Title: The post-captive movement ecology of endangered mountain caribou

FORD, AT[*,1]

NOONAN, MJ [1]

BOLLEFER, K [2]

GILL, R[3]

LEGEBOKOW, C [4]

SERROUYA, R [5]

*corresponding author: adam.ford@ubc.ca

1. Department of Biology, The University of British Columbia, 1177 Research Road, Kelowna, BC, Canada

2. Revelstoke Community Forest Corporation, Box 3199, Revelstoke, BC, V0E 2S0, Canada

3. Revelstoke Caribou Rearing in the Wild Society, PO Box 3199, Revelstoke, BC, V0E 2S0, Canada

4. Resource Stewardship Division, Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Province of British Columbia, Revelstoke, BC V0E 3K0, Canada

5. Caribou Monitoring Unit, Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Abstract

Translocation and captivity are important tools for conservation biology and wildlife management – they have the potential to restore populations, augment existing populations, and improve the fitness outcomes for individuals Efforts to understand the spatial extent of individual movement in novel terrain is critical to the choice of translocation release sites and management of the surrounding area, i.e., the management neighbourhood. We examined the movements of adult female caribou (N= 36) following their translocation to, and release from, a maternity pen ('penned caribou') and compared these movements to animals that were not translocated ('unpenned caribou', N = 22). A maternity pen is a temporary holding facility, within the animals' existing range, that enables them to bear and raise their young in the absence of predators and with augmented resources. Penned and unpenned animals had similar home range sizes (1052.2 km^2 and 1314.6 km^2, respectively, $P = 0.46$) though penned animals moved through the landscape in a faster yet less directed manner. We found some evidence that memory may improve the efficiency of space use. Home ranges with higher quality habitat tended to be smaller than home ranges with poorer quality habitat irrespective of penning status. Penned animals ranged at lower elevation (~150m) than unpenned animals, particularly in spring and early winter. For penned animals, we did not detect evidence of homing back to the original capture site. The best predictor of how they will use the landscape appears to be driven by the location of the release site. To maximize the fitness of post-released animals, future plans for maternity pens and captive breeding programs need to consider the management of food, predators, and habitat across the 1000-2000 km^2 home ranges that will form near the release site.

Keywords: maternity pen, movement ecology, restoration, translocation

Introduction

Habitat loss is one of the most important factors leading to the global decline of biodiversity (Ceballos, Ehrlich, & Dirzo, 2017; Bradshaw et al., 2021). Efforts to curb human-driven extinctions may include the creation of protected areas (Le Saout et al., 2013), changes in harvest regulations (Williams & Johnson, 1995), and population-level management (Tilman et al., 2017). Broadly speaking, these efforts are intended to improve the survival and reproduction of individuals, thereby increasing population growth rates to a point where self-regulating mechanisms are influential enough that human intervention can be withdrawn and invested elsewhere.

One of the more intensive strategies to improve population recovery separates vulnerable animals from threats faced by predators, food shortages, or illegal harvest. For example, captive rearing, with appropriate genetic support (Fraser, 2008), can provide a source population for augmentation or reintroduction efforts in the wild, and/or reduce the exposure of animals to threats until such time that conditions in the wild improve (Tribe & Booth, 2003). In some cases, captivity is long term, with very limited prospects for wild reintroduction or translocation of individuals (Witzenberger & Hochkirch, 2011). In other cases, captivity is designed to minimize human intervention while maximizing fitness. Captive facilities could be quite large and permanent, with active management occurring at low intensities (e.g., predator removal from pen) (Ali et al., 2018). Other facilities could require more intensive management over shorter periods and less space. In caribou (*Rangifer tarandus*), for example, maternity penning provides a brief respite for young animals who may have survival rates below 19% over the first year of life in the wild (Adams et al., 2019). In contrast, survival for penned and released young may be closer to 57% (Adams et al., 2019).

