compared (AIC_P = 11,941.9; AIC_{NB} = 12,183.3, theta = 10). Generalized additive mixed models allow for both linear and non-linear effects in the model. For variables with non-linear effects, we used spline smoothers and a non-parametric reverse iterative approach to create separate model estimates for sections of the regression line (Wood 2017). The procedure involves assessing how much model fit is improved as more spline smoothers are used to explain the non-linear effect, while simultaneously penalizing the model for each smoother added. The result of this was that an optimal number of smoothers, or effective degrees of freedom (EDF), was chosen for each non-linear effect. This method, however, did not yield a single model estimate for each non-linear effect as multiple smoothers were used when creating these model effects (Wood 2017, Wood and Scheipl 2020).

Our objectives were to understand moose habitat use with respect to roads and forest type and age, while controlling for the underlying effect of forest cover; thus, we included crown closure as a non-linear fixed effect. Because survey blocks are spatially autocorrelated, we also used the x and y coordinates of the transect lines as a non-linear effect (Kneib et al. 2009, Wood 2017). The remaining fixed linear effects were percent cover for each habitat type and the average distance to roads and surface water features. Survey year was used as a random effect to account for population differences between surveys.

For model selection, we fitted a global model and then used stepwise backward selection to remove non-important variables from the model. This involved sequentially removing the variable with the lowest Beta/SE absolute value until the AIC value stopped declining (Pagano and Arnold 2009). Once all non-important variables were removed form the model, we compared models using their AIC values and estimated model weights. These weights were then used to create model averaged estimates that were unlogged to generate incidence rate ratios (IRRs). An IRR indicates how the relative count of moose changes as you increase an independent variable by 1 unit. In the case of habitat type, one unit was the difference between a site without or devoid of a habitat type (0) or entirely composed of that type (1). For roads and water, this was measured as distance (km) from the feature.

To assess if our model was able to accurately predict moose abundance in the GHE, we compared historic abundance estimates from this area (historical estimates) to abundance estimates based on our model and the habitat and surface feature data from the survey blocks (model estimates). The model estimate included the random intercept for each survey year. We also used the survey block data to determine the road density across the GHE. Because moose abundance was calculated to account for the GHE and not the entire area surveyed with transects, we applied a multiplier of 6 to the model estimates to account for the entire area. We further needed to multiply our estimates by the SCF for each year to account for missed animals. After this adjustment, we compared the observed and estimated abundances using a Pearson's correlation coefficient. We calculated the average abundance in each survey block using the 1999, 2009, and 2020 forest inventories to determine the likely moose distribution during 3 time periods (2001–2005, 2006–2014, and 2015–2020), and visually assessed these data for temporal and geographic trends in abundance.

RESULTS

Our best supported model identified relationships between habitat use and several categories of forest type and age, as well as distance to water and roads (Table 3). While AIC values indicated an initial best model, (AIC = 11,933.5, variables = 16; Table 4), the removal of uneven aged coniferous forest (11,934.6) and < 25-year-old deciduous forest (11,934.4) separately, and together (11,935.3), increased the AIC value by < 2 points. Because of the small difference between these four models, we used model averaging based on model weights to generate the final estimates.

We found that the probability of observation was highest in moose meadows followed consecutively by younger coniferous forest types. The incidence rate ratios (95% CI) were 10.32 (8.25, 12.90) in moose meadows, 3.67 (3.02, 4.46) in < 25-year-old conifer forests, 3.16 (2.58, 3.88) in 25–40-year old conifer forests, and 1.30 (0.99, 1.69) in > 40-year old conifer forests (Table 3). Lower selection was found for >25-year-old deciduous forest, 25–40 year-old mixed wood forest, and > 40-year-old mixed wood forest: incidence ratios were 2.87 (0.98, 8.40), 3.12 (2.17, 4.50), and 4.33 (3.39,5.53), respectively. There was minimal chance of observation in uneven aged deciduous forest: incidence ratio = 0.45 (0.33, 0.610) (Table 5). Areas with greater average distance to roads had higher observations of moose: paved = 1.05 (1.03, 1.07), unpaved = 1.27 (1.24, 1.30). The opposite was true for areas with a greater average distance to surface water (0.07 (0.05, 0.11) (Table 5). Road density (km of road/km^2) was lowest in the CBHNP and highest in the area to the south: north of park = 0.29 (0.07, 0.51), park = 0.15 (0.03, 0.27), south of park = 0.71 (0.70, 0.73).

