The temporal niche and seasonal differences in predation risk to translocated and resident caribou (Rangifer tarandus caribou)

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The temporal niche and seasonal differences in predation risk to translocated and resident caribou (*Rangifer tarandus caribou*)

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Abstract

Mountain caribou are an endangered ecotype of woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788) that continue to decline ultimately due to habitat loss and proximately due to predation. A particularly imperilled population of mountain caribou was experimentally augmented with 19 northern caribou, a geographically distinct ecotype, from northern BC. We examined seasonal variation in risk of predation by cougars (*Puma concolor* L., 1771) to the translocated caribou with comparison to resident caribou. We applied a cluster analysis framework on space-use patterns of GPS radio-collared animals to determine biologically relevant seasons. Then we examined the spatiotemporal similarity in habitat use between caribou groups and cougars across these seasons. This analysis included a control group of caribou from the donor herd that were not translocated. Five resident caribou seasons, two donor caribou seasons, and two cougar seasons were identified. Resident caribou remained at high elevations year-round and primarily selected habitats not used by cougars. In contrast, translocated caribou tended to occupy low-elevation habitats extensively used by cougars, resulting in predation of eight translocated caribou, six of which were by cougars. We concluded that the translocated caribou did not adopt the predator avoidance strategies of resident caribou, rendering them more vulnerable to cougars. We make recommendations for future herd augmentations.

**Key Words:** Predation risk, *Puma concolor, Rangifer tarandus caribou*, mountain caribou, northern caribou, cougars, translocation.
Introduction

Woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788) have been decreasing in numbers for many decades throughout their circumpolar range (Vors and Boyce 2009). Caribou require large, undisturbed areas of old or mature coniferous forest relatively free of direct human disturbance (Kinley et al. 2003; Seip et al. 2007; Serrouya et al. 2007). In North America, woodland caribou are often categorized into mountain, northern, and boreal ecotypes (Serrouya et al. 2012). The first two are of concern in this paper. The mountain caribou ecotype numbers some 1,600 animals in British Columbia (BC), representing about 98% of the global population. Mountain caribou are red-listed (Endangered) (BC Conservation Data Centre 2014).

Habitat loss and fragmentation are believed to be the major agents for the long-term (i.e., ultimate) decline of mountain caribou (Bergerud and Mercer 1989; DeCesare et al. 2010; Wittmer et al 2005a). Predation has been identified as the proximate cause (Wittmer et al. 2005b; DeCesare et al. 2010; McLellan et al. 2012). Over the past few decades, populations of white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780), mule deer (*O. hemionus* Rafinesque, 1817), elk (*Cervus elaphus* Erxleben, 1777), and moose (*Alces alces* L., 1758) have significantly increased in caribou ranges as a function of increased regeneration of early and mid-seral habitat (Bergerud and Elliot 1986,;Latham et al. 2011a; Latham et al 2013). In turn, there has been a numerical response in their density resulting in habitat-mediated apparent competition, a general phenomenon described by Holt (1977) where there is asymmetrical influence of a shared predator. DeCesare et al (2010) discussed the role of apparent competition for endangered species such as a mountain caribou. The increased predator densities render caribou vulnerable to incidental predation (Wittmer et al. 2005b), and hence declining populations of mountain caribou. Small populations are also vulnerable to demographic stochasticity (Lande et al 2003).
Mountain and northern caribou differ in their foraging behaviour, migration patterns, and habitat use. Mountain caribou live at low densities in mountainous environments and forage principally on arboreal lichen in winter (Johnson et al. 2004\textsuperscript{a}; Wittmer et al. 2005\textsuperscript{a,b}). They occupy high elevation habitats in winter and during calving, and moving to lower elevations in summer (Apps et al. 2001; Johnson et al. 2004). Northern caribou are found in west-central and northern mountainous regions of BC. They use subalpine and alpine habitats during calving and summer, and low elevation pine forests where they forage on terrestrial lichens by cratering (Bergerud et al. 1984, Miller 2006). Both ecotypes are known to spatially separate from predators and alternate prey to reduce predation risk (Seip 1992; James et al. 2004).

One management strategy to aid recovery of small wildlife populations, including caribou, is translocation (Seddon et al. 2007; Pérez et al. 2012). Caribou translocations have been conducted in North America since 1924 with varied success (Bergerud and Mercer 1989). Many translocations in eastern North America failed due to disease transmission from white-tailed deer, primarily meningeal brain worm (\textit{Parelaphostrongylus tenuis} Dougherty 1945) within a few years post release (Dauphiné 1975). Predation was also a primary factor limiting success of caribou translocations (Bergerud and Mercer 1989). Cougar predation was the main cause of mortality of caribou translocated from BC to Idaho (Compton et al. 1995), and wolf (\textit{Canis lupus} L., 1758) predation was suggested as the cause of mortality for caribou released near Lake Superior (Gogan and Cochrane 1994). In Newfoundland, where white-tailed deer and wolves are absent, 17 of 22 caribou translocations conducted from 1961-1982 were successful. Anthropogenic disturbance and illegal harvest were thought to be responsible for those failed attempts (Bergerud and Mercer 1989). Recently, caribou translocations have received further attention as a possible management tool to enable caribou persistence for those populations that
have declined to perilously low levels (DeCesare et al. 2011; St-Laurent and Dussault 2012). DeCesare et al. (2011) modelled probabilities of caribou persistence in Jasper and Banff National Parks and concluded translocations may help enable recovery of some populations.

The Purcells-South (PS) mountain caribou herd, located in southeastern BC, is at high risk of extirpation. In 2011, the PS herd totalled 15 members. In an effort to increase the PS population, 19 northern caribou from the Level Kawdy (LK) herd were experimentally translocated to the PS herd in March 2012, with a plan to move another 20 caribou the following year. The overall conservation objective was to (1) increase the population size of the PS herd, thus decreasing the probability of extirpation; (2) decrease potential negative effects of genetic, demographic, and environmental stochasticity; and (3) reduce or eliminate Allee effects that cause the per capita growth rates to decline as populations decline (McLellan et al. 2010).