Animals released from captivity, translocation, and maternity pens will often be exposed to the same types of factors affecting wild populations – limited access to food, inclement weather, and mortality from predation. Some species subject to captive management respond to these limitations by remaining within close proximity to their release sites (Mertes et al., 2019), or returning to the release site during risky periods (Smith & Pittaway, 2011), which can impact the long-term viability of these conservation efforts. As such, managers seeking to enhance or maintain fitness for released animals need to better understand how space use changes over time following release (Van Dierendonck & Wallis De Vries, 1996). This post-release environment contributes to the survival of animals, and therefore could determine the success of the captive program as a whole, and ultimately, the trajectory of the population (Seddon, Armstrong, & Maloney, 2007; Hare et al., 2020). Understanding where such conditions are optimal for newly released animals may help guide facility placement – particularly for animals who are not returned back to the original capture site by managers. Likewise, the post-release home range of animals can guide the scope of a 'management neighborhood' –i.e., the area where habitat protections, forage supplementation, and predator reductions could be concentrated to provide the most efficient gains for recovering populations.

One of central questions in predicting the spatial dynamics of post-release home ranges is the extent to which animals' response to novel terrain will reflect their response to familiar terrain. Studies on animals encountering novel terrain reveal complex movement and navigation processes. For example, some species retain their aversion to people / disturbance following translocation (Ford & Fahrig, 2008), while other translocated species may travel farther, encounter more disturbances, and experience greater risks than non-translocated conspecifics (Ishii et al., 2019; Wright et al., 2020). Studies have shown that there can be an exploratory phase when an animal encounters a new environment before 'settling' (Fryxell et al., 2008), akin to home range formation following natal dispersal (Fattebert et al., 2015). Social interactions (Jesmer et al., 2018) and memory formation may further shape the extent of movement and interactions with novel terrain (Fagan et al., 2013).

Caribou are one of the most endangered terrestrial mammals in North America and are the first large mammal to be extirpated from the conterminous United States of America in the 21st century. For caribou, maternity penning is seen as a management intervention worthy of consideration and has been used on several caribou herds in Canada and the USA (Smith & Pittaway, 2011; Adams et al., 2019; Serrouya et al., 2019). While the results of many penning studies are still under development, early evidence suggests that the local conditions near the pen greatly affect post-release survival of adult and young caribou. With management of caribou facing intense scrutiny by the public and scientific community alike (Hebblewhite, 2017; Struzik, 2020), efforts to optimize actions in the management neighborhood around maternal pens is critical for caribou recovery and persistence.

Here we contrasted the movement ecology of sympatric penned and unpenned caribou to determine the extent of movement, and the interactions between movement and habitat. While we only examined the movements of free-ranging animals, we refer to the animals that were in the maternity pen and then released as 'penned' and the animals that were never penned as 'unpenned'. We hypothesized that unpenned caribou would have greater familiarity with their environment, such that we would expect these animals to have smaller home ranges and shorter displacement distances compared to penned caribou. We also examined effects of multiple releases and reproductive status (presence/absence of a calf at release) for penned animals. We compared seasonal use of a regional habitat model and elevation – a composite measure of resource availability, weather, and exposure to predation – for penned and unpenned caribou (Wittmer et al., 2007; Apps et al., 2013; MacNearney et al., 2016).

Methods

Study Site

This study took place near the town of Revelstoke, British Columbia (BC), Canada and centered on the Columbia North herd of southern mountain caribou (*Rangifer tarandus caribou*), with overlap into the herd ranges of the Groundhog herd to the west, Frisby-Boulder to the southwest, and Columbia South to the southeast. The Columbia North herd occupies a 4652 km^2 range situated in the Selkirk and Monashee mountains within the northern portion of the Columbia River basin (Wittmer et al. 2005). Caribou populations in this area exhibit a bimodal cycle pattern of elevational migrations utilizing upper parkland portions of the Englemann Spruce – Subalpine Fir and Alpine-Tundra biogeoclimatic zones in late winter when deep consolidated snowpacks support foraging on arboreal lichens (Apps et al., 2001). In early spring they briefly descend into closed canopy portions of the Englemann Spruce – Subalpine Fir and the Interior Cedar-Hemlock zones. By mid-May they return to the alpine-ecotone where they give birth and remain until late fall/early winter when they again descend before returning to late winter habitats in January.

