Wildlife Society Bulletin 38(4):878–883; 2014; DOI: 10.1002/wsb.475

Tools and Technology

Using Ungulate Biomass to Estimate Abundance of Wolves in British Columbia

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ABSTRACT Management of wolves (*Canis lupus*) in British Columbia, as with most other Canadian provinces, is conducted on a regional scale (38,557–252,776 km^2), yet there is no standardized, cost-effective methodology for providing reliable estimates of wolf abundance at this scale. Therefore, we used periodic estimates of ungulate abundance and incorporated them into an ungulate biomass regression model to estimate wolf abundance on a regional and provincial (900,402 km^2) scale over a 12-year period (2000–2011). In 2011, the provincial estimate was 8,688 (95% CI = 5,898–11,760) wolves (7–13 wolves/1,000 km^2), while regional wolf abundance estimates ranged from 149 (95% CI = 100–205) to 2,693 (95% CI = 1,818–3,608) with differences related to regional scale (km^2) rather than wolf densities (4–15 wolves/1,000 km^2). We suggest the ungulate biomass regression model is useful to estimate the abundance of wolves for management purposes when precise estimates are not required and wolf populations are not heavily exploited or recovering.

KEY WORDS abundance, British Columbia, *Canis lupus*, ungulate biomass, wolves.

It is challenging to estimate the abundance of wolves over large areas (> 20,000 km^2) because they occur at low densities, avoid humans, and are often in forested habitats where their detection is difficult (Mech et al. 1998, Patterson et al. 2004). It is also expensive, which poses additional logistical difficulties (Crête and Messier 1987). Consequently, wolf abundance has been typically estimated over small areas (e.g., $\leq$ 20,000 km^2) using techniques such as snow-tracking, radiomarked individuals, and DNA analysis (Mech et al. 1998, Hayes et al. 2003, Caniglia et al. 2012, Webb and Merrill 2012). In these cases, wildlife managers are often left extrapolating wolf abundance estimates from small study areas to a larger scale on which wolves are managed; but extrapolation is always questionable and sufficient studies are often lacking (Hayes and Gunson 1995). Therefore, government agencies who manage wolves over a broad landscape face an important challenge because there is no reliable cost-effective methodology to estimate abundance of wolves on a jurisdictional scale (e.g.,$\geq$ 20,000 km^2).

One indirect method to predict carnivore abundance is using prey biomass (Fuller and Sievert 2001, Carbone and Gittleman 2002, Karanth et al. 2004). Keith (1983) found a strong positive relationship ($n = 7$, $r^2 = 0.94$) between an ungulate biomass index (UBI/km^2) and wolf densities (wolves/1,000km^2). This method was validated using additional studies across North America ($n = 24$, $r^2 = 0.72$) by Fuller (1989). Fuller et al. (2003) further increased the number of study areas and reaffirmed that most of the variation in wolf abundance was related to ungulate biomass ($n = 32$, $r^2 = 0.64$). This relationship between ungulate biomass and density of wolves, which we refer to as the ungulate biomass regression model, is now widely accepted (e.g., Messier 1995, Cariappa et al. 2011).

We suggest the ungulate biomass regression model is sufficiently reliable under most conditions to enable wildlife management agencies to predict wolf density from ungulate populations at a level of accuracy and precision that is adequate for most management purposes. We considered the data compiled by Fuller et al. (2003) to be applicable to British Columbia, Canada, because of the diversity of ungulate prey in the province. We thus explored the potential of the well-established relationship between wolf density and ungulate biomass to estimate the abundance of wolves in British Columbia on a regional and provincial scale.