Our overarching objective was to evaluate habitat use and post-release movements of translocated northern caribou compared to resident mountain caribou with a view to risk of predation. We invoked the Movement Ecology Paradigm (MEP) (Nathan et al. 2008) that postulates there is a relationship between the environment, the internal state of an organism, and its movement patterns as fitness-influencing factors, such as the search for food and mates or finding escape terrain. Central to this paper, the MEP also speaks to “when to move.” As noted by Winkler et al. (2014), “timing is key” in terms of making fundamentally important decisions on moving in relation to multiple, and potentially divergent environmental conditions.

In terms of time and timing, caribou are exposed to seasonal changes in environmental conditions such as variation in temperature, snow condition, forage availability and vulnerability to predation (Miller 2006; Fryxell and Holt 2013). However, from a research perspective defining what is meant by “season”, and how these factors vary over a seasonal scale, may be
problematic. Some studies categorize seasons by the Julian calendar (Bearzi et al. 2008), climate (Owen-Smith 2008), or expert opinion (Mejlgaard et al. 2013). While of heuristic value, these delineations may not correspond to biological reality (Vander Wal and Rodgers 2009; Basille et al. 2012). Failure to accurately define seasons may lead to inconclusive or inaccurate inferences when examining ecological phenomena including seasonal risk of predation.

Our specific goals are to use the MEP to frame questions related to the translocation, namely to (1) what is the nature of the spatial differences in habitat use by translocated and resident caribou? (2) how is habitat use is affected by variation in biologically meaningful seasons? (3) in what ways from a perspective of habitat overlap did cougars and cougar predation affect this conservation effort? and (4) what lessons can be learned from this translocation of northern caribou, a different ecotype, to an imperilled population of mountain caribou?

Study area

Capture site – Level Kawdy study area

The 17,000 km$^2$ LK study area was located in northwestern BC (57°59’N - 59°53’N and 129°51’W - 132°24’W) (Figure 1). The climate, vegetation, and topography is alpine-subalpine with Arctic affinities (Bergerud and Elliot 1986). Mean daily temperatures range from -22°C in January to 19°C in July, and mean annual precipitation is 426 mm (Government of Canada 2013). Snow depth at the nearest weather station, Dease Lake, generally reaches a maximum of 60 cm in March (Ministry of Environment 2013). Elevations range from 470 to 2,240 m, with moderate slopes and few peaks (Bergerud and Elliot 1986). Between 900 and 1,500 m, the Spruce-Willow-Birch (SWB) zone in BC’s Biogeoclimatic Ecosystem Classification (BEC)
system (Ministry of Forests, Lands and Natural Resource Operations (MFLNRO) 2013), is
dominant and is punctuated by areas of Boreal Altai Fescue Alpine (BAFA) zone at higher
elevations. Below this is the Boreal White and Black Spruce (BWBS) zone, dominated by white
spruce (Picea glauca Moench, Voss), black spruce (Picea mariana L), and lodgepole pine (Pinus
contorta Dougl. ex Loudon var. latifolia Englem.) (MFLNRO 2013). Moose, Stone’s sheep
(Ovis dalli stonei Nelson 1884), and mountain goats (Oreamnos americanus de Blainville 1816)
are the other ungulates in the study area. Large and meso carnivores include wolves, grizzly
bears Ursus arctos L., 1758, black bears (U. americanus Pallas, 1780), wolverines (Gulo gulo L.,
1758), and lynx (Lynx canadensis Kerr 1752).

**Release site – Purcells-South study area**

The 14,500 km² PS study area (49°04’N - 50°39’N and 115°18’W - 116°50’W) was located
within the Purcell South Mountains (Figure 1). Terrain varies in elevation from 535 to 3,040 m,
but most alpine ridges do not exceed 2,300 m. Mean daily temperatures range from -12°C in
January to 26°C in July, while mean annual precipitation is about 380 mm at the nearest weather
station in Cranbrook, BC (930 m), in the rain shadow of the Purcell Mountains (Government of
Canada 2013). Mean snow depth at 2,100 m generally reaches a maximum of 270 cm in April
(Powder Creek Lodge 2013). Both the dry and wet BEC subzones of Engelmann Spruce -
Subalpine (ESSF) are at higher elevations White spruce dominate the climax forest, with
subalpine fir (Abies lasiocarpa Hook.) Nutt) composing the understory, and lodgepole pine
(Pinus contorta) common following fire. The Montane Spruce (MS) and Interior Cedar –
Hemlock (ICH) zones are at lower elevations. The Montane Spruce zone is dominated by
Engelmann Spruce, subalpine fir, Douglas-fir (Pseudotsuga menziesii Mirb. Franco), white
spruce and lodgepole pine. In the ICH zone western red cedar (Thuja plicata Donn ex D. Don)
and western hemlock (*Tsuga heterophylla* Raf. Sarg.) are the dominant tree species in mature forests, with black cottonwood (*Populus balsamifera trichocarpa* Torr. & A. Gray) Brayshaw) the climax successional species in more moist areas. Other ungulates in the region include moose, white-tailed deer, mule deer, mountain goats, and elk. Large and meso carnivores include wolves, coyotes (*Canis latrans* (Say, 1823)), grizzly bears, black bears, wolverines, bobcats (*Lynx rufus* (Schreber 1777)), lynx, and cougars.