Table 3. Removal of non-informative variable from the habitat use model generated from transects flights over the Greater Highland Ecosystem of Nova Scotia (10 surveys, n = 8674). Variables were sequentially desegrated (**bolded**) based on their Beta/SE absolute values until the simplified model's AIC value began to increase. All models were general additive models with Poisson distributions and with year as a random factor. Transect location and % crown closure were treated as non-linear factors.

Model	# of variables	AIC	ΔAIC
CE, CY, CM, CU, DE, DY, **DM**, DU, ME, MY, MM, MU, MOO, NF, Paved roads, Unpaved, Water	21	11,941.85	8.35
CE, CY, CM, CU, DE, DY, DU, ME, MY, MM, **MU**, MOO, NF, Paved roads, Unpaved, Water	20	11,939.90	6.40
CE, CY, CM, CU, DE, DY, DU, **ME**, MY, MM, MOO, NF, Paved roads, Unpaved, Water	19	11,937.90	4.40
CE, CY, CM, CU, DE, DY, DU, MY, MM, MOO, **NF**, Paved roads, Unpaved, Water	18	11,935.96	2.46
CE, CY, CM, CU, DE, **DY**, DU, MY, MM, MOO, Paved roads, Unpaved, Water	17	11,934.31	0.81
CE, CY, CM, **CU,** DE, DU, MY, MM, MOO, Paved roads, Unpaved, Water	16	11,933.50	0.00
CE, CY, CM, DE, DU, MY, MM, MOO, Paved roads, Unpaved, Water	15	11,934.50	1.00

Habitat types: <25 year conifer (CE), 25–40 year conifer (CY), >40 year conifer (CM), uneven year conifer (CU), <25 year deciduous (DE), 25–40 year deciduous (DY), >40 year deciduous (DM), uneven year deciduous (DU), <25 year mixed (ME), 25–40 year mixed (MY), >40 year mixed (MM), uneven year mixed (MU), moose meadow (MOO), non-forest (NF)

Table 4. Comparison of models generated from flown transects over the Greater Highland Ecosystem of Nova Scotia using AIC to determine which habitat type and surface features best predict moose counts (10 surveys, n = 8674). All models were generalized additive mixed models with Poisson distributions and with year as a random factor. Transect location and % crown closure were both treated as non-linear factors.

Model	# of variables	AIC	ΔAIC	Weight
CE, CY, CM, CU, DE, DU, MY, MM, MOO, Paved roads, Unpaved, Water	16	11,933.5	0	0.38
CE, CY, CM, CU, DU, MY, MM, MOO, Paved roads, Unpaved, Water	15	11,934.4	0.9	0.25
CE, CY, CM, DE, DU, MY, MM, MOO, Paved roads, Unpaved, Water	15	11,934.6	1.1	0.22
CE, CY, CM, DU, MY, MM, MOO, Paved roads, Unpaved, Water	14	11,935.3	1.8	0.15
Null	4	13,077.7	1144.2	0

Habitat types: <25 year conifer (CE), 25–40 year conifer (CY), >40 year conifer (CM), uneven year conifer (CU), <25 year deciduous (DE), uneven year deciduous (DU), 25–40 year mixed (MY), >40 year mixed (MM), moose meadow (MOO)

Table 5. Model averaged incidence rate ratio ratios (IRRs) of seeing a moose on a transect in Nova Scotia's Greater Highland Ecosystem based on its habitat type and average distance from surface features (10 surveys, n = 8674). Results were generated from a generalized additive mixed model with a Poisson distribution, a with year as a random effect. Transect location and % crown closure were treated as non-linear effects. Habitat type IRRs are based on a 100% cover of that habitat type. EDF shows the number of spline smoothers used in each non-linear effect.

