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# Range Constraints for Introduced Elk in Southwest Yukon, Canada

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ABSTRACT. Forage availability, snow depths, and winter temperatures were assessed to determine if they might impose range constraints on introduced elk (*Cervus elaphus*) that voluntarily colonized a 95 $km^2$ area of southwest Yukon (Canada) in 1959. Parkland-like vegetation of stunted aspen (*Populus tremuloides*) and nonforest upland plant communities, which is atypical vegetation for a boreal forest environment, composed 30% of the colonized area. About 95% of the area produced less than 300 kg/ha of forage, which represents poor productivity compared to more southern elk ranges. In the remaining 5%, indigenous graminoid communities produced (average ± SD) 408 ± 131 kg/ha of forage, exceeded only by nonindigenous roadside vegetation with 652 ± 115 kg/ha. Data from radio-collared animals indicated that most elk occurrences (38% year-round) were associated with parkland-like vegetation, and fecal pellet groups were six times as frequent in indigenous graminoid vegetation as in forest vegetation. Late February 2011 snow depths of 41 ± 7 cm, during a year with a below-normal snowfall, suggested a potential for reduced winter access to forage. Meteorological data from 1981–2010 indicate that one-third of winter daily minima in the study area were likely lower than −20˚C, a threshold below which the metabolism of an elk calf must increase to maintain its body temperature. Each assessed habitat variable was unfavorable to elk compared with other western North American winter ranges, which may have limited the development of a more robust population in the southwestern Yukon.

Key words: boreal forest, *Cervus*, ecology, elk, forage, habitat, introduction, parkland, range, Yukon

RÉSUMÉ. La disponibilité des fourrages, l'épaisseur de couche de neige et les températures hivernales ont été évaluées afin de déterminer si elles sont susceptibles d'imposer des contraintes à l'aire de répartition du wapiti (*Cervus elaphus*) introduit en 1959 en vue de la colonisation volontaire d'une aire de 95 $km^2$ du sud-ouest du Yukon (Canada). La végétation de type forêt-parc composée de trembles rabougris (*Populus tremuloides*) et les communautés de plantes non forestières en montagne, soit une végétation atypique en milieu de forêt boréale, composent 30 % de la zone colonisée. Environ 95 % de la zone visée produisait moins de 300 kg de fourrage par hectare, ce qui constitue une productivité médiocre comparativement aux aires de répartition de wapitis se trouvant plus au sud. Dans le 5 % qui reste, les communautés graminoïdes indigènes produisaient (moyenne ± écart-type) 408 ± 131 kg/ha de fourrage, ce qui était dépassé seulement par la végétation non indigène en bordure de route de 652 ± 115 kg/ha. Les données obtenues grâce aux bêtes dotées de colliers émetteurs ont indiqué que la plupart des occurrences de wapitis (38 % à l'année) survenaient dans la végétation de type forêt-parc. Par ailleurs, les groupements de pelotes fécales se retrouvaient six fois plus souvent dans la végétation graminoïde indigène que dans la végétation forestière. L'épaisseur de couche de neige de 41 ± 7 cm enregistrée à la fin février 2011, une année où les chutes de neige ont été inférieures à la normale, suggèrent que l'accès au fourrage pourrait être réduit l'hiver. Les données météorologiques prélevées de 1981 à 2010 indiquent que le tiers des températures minimales quotidiennes hivernales dans la zone à l'étude étaient vraisemblablement inférieures à −20 ˚C, un seuil en dessous duquel le métabolisme d'un jeune wapiti doit s'élever pour maintenir sa température corporelle. Chacune des variables de l'habitat qui a été évaluée n'était pas favorable au wapiti, comparativement à d'autres aires de répartition d'hiver de l'Ouest nord-américain, ce qui pourrait avoir eu pour effet de restreindre la formation d'une population plus robuste dans le sud-ouest du Yukon.

Mots clés : forêt boréale, *Cervus*, écologie, wapiti, fourrage, habitat, introduction, forêt-parc, aire de répartition, Yukon

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## INTRODUCTION

The introduction of ungulates into unoccupied but potentially suitable habitat has been a common method for recovering locally extirpated populations or for introducing new species for social or economic reasons (Griffith et al., 1989; Spear and Chown, 2009). To optimize the potential success of contemporary introductions, pre-release assessments typically consider factors such as the availability of critical resources (e.g., Didier and Porter, 1999), biological and social conflicts, predation, and the transfer of pathogens (Corn and Nettles, 2001). Historically, however, such comprehensive assessments were not necessarily conducted. Extirpated ungulates tend to be more successfully reintroduced than other taxa (Griffith et al., 1989), with documented initial growth rates for reintroduced and introduced populations of 10%–30% per annum (Komers and Curman, 2000; Hundertmark and Van Daele, 2010 – Afognak Island, Alaska; C.C. Gates, pers. comm. 2012 – Suffield National Wildlife Area, Alberta). However, other ungulate (re)introductions that are far less successful raise the question of what limited population growth. Some possible limiting factors are demography of the released population (Komers and Curman, 2000; Forsyth and Duncan, 2001), pre-release animal handling effects (Rosatte et al., 2007), predation, unforeseen environmental circumstances, or chance synergistic affects. One example with limited success is the introduction of elk (*Cervus elaphus* or *C. canadensis*, Ludt et al., 2004) into the southwestern Yukon, which was north of its geographical range in northeastern British Columbia, where its abundance was typically low (Hatter et al., 2000; O'Gara and Dundas, 2002). Elk from Elk Island National Park (Hoefs, 1980) were introduced in the 1950s to provide another ungulate species for sport hunters in addition to the moose (*Alces americanus*) and caribou (*Rangifer tarandus*) that were traditionally harvested by Yukon residents (Soper, 1950; McCandless, 1985). However, despite a favorable pre-introduction habitat assessment by Soper (1950), growth of the elk population has been slow, and poor recruitment was thought to be a primary reason (Youngman, 1975; Hoefs, 1980).