Received: 27 August 2013; Accepted: 5 April 2014
Published: 11 September 2014

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STUDY AREA

The study area included most of the province of British Columbia (900,452 km^2), and excluded the Haida Gwaii archipelago where there are no wolves and Region 8 where wolf distribution was still expanding (Fig. 1). British Columbia is an ecologically diverse province with landscape and vegetation communities ranging from wet coastal and interior temperate rain forests to dry interior deserts (Meidinger and Pojar 1991). For wildlife management purposes, the province is divided into administrative areas (known as regions) ranging in size from 38,557 to 252,766 km^2 (Fig. 1). Hunting and trapping seasons for

Figure 1. Location of wildlife management regions in the province of British Columbia, Canada. Crosshatching denotes Haida Gwaii, which was excluded from the analysis used to estimate wolf abundance (2000–2011) due to the known absence of wolves. Region 8 was also excluded as wolves were still recolonizing (see text).

wolves occurred throughout British Columbia, with the exception of National Parks (< 1% of British Columbia land area) where harvest of wolves was prohibited. Wolves were found in all regions of the province and occurred on most of the larger coastal islands (Tompa 1983).

There were a diversity of ungulates in British Columbia (Shackleton 1999), including moose (*Alces alces*), elk (*Cervus elaphus*), Roosevelt elk (*C. e. roosevelti*), caribou (*Rangifer tarandus*), Stone's sheep (*Ovis dalli stonei*), Dall's sheep (*O. d. dalli*), California and Rocky Mountain bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), mule deer and black-tailed deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), plains bison (*Bos bison bison*), and wood bison (*B. b. athabascae*). In addition to wolves, there were 7 other medium-to-large carnivores (Nagorsen 1990), including coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Puma concolor*), lynx (*Lynx canadensis*), bobcat (*L. rufus*), and wolverine (*Gulo gulo*).

METHODS

Estimating Ungulate Biomass

Regional ungulate population estimates were available for 2000, 2003, 2008, and 2011. These estimates were based largely on information derived from ungulate surveys. All ungulate surveys are required to follow provincial standards, which are science-based techniques with defensible and comparable methodology. Protocols have been developed for ground-based surveys for moose, elk, and deer (RISC 1998, D'Eon et al. 2006). Standards for aerial-based surveys have been designed for bison, mountain goat, mountain sheep, moose, elk, deer, and caribou (RISC 2002). These provincial standards are based on methodologies for specific techniques and species derived from many published sources, including Caughley (1977), Gasaway et al. (1986), Samuel et al. (1992), Unsworth et al. (1994), and White (1996). Ungulate survey standards for accuracy and precision are 90% confidence intervals with an allowable error ranging from ±15% to ±25% (RISC 2002). Sightability correction factors are also commonly employed for aerial surveys (RISC 2002). There were 825 ungulate surveys conducted in British Columbia during 2000–2011 ($\bar{x} = 68$/yr).

Notwithstanding the rigor associated with ungulate surveys, there is still uncertainty when extrapolating area-based survey results to larger areas. A variety of approaches have been used in British Columbia to estimate regional ungulate abundance depending upon the availability of information. These include 1) extrapolating survey densities to sub-regional areas, after removing unoccupied areas and adjusting for differences in habitat suitability; 2) estimating ungulate abundance from population models based on survey information (White and Lubow 2002); and 3) using expert opinion where there is a paucity of survey information. Expert opinion is largely based upon harvest data and hunter success information, but frequently also includes observations and information from other knowledgeable individuals such as local hunters, guide-outfitters, First Nations, and other resource managers. Regional estimates included a minimum and maximum estimate to show the range of uncertainty in estimated ungulate populations.