**Methods**

**Data collection**

Four female PS caribou (henceforth “resident caribou”) were captured using helicopter-based net gunning techniques and then instrumented with Advanced Telemetry System G2110E GPS collars (ATS, Isanti, MN) in February 2011. We chose to collar only four resident caribou so as not to risk increased capture myopathy in the already small population. Also, these caribou travel in herds for the bulk of the year, except during calving when females briefly break away from the herd to calve alone, so GPS information from the four caribou is representative of the herd. Between February 29 and March 1, 2012, 19 LK translocated caribou (henceforth “translocated caribou”; 3 males and 16 females) were similarly captured and instrumented, transported by truck to the PS study area, and released on March 3, 2012. Fifteen female LK resident caribou (henceforth “donor caribou”) were fitted with the same collars but not translocated. These caribou were to serve as a control group to compare their patterns of movement to the translocated conspecifics. Between December 2011 and March 2012 seven cougars were tracked by hounds, sedated using a dart gun, and fitted with ATS G2100E or LOTEK TrackM 2D collars (Lotek Engineering, Newmarket, ON). GPS collared caribou and cougars were monitored through February 2013. Animal handling and capture was conducted in
accordance with all governmental and institutional laws and rules, and conformed to the guidelines of the Canadian Council on Animal Care. Capture and handling of resident caribou was conducted under University of Victoria protocol #2010-32 and BC Environment permit CB 11-68478, and BC Environment permit SM11-74596 for translocated caribou. Cougar capture and collaring was carried out by the British Columbia Fish and Wildlife Compensation Program following CCAC guidelines.

Caribou and cougar GPS positional fixes were taken four times daily, except between December 1 to March 15 and May 1 to August 1 when six daily fixes were taken. We excluded translocated caribou positional data for 3 days post-translocation because potential effects the translocation had on animal activity. Investigation of caribou mortalities were made within 6 days of a putative mortality signal from the GPS collars.

**Determining temporal clusters**

Caribou and cougar seasons were delineated using a cluster analysis framework following Basille et al. (2012). We based homogeneous space-use behaviour on land cover, elevation, and movement. The polygons were created based on the animals’ GPS fixes, thus those locations are 100% within the polygon. Land cover types were defined by BEC zones (MFLNRO 2013). BEC zones were grouped according to vegetation density, species composition, and elevation in the donor and recipient areas (Table 1 and Table 2). Using RESULTS (Reporting Silviculture Updates and Land status Tracking System) silviculture data, we reclassified regenerating cutblocks into two age classes (<5 years and 5-20 years) given that after about 5 years, the sightability of caribou by predators decreases because of increased shrub and tree height. Land cover classes were rasterized in ArcGIS 10.0 (ESRI, Redlands, CA) at a
25 m resolution grid. Road density (km/km\(^2\)) was calculated using a weighted system, giving a weight of one for loose or rough (low volume) logging roads and two for paved (high volume) roads (Chruszcz et al. 2003). Elevation was estimated using a 25 m resolution digital elevation model (DEM). These variables (e.g., BEC zone and elevation) were rasterized to match the 25 m cells.

A 15-day moving window was used to characterize the space-use of each caribou and cougar. For each Julian day, the moving window summarized movement and habitat characteristics based on GPS locations 7 days before and after a focal day. This smoothed temporal trends by removing fine-grained spatiotemporal variation (such as hourly or unusual daily variation in space-use), and thus offset erroneous (short) seasons (Tibshirani et al. 2001; Basille et al. 2012). For each 15-day window, we computed (1) mean travel rate (km/day); (2) tortuosity (turning angle); (3) average elevation (m); (4) average road density (km/km\(^2\)); and (5) proportion of locations in the moving window located in each habitat. Travel rate and turning angle were used to compare speed and path tortuosity. Travel rate was calculated by summing daily Euclidian distances between the current location and the next fixed location. Turning angle, defined as the average difference in direction for two successive moves, was determined between every successive animal location. Measurements were standardized for the entire study period so that each variable had the same clustering weight (Steinley 2006). Range standardization \((z_i)\) follows Steinley (2006), defined as:

\[
 z_i = (x_i - \min(x))/(\max(x) - \min(x)).
\]

where: \(z_i\) = the data point normalized between 0 and 1, \(x_i\) = each data point for a specific variable (e.g., elevation), \(\min(x)\) = the minimum of all the data points for a variable, and \(\max(x)\) = the maximum of all data points for a variable.
The optimal number of clusters (i.e., seasons) was determined using the difference of difference-weighted (DD-weighted) gap method (Yan and Ye 2007), which is based on the gap statistic (Tibshirani et al. 2001). The gap statistic is defined as:

$$gap_k = E^*\{\log(W_{kb})\} - \log(W_k)$$

where $E^*$ denotes expectation under a sample size of $n$ from the reference distribution and $W_k$ is the pooled within-cluster sum of squares around the cluster mean, based on the sum of the pairwise distances for all points in a cluster (i.e., points in a cluster are values for the variables (e.g., elevation, step-length, BEC zone) (Tibshirani et al. 2001). The gap statistic sometimes overestimates the “real” number of clusters ($k$) (Yan and Ye 2007; Basille et al. 2012). To overcome this problem, Yan and Ye (2007) proposed the DDgap method – a multilayer clustering approach ($D_{gap_k} = gap_k - gap_{k-1}$, and $DD_{gap_k} = D_{gap_k} - D_{gap_{k-1}}$) used to estimate the number of clusters when $k>1$. When $k$ is equal to the true number of clusters, the DDgap$_k$ is maximized (Yan and Ye 2007; Basille et al. 2012).

**Defining biological seasons**

The number of clusters determined by the DD-weighted gap statistic was used to define the number of seasons. A cluster was defined as the space-use by each animal group on a given day of the year. Thus a cluster may not be continuous in time, but interrupted with a different cluster. Distance decay, the decrease in similarity between objects as the distance (in space or time) between them increases (Tobler 1970), was used to define temporal space-use trends as neighbouring days are likely to fall into the same space-use state. Therefore, a “season” is defined as a period of time where a species experiences the same space-use (Basille et al. 2012).

Bootstrapping was used to evaluate robustness of seasonal delineation using 100 sets of individual year units randomly re-sampled from the original dataset. $K$-means clustering was
used to estimate the total number of clusters. A distribution of daily weights corresponding to the likelihood a given day would start a new season was then estimated within the bootstrap samples, following Basille et al. (2012). Days in the top 20% of the weight distribution were retained as the start of a season and remaining values were removed (Basille et al. 2012). Putative seasons that were less than 10 days were added to the preceding season as they were deemed too short to be biologically realistic.