Elk were present in eastern Beringia during the late Pleistocene to early Holocene (Yesner, 2001; Burns 2010), having migrated from Asia during the Illinoian glacial period (Guthrie, 1966). They were subsequently extirpated, with the last known occurrence in Yukon dated to ~1540 $^{14}$C years BP (Farnell et al., 2004). Guthrie (1966) speculated that changing range conditions caused the extirpation. The introduction of elk into the southwestern Yukon began with the release of 19 animals near Braeburn Lake (~60˚28′ N, 135˚46′ W), ~90 km NNW of Whitehorse in 1951, and an additional 30 animals were released in the same area in 1954 (Florkiewicz, 1994). After a major forest wildfire in 1958 (Englefield, 2003), an unknown number of the introduced elk became established ~70 km to the south in the Takhini Valley west of Whitehorse (Florkiewicz, 1994). During the early 1990s, an additional 119 elk were released,

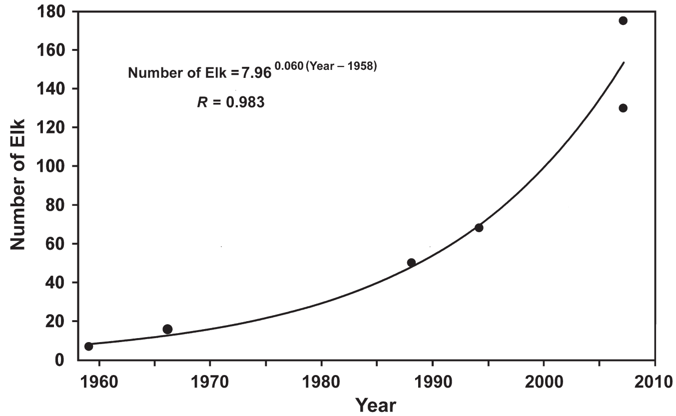


FIG. 1. Estimated growth rate of elk population in the Takhini Valley, Yukon, from 1959 to 2007 based on regression analysis. Individual population values were based on the following sources: 1966 – Hoefs (1980); 1988 – Florkiewicz (1994); 1994 – Florkiewicz (1994) plus 18 introduced animals (Yukon Elk Management Team, 2008); and 2007 – upper and lower 95% confidence limits developed by Florkiewicz et al. (2007). Because no initial population count was available, it was assumed that seven animals colonized the Takhini Valley in 1959, which was one year after a major wildfire.

18 in the Takhini Valley, 73 in the Braeburn Lake area, and 28 about 55 km southwest of Braeburn Lake (Yukon Elk Management Planning Team, 2008). For purposes of this study, the Braeburn Lake herd will not be considered further. Regression modeling suggests that the Takhini Valley population has grown steadily at ~6% per annum (including introductions) from 1959 to 2007 (Fig. 1**)**. By 2007, the Takhini Valley population was estimated at 144 (± 8.5 SD) animals (Florkiewicz et al., 2007).

In 2006, elk began to move from their area of most frequent use or core range in the Takhini Valley (~1 elk/km$^2$) into surrounding lands, causing conflict with agricultural interests (Yukon Elk Management Planning Team, 2008). In Scandinavia, Andersen et al. (2004) suggested that such range expansions by roe deer (*Capreolus capreolus*) were more rapid in marginal habitats and at higher latitudes, where climate and vegetation imposed constraints on population density (circumstances similar to those found in Yukon). Given the slow but steady increase in the size of the Takhini Valley elk population, coupled with its relatively small core range and recent range expansion, an important ecological and management concern was whether ecological conditions in the Takhini Valley were sufficient to support the current density of elk and further population growth (Yukon Elk Management Planning Team, 2008). The suitability of the core range was evaluated to address this concern. The specific objectives were to (1) classify and characterize the species composition and abundance of vegetation in the Takhini Valley core range; (2) determine the abundance (kg/ha) of late summer forage during a period of reduced elk presence on the range; (3) determine the relative use of vegetation by elk on the basis of radio-telemetry locations of collared animals and pellet group counts; (4) evaluate ambient winter temperatures and snowpack depths as possible constraints to growth over time; and (5) compare these factors to those of other occupied elk ranges

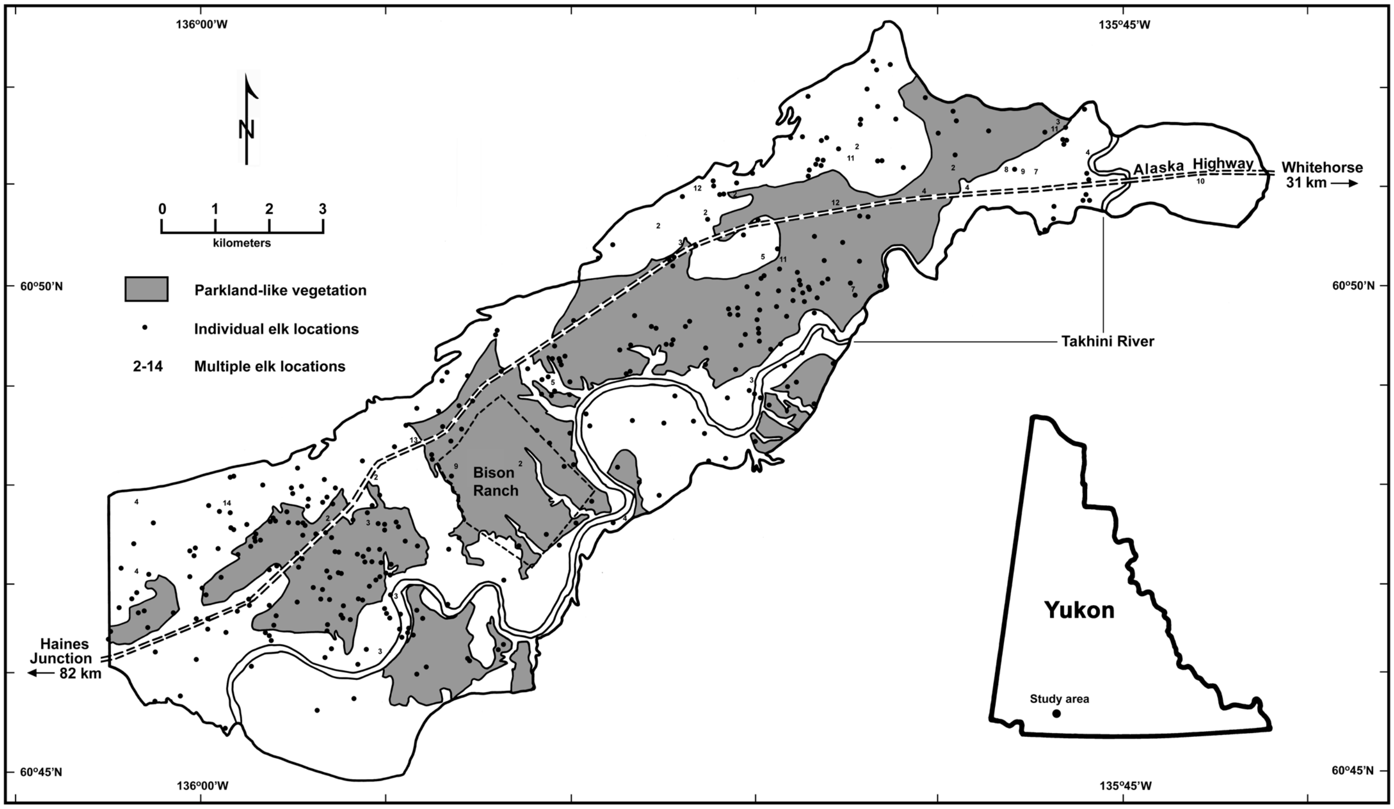


FIG. 2. Location and extent of the Takhini Valley elk core range in Yukon, with delineated parkland-like vegetation and elk radio-telemetry locations. The study area occurs on the bottomlands of the Takhini Valley, except for small discontinuous areas along the northwest edge and the eastern tip. The latter areas occupied toe and lower slope positions on the valley.