Linear variables

Variables	Incidence rate ratio	95% CI
(Intercept)	0.22	(0.16, 0.31)
<25 year conifer	3.67	(3.02, 4.46)
25–40 year conifer	3.16	(2.58, 3.88)
>40 year conifer	2.01	(1.54, 2.63)
Uneven year conifer	1.30	(0.99, 1.69)
<25 year deciduous	2.87	(0.98, 8.40)
Uneven year deciduous	0.14	(0.05, 0.42)
25–40 year mixed wood	3.12	(2.17,4.50)
>40 year mixed wood	4.33	(3.39, 5.53)
Moose meadow	10.32	(8.25, 12.90)
Avg. Distance paved road (per km)	1.05	(1.03, 1.07)
Avg. Distance unpaved road (per km)	1.27	(1.24, 1.30)
Avg. Distance surface water (per km)	0.07	(0.05, 0.11)

Non-linear spline smoothers

Variables	EDF	Chi^2
Location (x, y)	24.90	328.28
% Crown closure	3.17	27.39

Because the GAM analysis precluded calculation of model estimates for the non-linear variables (average percent crown closure and moose group location), we plotted these data to assess potential relationships. Observations increased as average percent crown closure rose to ~17%, and then declined. This decline slowed around 55% but continued to 80%, the upper end of the range (Fig. 2). Moose groups were highly clustered across the
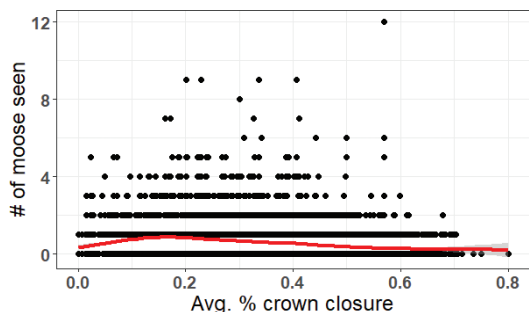
Fig 2. The relationship between average % crown closure of a transect line and the number of moose seen on that line during flights over the Greater Highland Ecosystem of Nova Scotia (10 surveys, n = 8674). The regression line used was fitted using spline smoothers.

landscape, creating distinct high and low abundance areas (Fig. 3). Both these patterns fit with our expectations based on the best model (EDF values; crown closure = 3.17; moose location = 24.90) (Table 5).

When we estimated moose abundance for the entire GHE, the abundance estimates based on the model were highly correlated with the historical estimates (R^2 = 0.94; Fig. 4). When examining the average moose distribution across the GHE in the 3 time periods (2001–2005, 2006–2013, and 2015–2020), we found that moose occupied the same areas throughout, although distribution contracted especially south of CBHNP (Fig. 3). The principal areas of consistent occupation were just north of CBHNP, the western side of the CBHNP, and to a lesser extent an area southeast of CBHNP, all protected areas with poor road access and limited forestry.