**Habitat selection**

We used 90% kernel density estimations (KDEs) for each animal group to determine available habitat by season following Johnson’s (1980) second order selection. Availability was assumed using one random location within the KDE for each location (Johnson et al. 2006; Latham et al. 2011b, 2013). Habitat use within KDEs was then estimated using Jacobs’ index (D), calculated as:

\[ D = \frac{(r - p)}{(r + p - 2rp)} \]

where \( r \) is the proportion of habitat used and \( p \) is the proportion available (Jacobs 1974, Kauhala and Auttila 2010). \( D \) ranges from -1 (maximum avoidance) to +1 (maximum preference), and near zero values indicate habitat used in proportion to its availability (Jacobs 1974; Kauhala and Auttila 2010). Bandwidth was based on the least-squares method (Kie 2013). Chi-square goodness-of-fit tests determined whether habitat selection was independent of availability (\( \alpha < 0.05 \)) (Jelinski 1991).

**Habitat similarities between animal groups**

Jaccard’s index (Birks 1987; Real and Vargas 1996) was used to estimate habitat similarity between each animal group. Travel rate and turning angle were also compared between the resident, translocated, and donor caribou. Similarity (\( J \)) was measured as the
intersection between any two groups divided by the size of the union based on minimum and maximum values of each variable such that:

\[ J(A,B) = \min[\max(A), \max(B)] – \max[\min(A), \min(B)] \]

\[ \max(A, B) – \min(A, B) \]

The index ranges from 0 (no similarity) to 1 (total similarity), where negative values are set to zero. Indices were averaged for each variable to determine overall habitat similarity, as well as by resident caribou season for the resident caribou, translocated caribou, and cougars.

Cougar harvest data reported by hunters and problem kills reported by conservation officers in the Kootenay Region were obtained to estimate cougar population trends from 1976 to 2013 (MFLNRO unpublished data). One-way ANOVAs with Tukey’s HSD post hoc tests were used to compare all metrics, except habitat similarity, between seasons for resident, translocated, and donor caribou, and cougars. For statistical analyses we used R 2.15.3 (R Core Team 2014) with the R packages: aspace (Bui et al. 2013) for determining turning angles, seasonality (Basille 2013) for calculating cluster statistics and biological seasons, and adehabitatHR (Calenge 2013) for establishing KDEs.

**Results**

Harvest data showed a peak in cougar kills between 1996 and 1998, as well as an increased trend from 2005 to 2013 (Figure 2). Of the 19 translocated caribou, 8 died due to predation (6 by cougars and 2 by wolves), and an additional 9 died of accidental or unknown causes (3 by falling or injury, and 6 by unknown causes) within the first 13 months following translocation. These deaths decreased the \( n \) value to 2, and would have increased the contribution that remaining translocated caribou had to any statistical analysis; for this reason, we did not estimate seasons for translocated caribou.
**Defining seasonality**

**Resident caribou**

The DD-weighted gap statistic for resident caribou clustered into three groups (DD-gap = 0.268), corresponding to five seasons. Start dates of the five seasons were May 5, June 10, July 11, September 19, and December 17 (Figure 3). September 19 was not within the top 20% of the weighted distribution, but was retained because caribou generally change their movement patterns at this time (Miller 2006). Resident caribou had the highest annual travel rate (2.66 ± 2.83 km/day) in spring (May 5 - June 9), and the lowest rate (1.14 ± 1.35 km/day, \( p < 0.001 \)) in calving season (June 10 - July 10). In the calving season, resident caribou moved to higher elevations (2090 ± 115 m) and increased use of ESSF Woodland zones. In summer (July 11 - September 18), they made extensive use of Other ESSF zones and travelled to lower elevations (1960 ± 117 m). In the early winter season (September 19 - December 16), they moved to higher elevations (2072 ± 111 m) and reduced use of Other ESSF zones, while use of ESSF Woodland and Parkland zones increased. In late winter (December 17 - May 4), they reduced travel rates (1.15 ± 1.46 km/day), use of higher elevations (2161 ± 81 m), and made increased use of ESSF Woodland and Parkland zones.

**Donor caribou**

Data from donor caribou clustered into two seasons (DD-gap = 0.648). Both were strongly weighted with start dates of May 12 and December 19 (Figure 3). Season 1 (May 12 - December 18) corresponded to caribou moving quickly (3.52 ± 4.50 km/day, \( p < 0.001 \)) at high elevations (1427 ± 213 m, \( p < 0.001 \)). In Season 2 (December 19 - May 11) they reduced rate of travel (2.33 ± 5.50 km/day, \( p < 0.001 \)), and used subalpine and mid-elevation habitats (912 ± 127 m, \( p < 0.001 \)).
**Translocated caribou**

Data from translocated caribou clustered into two groups (DD-gap = 0.634) with breakpoints within the top 20% of the weight distribution delineated by March 6 and October 26 (Figure 3). The first breakpoint occurred on March 6, the day data collection began (3 days post-translocation). At this time, translocated caribou had high travel rates (3.02 ± 5.09 km/day, \( p<0.001 \)), and used high elevations (1618 ± 443 m, \( p<0.001 \)) and areas of high road density (1.21 ± 0.93 km/km\(^2\), \( p<0.001 \)) relative to the second break point. They also used ESSF Woodland and Other ESSF zones during this time. The second break point, October 26, was characterized by lower travel rates (1.04 ± 1.81 km/day, \( p<0.001 \)), and use of lower elevations (1171 ± 386 m, \( p<0.001 \)), and areas of lower road density (0.71 ± 0.36 km/km\(^2\), \( p<0.001 \)). They made extensive use of ICH zones at this time.