in western North America to better understand the possible constraints imposed by local environmental conditions. A more complete understanding of these environmental conditions might provide greater insight into the future for elk in the Takhini Valley, facilitate the maintenance or enhancement of range conditions, and aid in identifying locations for additional introductions elsewhere in northwestern North America.

## MATERIALS AND METHODS

### *Study Area*

Within a 1144 km$^2$ range in the Takhini Valley area, elk most frequently use a 95 km$^2$ core range located ~31 km west of Whitehorse, Yukon (Yukon Elk Management Team, 2008). The core range extends 24 km WSW along the Alaska Highway from 2.5 km east of the Takhini River and is ~5 km wide (Fig. 2). The core range (Yukon Elk Management Team, 2008) was delineated on the basis of expert opinion of elk managers (R.R. Florkiewicz and R.M.P. Ward, pers. comm. 2012), as informed by three decades of aerial surveys, telemetry data, and anecdotal observations by local people. The overall distribution of elk in the area was derived from radio-telemetry data. The boundaries of the current study were aligned with topographic breaks and major changes in vegetation physiognomy that approximated the elk core range. These vegetation boundaries often coincided with the limits of a major burn that occurred in 1958 (Englefield, 2003). A disjunct site (~16 km$^2$) located farther west had numerous elk occurrences, but it was excluded from the analysis because it included residential and agricultural development. Elk in the Takhini Valley were free-roaming, except between mid-March and early August 2008, when Yukon Fish and Wildlife staff rounded them up and penned them to control an infestation of winter tick (*Dermacentor albipictus*). A limited hunt was first instituted in September 2009 (21 elk harvested, Yukon Department of Environment, unpubl. data 2013) to reduce the elk population size in the Takhini Valley. In 2008, potential forage competitors in the Takhini Valley elk core range included ~30 mule deer (*Odocoileus hemionus*) and at least 20–30 semi-feral and feral horses (*Equus ferus caballus*). If population estimates from nearby studies are representative, carnivores such as grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) had average densities of 1.3–2.2 and 1.3 per 100 km$^2$, respectively, in and around the study area (Larsen and Markel, 1989). Black bear (*Ursus americanus*) also occur in the study area and potentially prey on elk calves, but no population density estimate was available.

The Takhini elk core range is part of the Mid-Cordilleran Boreal (MCb) ecoclimatic region, which occurs south of 61° N latitude in Yukon (Strong, 2013) and extends southward into northern British Columbia (Ecoregions Working Group, 1989). Regionally, lodgepole pine (*Pinus contorta* var. *latifolia*) forms the zonal vegetation at low elevations in this portion of Yukon; however, this species had limited abundance in the elk core range and farther west. A review of 1948 aerial photographs (A11478 and A11539, Yukon Energy, Mines and Resources Library) indicated that before the 1958 wildfire, open-growing spruce (*Picea* spp.) dominated moderately well drained sites throughout the elk core range. One exception was the present-day bison ranch area (Fig. 2), which had mixed aspen (*Populus tremuloides*) and spruce cover that may have been due to a burn several decades earlier. During the study, seral postfire vegetation dominated most of the landscape in the core range. Along the western and southwestern edges of the core range, mature stands of western white spruce (*Picea albertiana* ssp. *albertiana*) were common. Mature lodgepole pine forests with some aspen occurred to the south and southeast, and relatively dense post-1958 aspen regeneration occurred to the east. To the north, aspen and mixed aspen–western white spruce stands were present, with nonforest patches of vegetation on steep southerly aspects. The valley bottom had level to undulating terrain blanketed primarily with late Wisconsinan glacial lacustrine deposits that were incised by the Takhini River (Rampton and Paradis, 1979; Morison and Klassen, 1991). Topographic relief between the valley bottom surface and the river ranged from 30 to 50 m.

Monthly data from 1981–2010 (values missing from January 1996 to November 1997) from the nearest long-term meteorological recording station (Whitehorse Airport, station identification 2101300, Environment Canada, 2013a) indicate that the region has average summer (May–September) temperatures of 11 ± 3˚C, with 156 ± 40 mm of precipitation. Winters (November–March) are cold (−9 ± 2˚C). One-third of 151 days in winter have minima of −20˚C or lower, and an average of 16 days per winter have minima of −30˚C or lower. Winters have moderate precipitation (81 ± 23 mm). Snow depths in February–March at the Whitehorse Airport average 24 ± 10 cm, with maxima of 50–55 cm. Prior to forage sampling, average May–July 2008 temperatures were slightly cooler than normal (10˚C versus 11 ± 1˚C), with total precipitation within one standard deviation of the average.

### *Vegetation Sampling*

Different vegetation cover types (aspen, lodgepole pine, western white spruce, shrublands, and herbaceous areas) were sampled in late June and July 2008, during the period of elk impoundment for winter tick control. Sampling plots were distributed throughout the elk core range. Individual plots were located within relatively homogenous portions of stands as determined by overstory and understory structure and composition. During sampling, 10 stands were assessed per vegetation type, when sufficient stands were available.

Stand composition sampling was based on a 20 m × 30 m macroplot with a centrally located 30 m transect, along which five sets of nested quadrats were spaced at 5 m intervals. Each set of nested quadrats consisted of a 2.5 m × 2.5 m and a 1 m × 1 m plot within which plants 1–2.5 m tall and less than 1 m tall, respectively, were assessed for percent canopy cover (Daubenmire, 1968) by ocular estimation. The canopy cover of trees and shrubs more than 2.5 m tall was estimated in each macroplot from three evenly spaced locations on each side of the central plot transect. Naming of vegetation types was based on dominant species by stratum; a slash (/) between plant names indicates a change in stratum, and a dash (–) indicates codominants. Plant nomenclature follows ITIS Partners (2012), except for spruce (Strong and Hills, 2006). To determine the abundance of individual vegetation types, the elk core range was mapped in 2011 at a scale of ~1:34 500 on the basis of stereoeoscopic interpretation of 2007 aerial photographs (A28543 and A28544; Yukon Energy, Mines and Resources Library) followed by field verification of the mapped polygons.