The Columbia North subpopulation declined steadily from the mid-1990s to 2004, then stabilized for 10 years during an experimental moose reduction that led to lower predator numbers (Serrouya et al. 2017). Population growth for caribou, however, was elusive (or did not occur). In further support population growth in the Columbia North, a multi-sector partnership formed - Revelstoke Caribou Rearing in the Wild - to create and manage a maternity pen aa a pilot study from 2014 to 2018.The initial goal of this pen was to test the concept on a low proportion of animals, with the possibility of scaling up the treatment to a level that would affect population growth. The pen was located 100 km north of the City of Revelstoke, in a sparsely restocked clearcut at 580 m elevation on the west shore of Lake Revelstoke. This location is approximately centered within the Columbia North's population bounds. The site's microclimate is typified by warm, wet summers and cool winters with moderate snowfall. Although not within typical alpine-ecotone calving range, the site was chosen because of a lower late-winter snowpack (approximately 1–2 m) compared to in-situ conditions (3+ m) where logistical aspects of the project would have been extremely challenging.

The 9.3 ha maternity pen consisted of a 4-m high geotextile wall surrounded by a 2.4-m high 5000 volt electric fence. Water was provided and animals were fed at a rate of 3.2 kg/animal/day (Cook, *personal comm.)* using a commercial pelleted ration developed for the Calgary Zoo (Wetaskiwin Co-op Association, Calgary Zoo Winter Herbivore Ration Formula Code M800710). Transitioning from their natural diet of arboreal lichens to pelleted feed occurred over a 10-day period. Personnel continuously monitored the animals through a combination of direct observation, radiotelemetry, and a live feed remote camera. Camera traps were used to detect predators on the perimeter of the pen, which included wolf (*Canis lupus*), black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), wolverine (*Gulo gulo*), cougar (*Puma concolor*) and lynx (*Lynx canadensis*), however, no predators entered the pen during its five years of operation.

Data Collection

Animals were captured in late March or early April when gravid females were still approximately two months pre-parturition and fresh, deep soft snow increased animal detection and safety during capture. By that time, adult males had dropped their antlers allowing for easier identification of target adult females, who retained their antlers. Capture protocols were adapted from those used by Level-Kawdy/Purcell translocation (Kinley 2010). All animals were captured by a net-gun from a helicopter using a qualified contractor and crew. After sedation with medetomidine administered by an intranasal atomizer device, animals were hobbled, blindfolded, secured in a transport bag and transported with an attendant inside a helicopter to the pen site for final processing. Authority to capture, transport, possess, and release the caribou was provided under BC *Wildlife Act* Permit CB16-220408.

Captured animals were fit with one of three models of Vectronic Aerospace GmbH radiotelemetry collars. Some collars were programmed to acquire 12 location fixes/day, while in year 3 the number of location fixes/day was reduced to 6 in order to extend battery life. In year 4 Vectronic Vertex Lite Globalstar adult collars were deployed and programmed to acquire 2 location fixes/day. These collars had a 54% failure rate due to inherent flaws with the GPS and VHF transmitters so in year 5 of the penning project Vectronic GPS PLUS Globalstar collars were used and programmed to provide a location fix every 13 hours. These failure rates are similar to global averages (Hofman et al., 2019).

Data analysis

For each location estimate, the GPS collars we used recorded a unitless Dilution of Precision (DOP) value as a measure of the accuracy of each positional fix. To prepare the data for error-informed analyses (C. H. Fleming et al., 2020) we converted these unitless DOP values into calibrated error circles by assigning a User Equivalent Range Error (UERE) of 10 m to the tracking devices, which tends to be the standard value for most GPS devices (Noonan, Fleming, et al., 2019; C. H. Fleming et al., 2020). For each individual dataset, we then filtered out outliers based on error-informed distance from the median longitude and latitude, and the minimum speed required to explain each location's displacement (for further details see Additional File S2 in Noonan et al. 2019). We did not measure movements of penned caribou while they were in the pen.