**Cougars**

Cougar data clustered into two groups (DD-gap = 0.135) beginning July 11 and October 5 (Figure 3). From July 11 to October 4, their birthing season, cougars used higher elevations (1546 ± 351 m, \( p<0.001 \)) and areas with lower road density (2.23 ± 0.94 km/km\(^2\), \( p<0.001 \)) than the other season. At this time, cougars primarily used ESSF Woodland and Other ESSF zones, and regenerating cutblocks less than 5 years old. From October 5 to July 10, the non-birthing season, cougars used lower elevations (1164 ± 233 m, \( p<0.001 \)) and areas with higher road density (2.79 ± 0.85 km/km\(^2\), \( p<0.001 \)), as well as ICH and IDF zones. Cougar travel rates between birthing and non-birthing seasons were comparable (3.77 ± 3.38 and 3.44 ± 3.18 km/day, respectively, \( p=0.2239 \)).
**Habitat selection**

Resident caribou selected ESSF Woodland zones (Jacobs index of 0.628, $\chi^2$ test, $p<0.001$), and used ESSF Parkland zones in proportion to availability (Jacobs index of -0.010, $\chi^2$ test, $p<0.637$) (Table 3, Figure 4). They avoided ICH (Interior Cedar-Hemlock) zones and both ages of regenerating cutblocks (Jacobs index of -0.985, -0.836, and -0.780, respectively, $\chi^2$ test, $p<0.001$) (Table 3, Figure 4). Conversely, translocated caribou selected ESSF Woodland zones and Other ESSF zones (Jacobs index of 0.301 and 0.088, respectively, $\chi^2$ test, $p<0.001$; Table 3, Figure 4). The donor caribou strongly selected alpine habitat, followed by mid-elevations (Jacobs index of 0.148 and 0.153, respectively, $\chi^2$ test, $p<0.001$) (Table 4, Figure 5), and avoided subalpine habitat (Jacobs index of -0.191, $\chi^2$ test, $p<0.001$) (Table 4, Figure 5).

Cougars selected ICH zones, which resident caribou avoided. Additionally, cougars avoided Woodland, Parkland and Other ESSF zones, and regenerating cutblocks less than 5 years old (Jacobs index of -0.628, -0.560, -0.578, and -0.553, respectively, $\chi^2$ test, $p<0.001$) (Table 3, Figure 4).

**Habitat similarities between caribou and cougars**

There was little habitat similarity between resident caribou and cougars (Table 5). With the exception of Other ESSF zone ($SI = 0.309$), regenerating cutblocks less than 5 years old ($SI = 0.072$), and regenerating cutblocks 5-20 years old ($SI = 0.208$). Habitat similarity was greater between translocated caribou and cougars, except in Other ESSF zones (Table 5). When comparing resident caribou and cougars to translocated caribou and cougars, the greatest difference in habitat similarity was found in use of ICH zones (difference of 0.786, Table 5). Here resident caribou and cougars had no habitat similarity, while translocated caribou and
cougars had high similarity ($SI = 0.786$, Table 5). Translocated caribou and cougars also had a high degree of elevational similarity ($SI = 0.386$, Table 5).

Habitat similarity between translocated caribou and cougars was high year-round except during spring. Conversely, habitat similarity between resident caribou and cougars was low year-round (Figure 6). Differences in habitat similarity between both resident and translocated caribou and cougars were greatest in summer, late winter, and early winter seasons (Figure 6). Resident caribou and cougars had the greatest degree of habitat similarity in spring and early winter seasons, with no habitat similarity during summer season (Figure 6). Habitat similarity between translocated caribou and cougars was greatest in winter seasons and lowest during spring.

**Habitat similarities in resident, translocated, and donor caribou**

Habitat similarity between resident and translocated caribou was generally low year-round (Table 6), with the greatest similarity for using ESSF Parkland zones, Other ESSF zones, and 5-20 year old regenerating cutblocks. No habitat similarity was found for use of the ICH and IDF zones (Table 6). We found high similarity between the travel rate and tortuosity variables (Table 6), indicating that translocated and resident caribou had similar movement patterns on an annual basis.

Translocated and donor caribou used elevations more similarly than translocated and resident caribou (Table 6). There was low to no similarity of road density use for any caribou comparisons (i.e., resident-translocated, donor-translocated, and donor-resident). Resident and translocated caribou had the highest habitat similarity in ESSF Parkland zones and zero similarity in their use of ICH and IDF zones. Travel rate and tortuosity were most similar
between resident and translocated caribou and least similar between donor and resident caribou (Table 6).

Discussion

Biological conservation often deals with crises situations that demand hard choices (Tulloch et al. 2014). Woodland caribou are a conservation-reliant species, and major efforts are needed to reverse their decline (Vors and Boyce 2009). One of the most imperilled herds of mountain caribou was augmented with 19 caribou from northern BC, which were a different ecotype. Within the first 16 months post-augmentation, 17 of the 19 translocates died, including at least 8 due to predation, and 6 by cougars. In a retrospective analysis, we sought to better understand why the herd augmentation failed. We found resident caribou spatially separated from risk of predation by cougars by occupying high-elevation habitat year-round. Unfortunately, translocated caribou used lower-elevation habitats more similar to that used by cougars, thus resulting in the high rate of cougar predation.

Seasonality

According to the spatial separation hypothesis (Bergerud and Elliot 1986; Seip 1992; James et al. 2004), mountain caribou migrate to high elevations to reduce risk of predation. Highest elevations were used during the calving season, when adult females are most vulnerable to predators owing to reduced mobility and agility, and later with a calf at heel (see Magnhagen 1991). Similarly, in late winter, mountain caribou travelled to high elevations to separate from alternate prey typically found at lower elevations in winter. At this time, the snowpack is sufficiently deep and consolidated to access arboreal lichens. Slightly lower elevations were used in spring and early winter seasons, and the lowest elevations were used in summer. By
comparison, Kinley and Apps (2001) found predation by cougars on the resident herd was highest in summer and fall, suggesting lower elevations used by resident caribou in these seasons increase their risk of cougar predation.

The donor caribou moved to alpine areas from May 12 to December 18, and to lower elevations between December 19 and May 11. This mirrored a migration pattern similar to that of northern caribou in their native habitat, as described by Johnson et al. (2004) for a herd located approximately 300 km southeast of the donor population.