Late summer forage biomass was sampled at the end of the growing season in early August 2008. The summer's growth of species 2–250 cm tall and thought to be acceptable elk forage (Kufeld, 1973; Florkiewicz, 1994; Cook, 2002; R.R. Florkiewicz and R.M.P. Ward, pers. comm. 2008; also see Chambers, 2010:21–22) was clipped within a separate set of five quadrats (50 × 100 cm) spaced at 5 m intervals along a 30 m transect located within the 20 m × 30 m vegetation macroplot. If an adequate biomass sample could not be obtained, the quadrat size was doubled. The collected material was separated into graminoids, forbs, and shrub foliage and then placed in separate paper bags. Samples were air-dried and then oven-dried at 60˚C for 48–72 hours before weighing and conversion to kg/ha.

### *Habitat Use*

Radio-telemetry locations from 12 female and three male adult elk wearing VHF radio-collars (LMRT series; Lotek Engineering, Newmarket, Ontario) were collected by Yukon Department of Environment (unpubl. data 2011) and used in this study to assess the relative use of vegetation types by these animals. Radio-collared elk (excluding animals that were impounded during the tick control period) were located between 19 March 2007 and 16 March 2010 using ground-based telemetry at intervals of 8 ± 5 days during the first 92 weeks and 34 days (on average) during the last 64 weeks. Locations were determined between 0830 and 1740 h, with half obtained between 1125 and 1413 h. Measurements were made mostly during daylight hours, although the number of available hours varied by season. Locations were taken primarily from the Alaska Highway. Radio-telemetry signal bearings were taken from three or more positions determined by global positioning system (GPS). The software program Locate II was used to determine elk locations on the basis of 95% error ellipses using maximum likelihood estimators. Using the area values associated with the ellipse error of each location, a standard deviation of under 274 m was determined for half of the available 448 location error values, whereas an additional 25% (median to 3rd quartile) had error values of 275 – 759 m. The remaining locations had standard deviations greater than 759 m; most of these were located at least 3 km from the closest point of measurement in or near the incised riparian area of the Takhini River or farther to the southeast (Fig. 2).

Elk pellet groups were counted along a 5 m wide belt transect located in the vegetation macroplots. Pellet groups were not separated by age as decay rates likely varied among vegetation types (Prugh and Krebs, 2004). Our field protocol approximated the standing crop method (Campbell et al., 2004), as pellets were not removed before sampling.

### *Snow Depth Sampling*

Snow depths along 10 traverses with a combined length of 3040 m were sampled within the core range from 19 to 22 February 2011. On these dates, snow depth was at or near the winter maximum since there was no substantial snowfall during the subsequent two months of winter (Environment Canada, 2013a; W.L Strong, pers. obs. 2011). Sampling involved measuring the vertical depth of snow at 5 m paced intervals along arbitrary compass headings across the landscape in forested and non-forested indigenous vegetation areas and an agronomic area. The locations of these traverses were independent of vegetation composition and related sampling because of the scattered distribution of macroplots and the limited road access at the time of sampling. Because neither the composition, horizontal, and vertical structure of the vegetation nor the terrain conditions (i.e., slope gradient, orientation, configuration, wind exposure) were uniform along each traverse, each snow depth measurement was treated as a separate entity for analysis purposes. Major changes in terrain configuration (e.g., level to rolling versus steep unidirectional slopes) and vegetation overstory composition (e.g., aspen versus spruce) were noted for each sample point. Snow depths at the Whitehorse Airport from 1981 to 2010 were used as a control for comparison with the core range because no snow depth data were available for the study area or from any immediately adjacent site. No effort was made to estimate missing values in the station's record.

### *Data Analysis*

Cluster analysis (McCune and Mefford, 1999) based on relative squared Euclidean distance as the distance (dis)similarity measure and Ward's method as the linkage method was used as a guide for classifying vegetation plots in conjunction with stand structure and species constancy. Constancy was defined as the percent occurrence of a plant taxon within a vegetation type.

Data were assessed for normality prior to analysis using Shapiro-Wilk tests (Statsoft, 1995). As the data were not normally distributed and variables were often difficult to transform, Kruskal-Wallis tests with adjustments for duplicate values (Sokal and Rohlf, 1981:430 – 432) were used to identify statistically significant ($p < 0.05$) differences among more than two groups and Mann-Whitney U-tests (Statsoft, 1995) to detect significant differences between paired groups. Nonparametric Scheffé rank tests (Miller, 1966: formula 110) were used to identify pair-wise group differences within significant Kruskal-Wallis tests. G-tests for goodness of fit were used to determine whether significant differences occurred between expected elk frequencies and those measured by radio-telemetry (Sokal and Rohlf, 1981: equation 17.1). Expected values were based on the amount of land associated with each compared group (i.e., an extrinsic hypothesis). The probability value ($p$) for all comparisons was based on the number of compared groups minus one (i.e., degrees of freedom or df).

TABLE 1. Vegetation types and their abundance in the Takhini Valley elk core range (95 km$^2$). See Chambers (2010) for a detailed species composition summary of each vegetation type.

| Vegetation type | Percent of study area |
|---|---|
| Forest types: | |
| Open-growing aspen//bearberry | 18.8 |
| Aspen//buffaloberry – wild rose | 12.3 |
| Aspen//wildrose – bearberry | 1.0 |
| Open-growing western white spruce/willow | 10.3 |
| White spruce//stairstep moss | 8.8 |
| Western white spruce//bearberry | 9.7 |
| Lodgepole pine//purple reed grass | 5.4 |
| Shrub types: | |
| Wild rose – strawberry | 11.2 |
| Graminoid types: | |
| Purple reedgrass | 2.2 |
| Needleleaf sedge – pasture sage | 1.5 |
| Weak arctic sedge | 0.2 |
| Smooth brome – wild rose | 1.5 |
| Other indigenous vegetation | 6.7 |
| Agricultural development | 3.0 |
| Unvegetated natural disturbances | 6.6 |
| Unvegetated anthropogenic disturbances | 0.8 |
| Total | 100.0 |

## RESULTS

### *Vegetation*

Twelve indigenous vegetation types dominated the elk core range (Table 1). Indigenous vegetation covered ~82% of the core range, with forests comprising the majority. About 12% of the area was not vegetated by indigenous plant communities because of erosion and anthropogenic disturbances such as residential, road, and agricultural development.