Estimating Abundance of Wolves

Regional ungulate estimates for 2000, 2003, 2008, and 2011 were used to calculate indices of ungulate biomass (Fuller et al. 2003). One region (see Region 8 in Fig. 1) was excluded because wolves were recolonizing this area during those years and it was unlikely that wolf abundance was associated with ungulate biomass. Wolf abundance for all other regions was estimated from the data compiled by Fuller et al. (2003). We modified the ungulate biomass regression model used by Fuller et al. (2003) in 2 ways to improve its utility to predict wolf abundance in British Columbia. First, we used a quadratic, rather than linear, equation to recognize the curvilinear relationship in the data and fixed the ordinate intercept to zero (Cariappa et al. 2011). Secondly, we removed 6 data points (Fuller et al. 2003: table 6.8) where wolf densities were considered to be independent of ungulate biomass. Adams et al. (2008) reviewed 41 wolf studies in North America and provided evidence that wolf populations compensate for human exploitation rates of $< 30\%$. We therefore removed 4 studies (southwestern MB; south-central AK; interior AK; southern YT) from Fuller et al. (2003) where exploitation rates exceeded 30%. Similarly we removed 2 studies (northwestern MN; east-central YT) where wolves were still recolonizing and thus may not have had time to adjust to ungulate biomass. The ungulate biomass coefficients, which standardize body mass of each ungulate species, are universally applicable (Keith 1983, Fuller 1989, Fuller et al. 2003). Therefore, we used the same ungulate biomass coefficients as Fuller et al. (2003) to convert ungulate densities to ungulate biomass; but, since their study did not include black-tailed deer, we used a 0.75 coefficient because of the smaller body size of black-tailed deer as compared to white-tailed deer and mule deer (Shackleton 1999).

To accommodate uncertainty in regional ungulate biomass estimates, we first calculated minimum and maximum biomass estimates from the minimum and maximum abundance estimates. We then converted the biomass estimates to a normal distribution by assuming the minimum and maximum ungulate biomass index (UBI) were estimates of the lower and upper 95% confidence intervals, respectively. The mean biomass was calculated as (max. + min.)/2 and the standard deviation as (max. − mean)/1.96.

We used PopTools 3.2 (Hood 2011) for Microsoft Excel© (Redmond, WA) to bootstrap 95% confidence intervals (CIs), and prediction intervals (PIs), for the wolf density–ungulate biomass regression (Davison and Hinkley 1997, Eberhardt 2007). We used 25,000 repetitions for the bootstrapping, each time re-sampling the residuals of the regression with replacement and re-estimating the regression coefficients using the LINEST function in Excel (i.e., for each repetition of the quadratic equation, we re-estimated the regression coefficients by re-sampling the regression residuals as well as a normally distributed random estimate of the UBI). We then repeated this procedure to estimate regional and the provincial wolf densities in British Columbia for 2000, 2003, 2008, and 2011. We then converted these estimates of wolf density to abundance by multiplying the wolf density (wolves/km^2) by the km^2 of each region. We used Arc Geographic Information System Version 10 to estimate the km^2 in each region.

RESULTS

Using the data in Table 1, we estimated the relationship between wolf density and ungulate biomass to be $\hat{y} = 5.40x - 0.166x^2$ where $\hat{y}$ = wolves/1,000 km^2 and x = biomass/km^2. The quadratic model fit the data well ($r^2 = 0.85$, $p < 0.001$). The resulting model estimates of regional density of wolves ranged from 4/1,000 km^2 to 15/1,000 km^2 in 2011 (Table 2). The provincial density of wolves ranged from 8/1,000 km^2 in 2000 to 10/1,000 km^2 in 2011 (Table 3).

Table 1. Estimated ungulate abundance and relative biomass values from 2000 to 2011 in British Columbia, Canada. Ungulate numbers are not included for Region 8 because wolves were known to be recolonizing this region, and for Haida Gwaii because of the known absence of wolves.

		2000		2003		2008		2011	
Species	Relative biomass values	Minimum number	Maximum number	Minimum number	Maximum number	Minimum number	Maximum number	Minimum number	Maximum number
Bison	8	850	1,300	900	1,200	1,300	2,300	1,500	2,400
Moose	6	126,600	195,500	130,100	223,000	129,900	221,900	142,100	231,200
Elk	3	34,700	45,950	38,600	54,900	47,000	75,900	42,900	77,150
Caribou	2	15,600	20,550	16,220	22,650	17,420	26,070	15,690	26,950
Thinhorn sheep	1	10,800	13,700	8,600	12,400	9,600	13,400	9,850	14,900
Bighorn sheep	1	4,900	6,750	3,800	5,100	4,310	5,440	4,850	5,950
Mountain goats	1	35,000	62,000	39,100	66,600	38,600	65,200	41,000	65,300
Mule deer	1	68,000	127,500	77,000	131,000	80,000	152,000	89,000	161,000
White-tailed deer	1	22,950	31,400	34,200	46,900	50,510	85,030	55,520	95,550
Black-tailed deer	0.75	73,300	137,700	92,500	170,000	78,500	136,000	79,000	127,000

Table 2. Regional ungulate biomass index (UBI/km^2), wolf densities (wolves/1,000 km^2), and wolf abundance estimates in British Columbia, Canada, for 2011. Region 8 excluded because wolves were recolonizing.