The two cougar seasons, which we referred to as birthing and non-birthing, were consistent with the female cougar birth pulse from July to September in North America (Pierce and Bleich 2003; Laundre and Hernandez 2007). After kittens are born, female cougars exploit additional predation opportunities to meet the demands of the litter (Knopff et al. 2010) including the potential for caribou predation. The cougar harvest data showed an increasing trend in cougar numbers leading up to the time of translocation; we believe the high predation rates of translocated caribou is partly due to increased cougar abundance. Kinley and Apps (2001) found the resident herd declined from 78 to 18 between 1995-2000, which corresponded to a peak in cougar numbers at that time.

**Habitat selection and predation risk**

Habitat selection is a hierarchical process involving a series of innate and behavioural decisions (Johnson 1980, Lima and Dill 1990). For caribou, this may involve a trade-off in selecting sub-optimal habitat to reduce risk of predation (Bergerud et al. 1984; Rettie and Messier 2000). We found that resident caribou minimized habitat similarity with cougars, consistent with the spatial separation hypothesis (Bergerud and Elliot 1986; James et al. 2004)
and thus possibly trading off high-quality habitat for a lower risk environment. Most research on this hypothesis insofar as caribou focuses on wolves (Bergerud et al. 1984; Seip 1992; James et al. 2004). There are wolves in our study area, and they are known to prey on caribou (Kinley and Apps 2001, Jelinski unpublished data). However, cougars use structurally more complex habitat (Bartnick et al. 2013). More research would be useful on how caribou habitat use when both cougars and wolves are present in significant numbers.

Somewhat paradoxically, resident caribou and cougars shared habitat similarity in their use of both age categories of regenerating cutblocks. Resident caribou may sometimes be found in regenerating cutblocks simply owing to the high proportion of this habitat type adjacent to preferred habitats, as noted by Beauchesne et al. (2014) for caribou in Quebec. In contrast, predators may select regenerating cutblocks because of the high availability of browse for ungulates such as moose and deer (Smith et al. 2000).

Translocated caribou displayed apparently risky behaviour by residing in habitats used by cougars and travelling at higher rates than resident caribou. Wide ranging movements of translocated animals is a major concern for translocation efforts (Seddon et al. 2007). Large-scale movements by translocated caribou may be, in part, due to their inexperience with the landscape or an attempt to reach their native home range (Stamps and Swaisgood 2007; Scillitani et al. 2013). Translocated Alpine ibex (Capra ibex ibex) had larger home range sizes than residents until 1 to 2 years post-translocation (Scillitani et al. 2012). Similarly, elk translocated from Alberta to Ontario dispersed 20-140 km from the release site (Rosatte et al. 2007).

In this conservation effort, translocated caribou encountered cougars, a novel predator as cougars are seldom found in the far north of BC. The ability of prey to recognize and respond to the threat of predation is critical to the survival and persistence of prey populations (Lima and
Naïve prey may lack sufficient antipredator behavior and, as a result, suffer increased mortality (Martin 2014). Accordingly, the inexperience of translocated caribou with cougars may have led to riskier behaviour in terms of habitat use and/or failing to adopt a spatial separation strategy similar to that of the resident caribou. Atwood et al. (2007) found that elk learned about new predation risk within 1 year, and shifted their habitat selection from simple grassland habitats to structurally complex refugia in attempts to reduce the predation risk from recolonizing wolves.

In our study, translocated caribou did not herd with resident caribou. In fact, based on our GPS data we have no evidence of any interaction between the translocated and caribou. On one occasion they were within about 0.5 km of one another. Herd formation reduces predator search efficiency by creating void spaces across the landscape that may otherwise be filled by asocial prey (Fryxell et al. 2007). Grouping behaviour also dilutes predation risk by increasing vigilance to detect predators (Dehn 1990, Hebblewhite and Pletscher 2002). In addition social animals learn from each other, allowing individuals to benefit from the experience of others insofar as as food source selection or locating refugia from predators, the combination of which may provide a survival advantage (Galef and Laland 2005; Seppanen et al. 2007). Last, juveniles can be more behaviourally plastic than sub-adults and adults (Letty et al. 2007). Therefore, it is possible that translocating northern calves in late winter or captive penning of calves in the PS Mountains with resident caribou may have increased site fidelity, and the potential for young caribou to learn resident caribou behaviours.

A range of factors affect the success of wildlife translocations including using a suitable donor population (Pérez et al. 2012). In the mid-1990s, a mountain caribou herd in northern Idaho was augmented with both mountain and northern caribou ecotypes (Warren et al. 1996).
As in our study, the northern ecotype exhibited more variable habitat use, especially in the first year following translocation. Survival of translocated mountain caribou was higher (67% survived after 3 years) compared to the northern ecotype (36% survived after 3 years). It is clear from the Idaho translocation and our findings that the the Purcells herd, and indeed other mountain caribou populations in like state of extirpation may fare better with a donor population of the mountain caribou ecotype. For example, Griffiths (2011) modelled the population dynamics of the Itcha-Ilgachuz mountain caribou herd in BC to determine the effects of removal of 40 caribou over 2 years. Griffiths used three model variations to reflect different hypotheses about the current dynamics of the Itcha-Ilgachuz herd, and concluded that removals would have little to no effect on the abundance and age and sex ratios of the Itcha-Ilgachuz herd. In hindsight the donor caribou from Itcha-Ilgachuz herd may have resulted in a more positive conservation outcome.

On the other hand there is no reason, \textit{apriori}, that northern caribou should not have been translocated. Using microsatellite markers Serrouya et al (2012) found no genetic differences between populations of both ecotypes. However as they and others note, there are behavioral differences in foraging and seasonal migration patterns characteristics between caribou ecotypes. Serrouya et al. (2012) surmised that these differences may be too recently derived and genetically complex to be expressed in mitochondrial DNA. Alternatively had a range of ecological factors been different, including lower cougar densities, the outcome may have been more favorable. We recommend that future herd augmentations effort should use donor caribou that have greatest genetic or clinal similarity to the recipient population. The donor animals should also have exposure to the same complex of predators, similar seasonal patterns of habitat
use and associated behavioural repertoires, particularly where caribou may be released into a predator-rich landscape.