Aspen stands 10 m or more tall comprised 32% the area. Stands in the eastern two-thirds were often 4 – 7 m tall. Tree ages were variable among aspen stands, but 2nd and 3rd quartile values indicated they ranged from 28 to 44 years. Western white spruce stands to 20 m tall constituted

TABLE 2. Forage availability in Takhini Valley elk core range and associated number of elk fecal pellet groups, by stand type.

| Dominant stand type | Percent of area | Number of samples | Forage availability (kg/ha) Graminoids | Forbs | Shrubs | Total | Number of samples | Number of pellet groups |
|---|---|---|---|---|---|---|---|---|
| | | | Average [SD] Scheffé rank test results[1] | | | | | |
| Coniferous tree[2] | 34 | 20 | 17 [27]a | 20 [22]a | 33 [39]a | 70 [51]a | 15 | 2.0 [2.5]b |
| Deciduous tree[3] | 32 | 21 | 61 [63]b | 85 [77]b | 117 [218]b | 263 [301]b | 11 | 0.2 [0.4]a |
| Graminoid[4] | 4 | 14 | 214 [118]c | 157 [79]cd | 37 [53]a | 408 [131]c | 11 | 15.9 [18.4]c |
| Shrub[5] | 11 | 3 | 31 [13]b | 219 [57]d | 28 [11]a | 279 [77]bc | 2 | 1.5 [2.1]ab |
| Disturbances[6] | < 2 | 5 | 499 [156]d | 122 [49]c | 30 [21]a | 652 [115]d | 5 | 2.4 [2.2]b |
| Other[7] | 17 | 0 | – | – | – | – | – | – |
| *p* value (Kruskal-Wallis test) | | | < 0.001 | < 0.001 | 0.020 | < 0.001 | | < 0.001 |

[1] Biomass growth-forms and number of pellet groups with the same letters are not significantly different at the α 0.05 level.
[2] Includes the western white spruce//stairstep moss, open-growing western white spruce/willow, western white spruce//bearberry, and lodgepole pine//purple reedgrass vegetation types.
[3] Includes the open-growing aspen//bearberry, aspen//buffaloberry – wild rose, aspen//wild rose – bearberry vegetation types.
[4] Includes the needleleaf sedge – pasture sage, weak arctic sedge, and purple reedgrass vegetation types.
[5] Includes the wild rose – strawberry vegetation type.
[6] Smooth brome – wild rose vegetation along roads and on other lands that were cleared of indigenous vegetation.
[7] Includes unvegetated areas such as roads, bedrock exposures, eroding slopes, and rivers (7%); agricultural land (3%); and miscellaneous vegetation types (7%).

29% of the area. The origin of most western white spruce stands predated the 1958 fire, with 2nd and 3rd quartile ages between 92 and 126 years (maximum 286 years). Approximately 30% of the vegetation on the study area (Fig. 2) consisted of aspen, shrub, and graminoid stands in a parkland-like mosaic too intricately mixed to be separated as individual entities at the mapping scale applied. The ratio of treed to non-treed areas in the parkland-like vegetation was approximately 56:44.

Bearberry (*Arctostaphylos uva-ursi*), wild rose (*Rosa acicularis*), and buffaloberry (*Shepherdia canadensis*) were the principal understory species of aspen stands and occurred in different proportions. Purple reedgrass (*Calamagrostis purpurascens*) with an average cover of 4% – 6% was the most common graminoid in aspen stands. Similar amounts of grass cover were also associated with lodgepole//purple reedgrass stands, which occurred on sandy soils. Between the two most common types, the open-growing aspen//bearberry type had greater total understory species cover than the aspen//buffaloberry – wild rose type (80% versus 41%). Wild rose stands less than 1 m tall that included various graminoids and forbs such as strawberry (*Fragaria virginiana*) were common in valley bottom areas. Purple reedgrass, weak Arctic sedge (*Carex supina*), and needleleaf sedge – pasture sage (*Carex duriuscula – Artemisia frigida*) vegetation types were mostly associated with dry, steep south-facing slopes, although the latter also occurred on the edges of wind-exposed upland areas and on saline soils. A variety of forbs and shrubs occurred in the western white spruce//stairstep moss type, but stairstep moss (*Hylocomium splendens*) with 51 ± 19% cover was the overwhelming understory dominant. In contrast, bearberry formed the dominant ground cover in drier western white spruce stands, whereas 1 – 1.5 m tall willows (*Salix* spp.) dominated riparian areas with imperfect to poor drainage. Roadsides and some cleared lands had smooth brome – wild rose vegetation, a result of agronomic seeding of smooth brome (*Bromus inermis*) and the natural re-establishment of indigenous plants.

### *Forage Availability*

Disturbed areas such as roadsides produced more than twice as much forage biomass as indigenous vegetation types (Table 2). Indigenous graminoid- and shrub-dominated types produced proportionally more forb biomass. Among indigenous vegetation types, graminoid-dominated stands produced the most total forage per hectare (Table 2). Coniferous tree-dominated stands produced an average of 70 kg/ha of forage. Deciduous tree stands produced 3 – 4 times as much shrub foliage as other vegetation types. Among sampled stands with indigenous vegetation, 69% had less than 300 kg/ha of late summer forage, with 93% producing less than 500 kg/ha (Fig. 3). Spatially, ~95% of elk core range produced less than 300 kg/ha of forage and 99% produced less than 500 kg/ha; these percentages are based on extrapolation from sampled areas (Table 2). Winter forage availability would be less than the totals indicated in Table 2 because of the loss of the deciduous shrub foliar component, although an unaccounted for additional amount of browse would be available.

### *Elk Occurrences*

Radio-telemetry locations (n = 882) indicate that the distribution of elk extended along the Takhini Valley for a distance of ~46 km, with the core range located approximately in the center. North-south elk occurrences were centered on the Alaska Highway. The majority of elk radio-telemetry locations outside the core range (n = 319) occurred directly

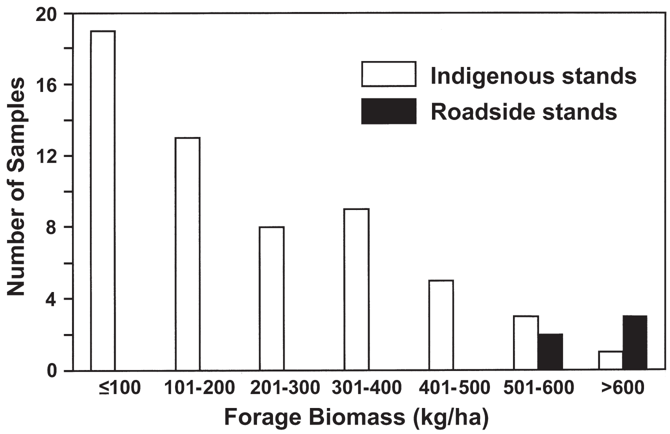


FIG. 3. Abundance of late-summer forage biomass (kg/ha) in the Takhini Valley elk core range based on samples collected in August 2008 (n = 63). Individual samples included graminoids, forbs, and shrub foliage.

east or west of the core range. Both areas external to the core range had residential or agricultural development, or both. During summer, 68% (equal to one standard deviation) of all measured elk locations occurred within 2 km of the Alaska Highway, whereas in winter elk were located within 1.2 km of the highway. The east-west variation in elk locations was less in summer (SD 5123) than in winter (SD 13 780 m) (Mann-Whitney *U*-test, df = 1, $p < 0.001$). Among all collared-elk locations that might have been obtained during telemetry sampling (n = 1021), 19 were unaccounted for in spring/fall and 45 in summer, whereas 75 were unavailable during winter. In combination, these missing locations constituted 14% of the potential number of locations.