Region	Area (km^2)	MeanUBI/km^2	Mean wolves/1,000 km^2	Mean abundance estimate	Lower 95% CI	Upper 95% CI
1	44,282	1.34	7	307	218	404
2	38,557	0.73	4	149	100	205
3	57,656	2.05	10	599	421	792
4	75,599	3.14	15	1,158	842	1,495
5	110,932	1.61	8	919	647	1,217
6	252,776	1.10	6	1,459	929	2,054
7A	130,210	2.00	10	1,320	896	1,785
7B	190,389	2.87	14	2,693	1,818	3,608

Table 3. Provincial ungulate biomass index (UBI/km^2), wolf densities (wolves/1,000 km^2), and wolf abundance estimates in British Columbia, Canada, for 2000, 2003, 2008, and 2011. Total excludes Region 8 because wolves were recolonizing.

Year	MeanUBI/km^2	Mean wolves/1,000 km^2	Mean abundance estimate	Lower 95% CI	Upper 95% CI
2011	1.90	10	8,688	5,898	11,760
2008	1.81	9	8,324	5,586	11,361
2003	1.73	9	7,981	5,376	10,852
2000	1.56	8	7,213	4,977	9,696

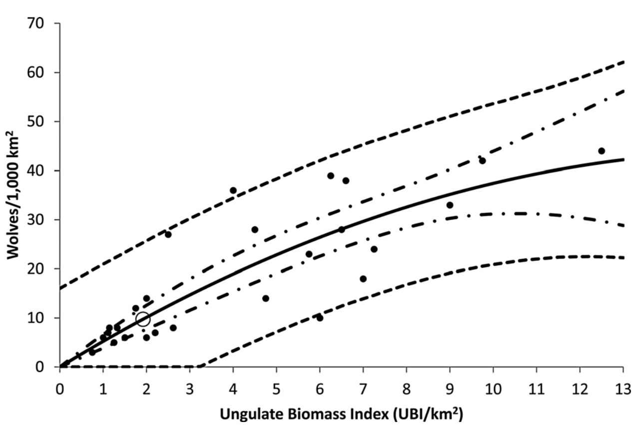

Figure 2. Predicted density of wolves based on an ungulate biomass index from 26 North American wolf studies where $\hat{y} = 5.40x - 0.166x^2$ and y is wolves/1,000 km^2 and x is ungulate biomass/km^2. The 95% prediction intervals (dashed line) and 95% confidence intervals (dot–dashed line) are also shown. The predicted density of wolves in British Columbia, Canada, for 2011 is depicted by the open circle.

We used the bootstrapped variance associated with the CI of the regression, and not the PI, when estimating uncertainty in the predicted British Columbia wolf densities because the PIs included estimates of 0 wolves/1,000 km^2 for all regions and the province despite harvest records showing that wolves were present (Mike Wolowicz, British Columbia Ministry of Forests, Lands and Natural Resource Operations, unpublished data). For example, the 2011 predicted wolf density estimate of 9.6 wolves/1,000 km^2 (open circle in Fig. 2) had a 95% PI that ranged from 0.0 to 25.4 wolves/1,000 km^2 (dashed lines in Fig. 2), while the CI ranged from 6.6 to 13.1 wolves/1,000 km^2 (dot–dashed lines in Fig. 2). Furthermore, our regional and provincial estimates of ungulate biomass/km^2 (Tables 2 and 3) occurred at the lower range of the ungulate biomass regression model (≤ 3/km^2; Fig. 2) where almost all wolf density estimates (12 of 13 study areas) were within or very close to the 95% CI of the regression (compare clustering of points around the dot–dashed line at ungulate biomass values ≤ 3/km^2 to scattering of points in the 4–7/km^2 range in Fig. 2).