DISCUSSION

As we predicted, moose showed higher use and preference for younger softwood forest and moose meadows. Young coniferous forests provide optimal moose forage, and
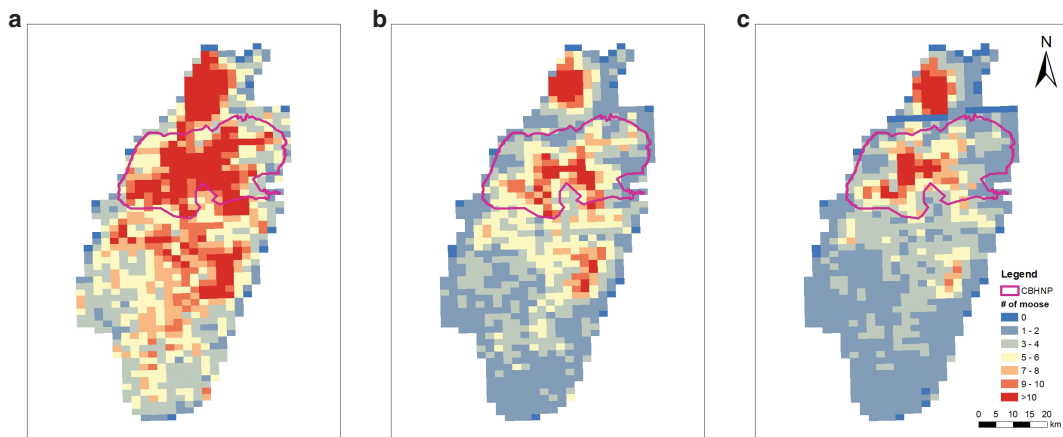
Fig. 3. Expected numbers of moose in each survey block in the Greater Highlands Ecosystem between 2001–2005 (a, est. pop. = 6883), 2006–2014 (b, est. pop. = 3563), and 2015–2020 (c, est. pop. = 3202) based on the best transect model and forest inventories in each period. The map also shows the location of Cape Breton Highlands National Park (CBHNP).
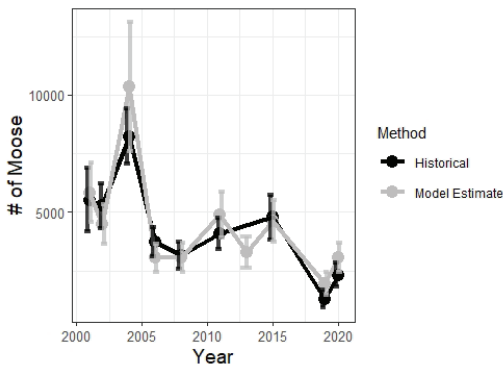
Fig. 4. Comparing the historical moose population estimates for the Greater Highland Ecosystem and estimates based on the habitat use model. Model estimates were extrapolated to the entire survey area and both sets of estimates have had the same set of sightability correction factors applied to them. Results for 2013 were not used to calculate the R^2 due to there not being an historical abundance estimate for this year.

moose meadows, although over-browsed, are dominated with early successional species (Schwartz and Franzmann 1998, Andreozzi et al. 2016). Our hypothesis that moose would avoid areas closer to roads was also supported. Roads pose a direct mortality risk to moose due to vehicle collisions and indirectly through habitat loss and fragmentation (Forman and Alexander 1998, Beazley et al. 2004, Eldegard et al. 2012). They also increase hunter access, which in turn leads to higher moose mortality (Forman and Alexander 1998, Beazley et al. 2004).

One factor we could not fully account for was how moose population changes might have affected habitat use. Moose numbers in the GHE changed dramatically (> 4-fold) during the study from a high of 8000 animals to a low of 1350 (Bridgland et al. 2007, Smith et al. 2015, Nova Scotia Lands and Forestry 2020a). We accounted for the annual variation in habitat use by using a random intercept to account for overall population differences among years, but other subtle and unmodelled differences may have influenced habitat use such as resource (forage) competition. Animals adjust foraging behavior and consumption to maximize caloric intake while minimizing energetic costs (Emlen 1966), which moose often accomplish by foraging on the most abundant vegetation rather than selectively feeding on the most nutritious plants (Wam and Hjeljord 2010, Bjornerass et al. 2012). Overall, this pattern is mediated by resource availability and competition (Wam and Hjeljord 2010).

Our decision to use a single sightability correction factor each year may have affected the relative accuracy of our surveys because sightability often varies widely among habitat types (Anderson and Lindzey 1996, Quayle et al. 2001, McIntosh et al. 2007). By not accounting for this variation, we likely reduced the accuracy of certain abundance estimates (Quayle et al. 2001). However, since this method was used to calculate the historical abundance estimates and we did not have sightability information for each habitat type, we adopted this approach to compare the two data sets and believe our estimates are reasonable.