Within the core range, elk telemetry occurrence frequencies were of greater density (5.9/km$^2$) than in the non-core portions (0.3/km$^2$) of their overall range (Table 3). They had a greater than expected frequency in parkland-like vegetation than in other (i.e., boreal forest) vegetation (frequencies from year-round locations; Table 3). Outside the parkland-like area, radio-collared elk occurred in a variety of habitats, ranging from conifer-dominated forests to grassy south-facing slopes, as well as roadsides, with no obvious patterns of occurrence. Seasonally, elk were more frequent in parkland-like vegetation in summer (when they had a greater than expected number of elk radio-telemetry occurrences), but not during other seasons (Table 3). The number of elk radio-telemetry locations within 250 m of the Alaska Highway was also greater than expected compared to areas farther away (Table 3). G-tests indicate greater use of the zone within 250 m of the road occurred during spring/fall ($p < 0.001$) and winter ($p = 0.004$), but not in summer (df = 1).

Elk fecal pellet groups were most frequent in graminoid-dominated vegetation (Table 2) and were especially common in the needle-leaf sedge–pasture sage vegetation type, with an average of 35.5 groups per transect (n = 4). The frequency of pellet groups among other vegetation types was less than 2.5 per transect.

*Snow Depths*

Snow depths in indigenous vegetation averaged 41 ± 7 cm in late winter (n = 580, Fig. 4), whereas level agricultural pasture had 34 ± 2 cm (n = 28). Scheffé rank tests showed no significant difference in snow depths between valley bottomland locations (n = 417) and steep south-facing slopes (30%–45% gradients, n = 163) , but riparian areas (n = 47) had greater depths of snow (average 49 ± 8 cm) (Kruskal-Wallis test, df 2, $p < 0.001$). Between 13 and 28 February 2011, or six days before and after snow depth sampling, an average of 12 ± 1 cm of snow was reported on the ground at the Whitehorse Airport, with a long-term late February average of 27 ± 11 cm based on daily values (n = 362, Environment Canada, 2013a). Maximum snow depths at Whitehorse Airport in late February were comparable to the most common Takhini Valley field values (Fig. 4).

## DISCUSSION

*Parkland-Like Vegetation Ecology*

Because parkland-like vegetation is atypical of Yukon (Strong, 2013) and important habitat for elk in the study area, its origin and ecology need to be considered. Such vegetation is more characteristic of drier segments of the aspen parkland, found over 1600 km to the southeast in Alberta and Saskatchewan (Gt, Ecoregions Working Group, 1989), than of high-latitude boreal forest. The nearest parkland physiognomic approximation directly to the south of the study area might be components of the Bunchgrass and Sub-boreal Pine zones in central British Columbia (Beil, 1969; Meidinger and Pojar, 1991). Aspen and graminoid-dominated vegetation do occur in close proximity elsewhere in southern Yukon, but the components tend to be segregated and associated with topographically diverse terrain (Vetter, 2000) and to lack shrub communities such as the wild rose–strawberry vegetation type.

The lack of a continuous forest cover where parkland-like vegetation occurs, poor local aspen height growth (< 7 m versus ~10 m site index age at 50 years, Strong, 2009; also Hogg and Wein, 2005), poor vigor, and deformed tree canopies suggest the presence of an environmental factor that negatively influences both normal tree growth and vegetation development. The presence of saline soils in the elk core range (Day, 1962; Mougeot and Smith, 1992) and the saline ponds nearby point toward the occurrence of soil salts in sufficient quantities to alter the ecology of the local vegetation. The occurrence of these excess salts is not a normal circumstance, particularly in boreal forest environments where leaching is a characteristic pedogenic process. Early summer aridity (Jätzold, 2000) and enhanced evapotranspiration due to increased annual temperatures during the past 50 years (Pinard, 2007) may have contributed to development of parkland-like vegetation in the elk core range, but the occurrence of excess soil salts likely had

TABLE 3. Comparison of radio-telemetry location frequencies of elk in different landscape components of the Takhini Valley (2007–10) based on G-tests for goodness of fit.

| Comparisons | Area (km²)[1] | Number of occurrences | G-test | $p$ value[2] |
|---|---|---|---|---|
| Core range versus overall range minus core range | 90:1044[3] | 548:319[3] | 1689 | < 0.001 |
| Within the core range | | | | |
| Parkland-like versus nonparkland-like vegetation | 23.3:66.7 | 207:341 | 37 | < 0.001 |
| Summer (May–September) | 23.3:66.7 | 148:148 | 78 | < 0.001 |
| Winter (November–March) | 23.2:66.7 | 30:102 | < 1 | 0.399 |
| Spring + Fall (April + October) | 23.3:66.7 | 29:91 | < 1 | 0.664 |
| Roadsides[4] plus 250 m versus core range | 13:82 | 104:459 | 10 | 0.002 |
| Roadsides plus 500 m versus core range | 25:70 | 157:406 | < 1 | 0.607 |

[1] Used to calculate expected frequencies.

[2] Probability values determined based on a chi-square distribution with one degree of freedom.

[3] Addition of these values represents the total for the Takhini Valley elk overall and core ranges, excludes bison ranch (~5 km²) due to high fences that excluded elk access.

[4] Overall disturbance zone was ± 10 m from road center line.