Regional wolf abundance estimates in 2011 (Table 2) ranged from 149 (95% CI = 100–205) to 2,693 (95% CI = 1,818–3,608). Estimates were higher in the northern regions, for the most part due to the larger size of those regions, as opposed to higher wolf densities. For 2011, the provincial population estimate was 8,688 (95% CI = 5,898–11,760) wolves (Table 3).

DISCUSSION

Our estimates of the number of wolves in British Columbia are similar to other previously published estimates. For example, our 2000 estimate is similar to the 1979 estimate of 6,300 wolves (Tompa 1983) based on expert opinion. Our 2003 and 2008 estimates are similar to the previously published estimates of 8,000 (Hayes and Gunson 1995) and 8,100 wolves (Theberge 1991), which were both based on expert opinion. Our estimated regional densities are within the range of those estimated for wolves using radio telemetry and snow-tracking within small study areas in British Columbia (Hatter 1988, Seip 1992, Bergerud and Elliot 1998, Hatler et al. 2008) and similar to those reported from neighboring jurisdictions (Bjorge and Gunson 1989, Hayes and Harestad 2000, Hayes et al. 2003, Kuzyk et al. 2006, Webb et al. 2011). Our estimated regional densities are also within the lower range of wolf densities from the western North America studies reported by Fuller et al. (2003).

There are limitations to using the ungulate biomass regression model to estimate the abundance of wolves in British Columbia and elsewhere. First, the wolf abundance estimate is dependent on the accuracy of regional ungulate population estimates. Second, ungulate biomass is a relatively imprecise estimator of wolf density. Third, the ungulate biomass regression model is only applicable if human-caused mortality rates do not exceed sustainable limits and wolf numbers have had time to adjust to prey biomass. Fourth, abundance of other predators such as cougars and bears could also influence ungulate abundance, especially in terms of the amount of vulnerable prey, which therefore could affect the prediction of wolf density. Finally, the ungulate biomass regression model may not applicable where wolves prey primarily on livestock. In our study, we tried to address issues of accuracy by including uncertainty about regional ungulate population estimates in our estimation procedure and by using confidence intervals rather than prediction intervals. With regard to human-caused wolf mortality, estimates in British Columbia (including harvest by hunters, trappers, and wolves removed because of livestock depredation) have been estimated to range between 650 and 1,400 per year from 2000 to 2011 (Mike Wolowicz, British Columbia Ministry of Forests, Lands and Natural Resource Operations, unpublished data). Our wolf estimates during this period were between 7,000 and 9,000; therefore, exploitation rates appear to be well below the 30% limit that Adams et al. (2008) reported as sustainable. Although cougars and bears are common in British Columbia, many of the studies reported by Fuller et al. (2003) also contained multiple predator species. Finally, although wolves prey primarily on livestock in certain areas of Europe (Vos 2000, Sidorovich et al. 2003), this is not likely to be a widespread concern in British Columbia.

Despite shortcomings of using the ungulate biomass regression model to predict wolf density, the method we have outlined is transparent, repeatable, and science-based. It fills a management need for estimating the abundance of wolves on a regional scale where other methods are neither practical nor affordable. The ungulate biomass regression model also enables wildlife managers with limited inventory funds to focus on ungulate inventories, while providing a cost-effective method to estimate abundance of wolves providing wolves are not highly exploited or recovering, and providing precise population estimates are not required.

ACKNOWLEDGMENTS

We thank the many regional biologists for gathering ungulate population estimates that enabled this analysis. D. Demarchi conducted the Geographic Information System mapping and P. Ott offered statistical advice on bootstrapping the confidence and prediction intervals. We appreciate the constructive reviews and input from L. Carbyn, M. Festa-Bianchet, A. Goddard, D. Heard, B. McLellan, C. Pasztor, C. Procter, T. Szkorupa, R. Ward, and anonymous reviewers, which greatly improved earlier drafts of this manuscript.

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Associate Editor: Boertje.