Additionally, it is likely that the crown closure values used in our analysis were not entirely representative of the field conditions during the surveys. Crown closure values came from forest inventories based on conditions during the growing season, whereas our surveys occurred during winter. Thus, areas with higher proportions of deciduous forest likely had inflated crown closure values due to the lack of leaves during the winter surveys. While only 10% of our site was dominated by deciduous trees (Table 1), the results in certain blocks were presumably biased to a degree.

We found that moose abundance increased more rapidly in response to increased distance to unpaved rather than paved roads. This suggests that hunter access, not vehicle collision, was the more import

risk factor driving moose avoidance of roads. Other studies have shown that moose avoid areas near roads year-round (Forman and Alexander 1998, Dussault et al. 2007, Van Beest et al. 2012). However, on Cape Breton this pattern might simply reflect the relative location of roads, as unpaved roads are mostly inland where we expect most moose activity to occur, whereas paved roads are largely near the coast where fewer moose are expected (Fig. 1). Further, the timing of the winter survey relative to the autumn hunting season may have some influence on winter abundance and location of moose, as animals in easily accessible areas may be harvested at higher rate. Because moose move little during winter (Wattles and DeStefano 2013), their ability to disperse and recolonize areas is limited until the following spring.

Roads also have a cumulative effect on moose populations. Beazley et al. (2004) suggested that areas with road density >0.6 km/km^2 in mainland Nova Scotia were incapable of supporting significant moose populations. We found that the average road density was 0.71 km/km^2 in the GHE south of CBHNP and most of this area supported low numbers of moose. The same pattern was observed in the moose management area directly south of the GHE, an area with even higher road density and fewer moose (Nova Scotia Lands and Forestry 2020a).

If managers seek to increase the number of moose south of the CBHNP, one course of action may be to decommission certain roads in this area, an action proposed in other parts of Nova Scotia to help local moose populations (Beazley et al. 2004). This action would be in accordance with Nova Scotia's Endangered Species Act (Government of Nova Scotia 1998) as several endangered species live within the area. If full decommissioning of roads is not feasible, managers could regulate access into areas of the GHE by using gates and signage during the

hunting season. This approach has been successful in maintaining and growing wildlife populations in other jurisdiction with high human access (Cole et al. 1997, Crichton et al. 2004). Our results provide further support for strategic planning and placement of new roads on the landscape.

Our predictive maps in the GHE show that moose generally used the same areas throughout the study, although their distribution was expected to contract given the measurable population decline. This same pattern was observed during the corresponding aerial surveys (Bridgland et al. 2007, Smith et al. 2015, Nova Scotia Lands and Forestry 2020a), suggesting that factors beyond habitat covariates were associated with the decline in the southern population; for example, the relative abundance of white-tailed deer (*Odocoileus virginianus*). When deer and moose are sympatric, their general abundance pattern is an inverse relationship in that as deer numbers increase, moose abundance declines (Snaith et al. 2002), a relationship believed to explain, in part, moose decline elsewhere in Nova Scotia (Pulsifer and Nette 1995, Snaith et al. 2002). This effect is unlikely to be direct competition between the species, rather, the increased spread and abundance of *Parelaphostrongylus tenuis*, or meningeal worm associated with high deer populations (Anderson 1972, Lankester 2010). White-tailed deer are the principal host of meningeal worm and rarely display symptoms or negative effects, whereas this parasite can be mortal to moose (Lankester 2010). Unfortunately, the prevalence of meningeal worm is unknown on Cape Breton and warrants further study.

To conclude, our aerial surveys provided a useful assessment of the annual and long-term winter abundance and habitat use of moose on Cape Breton. We found similarity between population estimates from historical aerial surveys and habitat use models

developed from aerial survey data. Our approach is applicable in many jurisdictions where long-term aerial survey data are available, but more specific GPS-telemetry data from marked individuals are lacking. We encourage further development of similar approaches and use of long-term data sets from various sources to assess wildlife populations and improve understanding of how change in environmental factors affects moose and other wildlife over time.

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