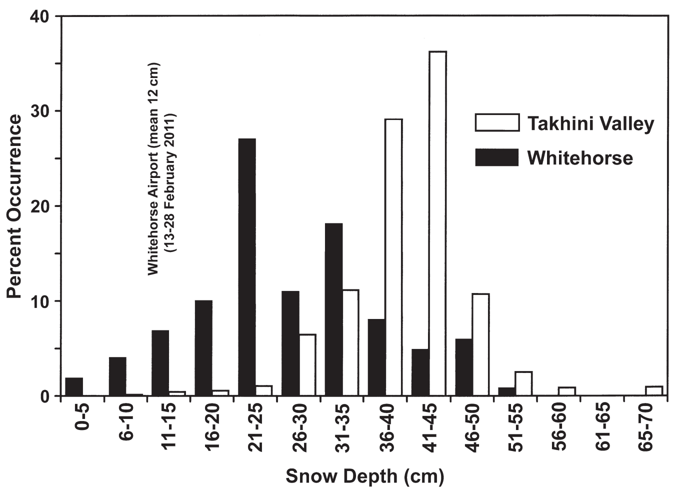


FIG. 4. Percent frequency of snow depths during the last half of February 1981–2010 at the Whitehorse Airport (n = 362; Environment Canada, 2013a) relative to values measured in the Takhini Valley elk core range in late February 2011. The Takhini Valley data include all samples taken in indigenous vegetation (n = 580).

a more direct influence through increased physiological drought stress.

*Elk Distribution Trends and Data Limitations*

The telemetry data indicate that most Takhini Valley elk were located at low elevations throughout the year, which suggests they did not migrate seasonally on an elevation or spatial basis. Elk, however, differed seasonally in distribution within their core range, with a less dispersed population and a greater bias toward parkland-like vegetation during summer than during winter. Elk also tended to occur near the Alaska Highway. These occurrence patterns seem ecologically reasonable because in the area of parkland-like vegetation the ratio between forage and cover is close to the range (from 40:60 to 60:40) considered optimal for elk use (Thomas et al., 1979; Skovlin et al., 2002). In contrast, other portions of the core range and surrounding areas are largely dominated by coniferous boreal vegetation. The attraction of elk to the Highway most likely reflects the greater availability of forage on the roadsides than in the indigenous vegetation.

Although the telemetry location errors were large (e.g., median 274 m) compared to errors from more refined measurement techniques such as global positioning systems (e.g., 50 m, Wolf et al., 2009), most individual elk location errors in the Takhini Valley were small relative to the size of the compared landscape units (Fig. 2), which were typically several square kilometres in area respectively (Nams, 1989). It should also be appreciated that the calculated telemetry error limits assume that elk were stationary during the entire measurement period. Non-stationary animals, however, might explain some of the very large telemetry error ellipse values.

*Range Constraints*

Table 4 summarizes selected characteristics of several areas in western North America that are used by elk as winter range as a basis for comparison with the Takhini Valley elk core range. The Takhini Valley core range produced much less late summer herbaceous biomass (kg/ha) than other areas used by North American elk during winter. Late summer forage was 3 to 10 times as abundant on other elk ranges as in the Takhini Valley (Table 4), with a trend of increasing availability with decreasing latitude. Low levels of forage production on upland sites were also reported by Johansen et al. (1989), Bailey and Willoughby (1990), and Florkiewicz (1994:41) in southern Yukon. In addition, elk ranges farther south often have grasslands dominated by fescues (*Festuca campestris* or *F. hallii*), needle grass (*Hesperostipa comata*), or blue grama (*Bouteloua gracilis*) (Table 4). As an indicator of forage value, these grasses typically have late summer crude protein contents of 5%–9% (Johnston and Bezeau, 1962; Uresk and Sims, 1975; Dragt and Havstad, 1987; Horton, 1991) compared to ~4% in purple reedgrass (Florkiewicz, 1994:18; Chambers, 2010:68).

TABLE 4. Number of cold days, typical snowpack depths, and reported herb forage abundance in selected locations used by elk in western North America during winter.

| Location[1] | Latitude (°N) | Average number of winter days with minima / averages:[2,3] ≤ −20°C | ≤ −30°C | Late winter snowpack depth (cm)[2,4] Average [SD] | Typical range of herb forage (kg/ha)[5] | Dominant grasses based on % cover | Source of forage information |
|---|---|---|---|---|---|---|---|
| Takhini Valley, YK[6] | 60.7 | 48 / 28 | 16 / 7 | 24 [10][7] | < 300[8] | Cp[9] | Field samples (Fig. 3) |
| Muskwa – Tuchodi area, BC | 58.8 | 74 / 43 | 17 / 7 | 49 [17] | 1700[10] | Li | Seip and Bunnell (1985) |
| Elk Island National Park, AB | 53.7 | 38 / 17 | 11 / 2 | 23 [13] | 477 – 1403 | Cc | Bork et al. (1997) |
| | | | | | 2900 – 3255 | Pp, E, Bc | Bishoff (1981:63) |
| Edson, AB | 53.6 | 32 / 13 | 9 / 2 | 21 [15] | 800 – 1100 | ND | Willoughby and Lane (2004) |
| Ya Ha Tinda, AB | 51.6 | 24 / 7 | 4 / 1 | < 25[11] | > 2150 | Fc | Robinson et al. (2010) |
| Suffield National Wildlife Area, AB | 50.3 | 25 / 12 | 6 / 2 | 3 [5] | 363 – 2157 | Hco, Bg, E | Adams et al. (2005) |
| | | | | | > 362 – 1000 | Hco, Bg | Coupland (1961) |
| Cypress Hills, AB | 49.6 | 27 / 10 | 5 / 1 | 26 [22] | > 1290 | Fh, Hcu | Adams et al. (2003, 2004) |
| Southwest Foothills, AB | 49.5 | 20 / 8 | 5 / 1 | 7 [9] | 2008 – 3363 | Fc | Adams et al. (2003) |
| Yellowstone National Park, WY | 44.6 | – | – | 20[12] | 1200 – 1600 | ND | Fortin et al. (2005) |
| | | | | | 2040 – 5890 | Variable | Frank and McNaughton (1992) |

[1] Areas used by elk as winter habitat.

[2] Based on 28 – 30 years of daily data (1981 – 2010, Environment Canada, 2013a), except for Cypress Hills (16 years) and Ya Ha Tinda (10 years).

[3] Winter defined as 01 November to 31 March.

[4] Based on February and March values.

[5] Includes only graminoid and forb biomass to allow direct comparison of the Takhini elk core range with other ranges, which did not typically include shrub forage.

[6] Climatic summary based on Whitehorse Airport meteorological station data.

[7] Thought to be underestimated based on Environment Canada (2013b) meteorological data, see *Snow Depths* section of Results and Fig. 4.

[8] This value represents 95% of study area, see Fig. 3.