Acknowledgements

We extend special appreciation to the Ktunaxa and Tahltan First Nations for assistance and cooperation. DEJ is grateful for financial support from the BC Habitat Conservation Trust Foundation, BC Ministry of Environment, Canadian National Sciences Research Council (NSERC), and the University of Victoria. We also thank the BC Hydro Fish and Wildlife Compensation Program for significant support. A large number of other dedicated individuals and NGOs contributed to this project, for which we are grateful. Special thanks to Dr. Rob Serrouya for generous contributions of time and valuable input on two earlier versions of this paper. We are also grateful to two anonymous reviewers of the paper. DEJ thanks Guinness Bell-Martin for constructive feedback on the final version of the manuscript.

References


Table 1. Biogeoclimatic Ecosystem Classification (BEC) zones to characterize caribou habitat in the South Purcell’s study area.

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>Description</th>
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</thead>
<tbody>
<tr>
<td>ESSF Parkland Zones</td>
<td>Subalpine parkland at upper elevations. Clumps of trees occur together in areas of heath, meadow, and grasslands. Includes krummholz life-form trees. Typical species include Sitka valerian (<em>Valeriana sitchensis</em>), Indian hellebore (<em>Veratrum viride</em>), arrow leaved groundsel (<em>Senecio triangularis</em>), western meadowrue (<em>Thalictrum occidentale</em>), bracted lousewort (<em>Pedicularis bracteosa</em>), common red paintbrush (<em>Castilleja miniata</em>), and various heather species (<em>Cassiope sp.</em> and <em>Phylloco p sp.</em>) Elevation range: 1,850 to 3,500 m</td>
</tr>
<tr>
<td>ESSF Woodland Zones</td>
<td>Open and continuous, upper elevation forest dominated by Engelmann spruce (<em>Picea englemannii</em>) and subalpine fir (<em>Abies lasiocarpa</em>) Elevation range: 1,650 to 2,650 m</td>
</tr>
<tr>
<td>Other ESSF Zones</td>
<td>Engelmann spruce and subalpine fir dominate wetter areas, with lodgepole pine (<em>Pinus contorta</em>) as a pioneer after disturbance and mountain hemlock (<em>Tsuga mertensiana</em>) in higher snowfall areas. Whitebark pine (<em>Pinus albicaulis</em>) and limber pine (<em>P. flexilis</em>) occur on drier sites. White rhododendron (<em>Rhododendron albi florum</em>) and false azalea (<em>Menziesia ferruginea</em>) are common understory plants.</td>
</tr>
</tbody>
</table>
Elevation range: 720 to 2,600 m

ICH Zones  Upland coniferous forests with high diversity of tree species.

Western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) dominate mature climax forests. Grand fir (*Abies grandis*) is common. Steeply sloping, mountainous terrain.

Elevation range: 300 to 1,980 m

IDF Zones  Open to closed, mature forests containing Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine. Ponderosa pine (*Pinus ponderosa*) occurs at lower elevations.

Elevation range: 440 to 1,500 m

<5 year cutblocks  High proportion of woody shrubs and herbaceous species

Elevation range: 440 to 2,200 m

5-20 year cutblocks  Woody shrubs with many conifer seedlings.

Elevation range: 436 to 2,400 m
Table 2. Biogeoclimatic Ecosystem Classification (BEC) zones to characterize caribou habitat in the native habitat of the Level Kawdy donor population.

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpine</td>
<td>High elevations. Temperatures are cold throughout the year, lowering the tree line by heavy and prolonged snow cover. Much of the land is covered by vegetated tundra, glaciers, or bare rock. Elevation range: 1,025 to 2,745 m</td>
</tr>
<tr>
<td>Subalpine</td>
<td>Higher elevation valleys and mountain slopes. White spruce (<em>Picea glauca</em>) and subalpine fir (<em>Abies lasiocarpa</em>) are the most common species. Engelmann spruce (<em>Picea englemannii</em>) and lodgepole pine are also found. Stands are often sparsely treed. Subalpine forbs, grasses, sedges, and some heath vegetation cover the ground. Elevation range: 800 to 1,880 m</td>
</tr>
<tr>
<td>Mid-elevation</td>
<td>Common tree species include: white spruce, trembling aspen (<em>Populus tremuloides</em>), lodgepole pine, black spruce (<em>Picea mariana</em>), balsam poplar (<em>Populus balsamifera</em>), tamarack (<em>Larix laricina</em>), common paper birch (<em>Betula papyrifera</em>), and Alaska paper birch (<em>Betula neoalaskana</em>). At higher elevations Engelmann spruce and subalpine fir are also found. Grassland and scrub communities occur in small pockets on steep slopes. Elevation range: 600 to 1,415 m</td>
</tr>
<tr>
<td>Low-elevation</td>
<td>Extensive old growth forests dominated by western and mountain</td>
</tr>
</tbody>
</table>

https://mc06.manuscriptcentral.com/cjz-pubs
hemlock forests (*Tsuga heterophylla* and *T. mertensiana*, respectively). Some white spruce, yellow cedar (*Chamaecyparis nootkatensis*), subalpine fir, and Western red cedar (*Thuja plicata*) are also found. Younger forest dominated by lodgepole pine, trembling aspen, and paper birch. Most of this zone consists of moist, cool climate.

Elevation range: 100 to 1,200 m

5-20 year cutblocks Woody shrubs with many conifer seedlings (Pypker and Fredeen 2003).

Elevation range: 300 to 1,460 m
Table 3. Numbers of GPS locations by Land Cover Type (BEC zones) for resident caribou, translocated caribou, and cougars in the Purcells-South study area February 2011 to February 2013.