[9] Bg – *Bouteloua gracilis*, Bc – *Bromus ciliatus*, Cc – *Calamagrostis canadensis*, Cp – *Calamagrostis purpurascens*, E – *Elymus* spp., Fc – *Festuca campestris*, Fh – *Festuca hallii*, Hco – *Hesperostipa comata*, Hcu – *Hesperostipa curtiseta*, Li – *Leymus innovatus*, Pp – *Poa pratensis*, and ND – No species composition data.

[10] Postfire Spruce – Willow – Birch biogeoclimatic zone vegetation.

[11] Robinson et al. (2010).

[12] Average depths for January and February, the months with the deepest snowpack (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wyyell).

Other common northern boreal forest grasses such as northern reedgrass (*Calamagrostis canadensis*) also have low crude protein content in late summer (3.6%, Strong et al., 2005). In comparison, mature smooth brome, an agronomic grass often used for roadside revegetation after disturbance, has a late summer crude protein content of 2% – 6% (Johnston and Bezeau, 1962). Among all of the above-mentioned grass species, the upper limit of crude protein content in early to mid summer can be similar (15% – 19%) and exceeds the 7.5% minimum necessary to maintain elk body weight (Cook, 2002). Purple reedgrass and northern reedgrass, however, are below the 7.5% minimum threshold in late summer. These data indicate that early and mid summer forage in the Takhini Valley elk core range is probably comparable in quality to forage in southern ranges.

Because of the low quantity and limited quality of post-summer forage, Takhini Valley elk may consume a greater proportion of browse (shrubs and tree twigs) than forage (graminoids and forbs) in winter, as intermediate mixed feeders (Hofman, 1989). This diet can have a negative effect on body weight (Christianson and Creel, 2009). Of the more commonly available browse species, aspen and some willows are considered highly valued (~8% protein content, Johnston and Bezeau, 1962; Bishoff, 1981), but wild rose, which is common in the elk core range, is of limited value (Cook, 2002). Browsing in winter may also be encouraged by deep snow. An analysis of midwinter elk fecal pellets from the Takhini Valley during a heavy snowfall year (2009) and a moderate one (2010) tends to support the hypothesis that browsing increases with increased snow depth: the woody plant component in the fecal pellets was 58% in 2009, but only 23% in 2010 (S. Stotyn, pers. comm. 2012). The woody plant components included willows and some aspen, but ground juniper (*Juniperus communis*) constituted 33% in 2010 compared to 55% in 2009. At best, ground juniper contains less than half (3% – 4%) the crude protein content of aspen (Gucker, 2012). In the elk core range, ground juniper is most commonly associated with steep south-facing slopes and rocky outcrops. The use of lower quality forage may reflect necessity rather than preference.

The characteristics of the forage suggest that during most of winter the diet of an elk in Yukon is constrained by limited availability and poor nutritional quality. As noted by Hoefs (1980) and the Yukon Elk Management Team (2008) and indicated by radio-telemetry data, the broad geographical dispersion of elk in the Takhini Valley area may represent an attempt to acquire adequate resources from discontinuous marginal habitats by a population that has exceeded the carrying capacity of its core range in winter (Chambers, 2010; cf. Andersen et al., 2004). Van Dyke (2007) reported similar expansion into marginal habitats by elk populations in Montana and suggested that this expansion was a density-dependent process.

The use of Whitehorse Airport snow depth measurements to characterize the Takhini Valley elk core range may lead to substantially underestimating the snow depths in the core range. For example, a 41 ± 7 cm snowpack occurred in the elk core range when 12 ± 1 cm was consistently measured at the recording station (Fig. 4). This differential implies that snow depths in the Takhini Valley elk core range could easily exceed a critical foraging depth of 50 cm (Poole and Mowat, 2005) at the same time that an average or above-average snowpack is recorded at the Whitehorse meteorological station. The discrepancy in snow depths between the Whitehorse Airport station and the field measurements likely relates to the lack of tall vegetation to retain snow and the channeling effect of the Yukon River Valley (Pinard, 2007). Steep south-facing slopes are often important habitats in winter because they are warmer and have less snow cover, which allows easier access to forage and potentially greater animal mobility. In this case, however, it was interesting to note that these slopes had the same snow depths as level terrain with indigenous vegetation. This phenomenon probably reflects local winds that are insufficient to redistribute or ablate snow and colder ambient temperatures that inhibit snow melting (winter average −9.3˚C). It may also reflect lower angles of solar incidence (winter range 12˚ – 32˚ azimuth at noon) and ~21% fewer daylight hours with an azimuth greater than 10˚ (March 1) than comparable sites at ~50˚ N latitude, which have an average temperature of −1.9˚C and azimuth of 23˚ to 43˚ (Environment Canada, 2013a; ESRL, 2013).

If temperatures of −20˚C or lower compromise elk calf survival by forcing increased metabolism to maintain body temperature where forage resources are limited (Parker and Robbins, 1984), then winters in southern Yukon are much less favorable than winters south of 55˚ N latitude (Table 4). However, immediately south of Yukon in northeastern British Columbia, the Muskwa – Tuchodi elk range experiences potentially similar snowpacks and more days with temperatures of – 20˚C or lower than the Takhini Valley experiences (Table 4), while supporting a much larger and denser elk population (~7 elk/km$^2$; Bergerud and Elliott, 1998). These facts suggest that deep snow (> 50 cm) and cold temperatures may not be severe range constraints provided that a sufficient volume of good quality forage is available. In most southern latitude elk ranges, average late-winter snow depths were much less than those measured in the Takhini Valley during a year of below-normal snow accumulation (Table 4).

Although forage availability, snow depth, and winter temperatures may create limitations for elk population growth, factors such as competition for resources with other species (e.g., deer and horses) and predation may also impose constraints in southwest Yukon, even though predation has previously been discounted as an important limitation (Hoefs, 1980).

## CONCLUSIONS

Reintroductions of animals to areas they formerly occupied are inherently more likely to succeed than introductions to new areas, because (assuming no extenuating factors) range conditions are presumably favorable to the organism. Although the Takhini Valley core range represents marginal elk habitat, it is the single largest and probably the best year-round elk habitat in the region. None of the range factors considered favored elk. Pellet group counts suggested that elk very strongly favored graminoid patches as habitat in the core range, but this vegetation is of very limited extent in the Takhini Valley. The expansion of elk into adjacent areas may indicate that the population has exceeded the carrying capacity of the Takhini Valley core range. Short of major interventions that would create artificial conditions, little can be done to substantially improve forage production or the nutritional value of the natural vegetation for elk, or to reduce the limitations of winter in Yukon. Such conditions are determined largely by the local climate. It is possible that future climatic warming might increase forage abundance within the Yukon landscape and possibly reduce the severity of winter temperatures. However, with current environmental circumstances, elk abundance and density will likely remain low in southwestern Yukon.

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