<table>
<thead>
<tr>
<th>Land Cover Type</th>
<th>Resident Caribou</th>
<th>Translocated Caribou</th>
<th>Cougars</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n = 4)</td>
<td>(n = 19)</td>
<td>(n = 7)</td>
</tr>
<tr>
<td>Number of GPS</td>
<td>Percent (%)</td>
<td>Number of GPS</td>
<td>Percent (%)</td>
</tr>
<tr>
<td>Locations</td>
<td></td>
<td>Locations</td>
<td></td>
</tr>
<tr>
<td>ESSF Woodland</td>
<td>7187</td>
<td>2872</td>
<td>65.8</td>
</tr>
<tr>
<td>ESSF Parkland</td>
<td>1289</td>
<td>344</td>
<td>11.8</td>
</tr>
<tr>
<td>Other ESSF</td>
<td>2277</td>
<td>3854</td>
<td>20.9</td>
</tr>
<tr>
<td>ICH Zone</td>
<td>5</td>
<td>4142</td>
<td>0.0</td>
</tr>
<tr>
<td>IDF Zone</td>
<td>0</td>
<td>890</td>
<td>0.0</td>
</tr>
<tr>
<td>Cut block &lt;5yrs</td>
<td>8</td>
<td>223</td>
<td>0.1</td>
</tr>
<tr>
<td>Cut block 5-20yrs</td>
<td>153</td>
<td>633</td>
<td>1.4</td>
</tr>
<tr>
<td>Total</td>
<td>10919</td>
<td>12958</td>
<td>100</td>
</tr>
</tbody>
</table>
Table 4. Relative use of land cover types by Level Kawdy donor caribou in native habitat for duration of study.

<table>
<thead>
<tr>
<th>Land Cover Type</th>
<th># GPS Points</th>
<th>Percent (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpine</td>
<td>837</td>
<td>11.1</td>
</tr>
<tr>
<td>Subalpine</td>
<td>4388</td>
<td>58.1</td>
</tr>
<tr>
<td>Mid-elevation</td>
<td>2330</td>
<td>30.8</td>
</tr>
<tr>
<td>Low-elevation</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Cut block 5-20yrs</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Total</td>
<td>7555</td>
<td>100.0</td>
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</table>
Table 5. Measure of habitat similarity (Jaccard’s Index) between resident caribou, translocated caribou, and cougars in relation to habitat attributes in the Purcells-South study area.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Resident-Cougar</th>
<th>Translocated-Cougar</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>0.000</td>
<td>0.386</td>
<td>0.386</td>
</tr>
<tr>
<td>Road Density</td>
<td>0.000</td>
<td>0.337</td>
<td>0.337</td>
</tr>
<tr>
<td>ESSF Woodland</td>
<td>0.000</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>ESSF Parkland</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Other ESSF</td>
<td>0.309</td>
<td>0.213</td>
<td>-0.096</td>
</tr>
<tr>
<td>ICH Zone</td>
<td>0.000</td>
<td>0.786</td>
<td>0.786</td>
</tr>
<tr>
<td>IDF Zone</td>
<td>0.000</td>
<td>0.370</td>
<td>0.370</td>
</tr>
<tr>
<td>Cut blocks &lt;5 yrs</td>
<td>0.072</td>
<td>0.220</td>
<td>0.148</td>
</tr>
<tr>
<td>Cut blocks 5-20 yrs</td>
<td>0.208</td>
<td>0.303</td>
<td>0.095</td>
</tr>
</tbody>
</table>
Table 6. Measure of habitat similarity (Jaccard’s index) between resident and translocated caribou based on their use of habitat attributes in the Purcells-South study area and movement (travel rate and tortuosity) between resident, translocated, and donor caribou.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Resident-Translocated</th>
<th>Donor-Translocated</th>
<th>Donor-Resident</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>0.112</td>
<td>0.245</td>
<td>0.000</td>
</tr>
<tr>
<td>Road Density</td>
<td>0.093</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>ESSF Woodland</td>
<td>0.014</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ESSF Parkland</td>
<td>0.823</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Other ESSF</td>
<td>0.691</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ICH Zone</td>
<td>0.000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>IDF Zone</td>
<td>0.000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cut blocks &lt;5 yrs</td>
<td>0.016</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cut blocks 5-20 yrs</td>
<td>0.685</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Travel Rate</td>
<td>0.650</td>
<td>0.450</td>
<td>0.304</td>
</tr>
<tr>
<td>Tortuosity</td>
<td>0.770</td>
<td>0.449</td>
<td>0.384</td>
</tr>
</tbody>
</table>
Figure Captions

Fig. 1. Location of the donor herd, Level Kawdy, BC and recipient herd, Purcells-South.

Fig. 2. Cougar harvest data for hunter kills (black square) and problem kills reported by conservation officers (grey circle) in the Kootenay Region, BC from 1976 to 2013. Data obtained from BC Ministry compulsory inspection reports, (Forests, Lands and Natural Resource Operations, unpublished data).

Fig. 3. Biological seasons for resident caribou and female cougars in the Purcells-South study area in southeastern BC, and donor caribou from the Level Kawdy region in northern BC. (Translocated caribou clusters may be a statistical artefact coincident with the date of translocation.) Abbreviations symbolize: LW – late winter, Sp – spring, Clv – calving, Sum – summer, EW – early winter, Sea1 – season 1, Sea2 – season 2, Clu1 – cluster 1, Clu2 – cluster 2, NB – non-birthing, B – birthing.

Fig. 4. Selection for land cover types by resident caribou, translocated caribou, and cougars in the study area of BC as shown by the Jacobs Index.

Fig. 5. Selection for land cover types by donor caribou, Level Kawdy region BC, as shown by the Jacobs Index.

Fig. 6. Seasonal changes in habitat similarity between cougars and resident caribou (solid black line), and between cougars and translocated caribou (dashed grey line) based on temporal patterns of habitat use including average elevation, average road density, and proportions of time spent in selected Biogeoclimatic Ecosystem Classification (BEC) zones.
<table>
<thead>
<tr>
<th></th>
<th>Jan</th>
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<tbody>
<tr>
<td><strong>Resident Caribou</strong></td>
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<tr>
<td><strong>Donor Caribou</strong></td>
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<td>Sea2</td>
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<td>Sea1</td>
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<tr>
<td><strong>Translocated Caribou</strong></td>
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<td>Clu1</td>
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