Movement metrics

Our primary aim was to determine whether penned animals exhibited movement behaviour that was significantly different from unpenned animals. To do this, we quantified 6 key movement metrics using the methods implemented in the `R` package `ctmm` (ver. 0.5.11;Calabrese et al. 2016): displacement distances, autocorrelation timescales, home range areas, and median movement speeds. We opted to use the continuous-time methods implemented in the `ctmm` package, as these are robust to differences in sampling protocols.

Displacement distances – We quantified the maximum and median distances that penned and unpenned caribou displaced from both the maternal pen and from each individual’s capture location. Displacements were calculated using the haversine great-circle formula implemented in the `R` package `geosphere` (ver. 1.5-10; (Hijmans, 2016).

Positional and velocity autocorrelation time scales – Following the workflow described in Calabrese et al. (2016), we fit a series of continuous-time movement models to the data using perturbative-Hybrid Residual Maximum Likelihood (pHREML; Fleming et al. 2019), and identified the best model for each individual via small-sample-sized corrected Akaike’s

Information Criterion (AICc). We then extracted the positional autocorrelation timescale (τ_p), which provides a measure of the home-range crossing time, and the velocity autocorrelation timescale (τ_v), which provides a measure of directional persistence, from each individual's best fit model.

Home-range area – We estimated the 95% home-range areas of each caribou using Autocorrelated Kernel Density Estimation (AKDE; Fleming et al. 2015). AKDE home-range estimates were conditioned on the autocorrelation structure of the best fit model identified above, and we implemented the small-sample-size bias correction of (Christen H. Fleming & Calabrese, 2017), and the location weighted of Fleming et al. (2018). In addition to estimating the home-range area, we also calculated the Euclidean distance between each individual's home-range centre and the maternal pen for both penned and unpenned animals.

Mahalanobis distances – In order to understand how each individual's post-collaring space use related to their original capture location, we calculated the Mahalanobis distances (MD; Mahalanobis 1936) between each animal's home range and i) its capture location; and ii) the maternal pen. The MD is a statistical measure of the distance between a point and a distribution that is typically used in outlier identification. In this context, if an animal's observed home range had a large MD from its capture location, this could be considered an 'outlier' and provide evidence of a range shift. Similarly, a short MD between an animal's observed home range and the maternal pen would suggest that the maternal pen can be considered as part of the animal's range. We calculated these using the `distance()` function in `ctmm`.

Median movement speed – We estimated the median daily movement speed (in km/day) using continuous-time speed and distance (CTSD) estimation (Noonan, Tucker, et al., 2019). CTSD uses a simulation-based approach to sample from the distribution of possible trajectories that are consistent with the data and a fitted continuous-time movement model, from which the median speed estimate and confidence intervals can be extracted. This approach is insensitive to the sampling schedule, enabling robust comparisons across individuals.

We were also interested in understanding whether repeated capturing and (re-)penning influenced individuals' movement over time. For the nine animals that were held in the maternity pen on > 1 occasion, we split individual datasets up by penning cycle (year) and estimated each of the above movement metrics for their annual data.

To explore for any underlying patterns in movement behaviour between penned and unpenned animals, we performed a principal component analysis (PCA), with scaling, across these movement metrics. Home-range areas, movement speeds, and model parameters were compared using the meta-regression model implemented in the `R` package `metafor` (ver. 2.1-0; (Viechtbauer, 2010), which allowed uncertainty in each individual estimate to be propagated into the population level estimate when making comparisons. All other metrics were compared using two-tailed permutation tests, as described by (Strasser & Weber, 1999), and implemented in the `R` package `lmPerm` (Wheeler, Torchiano, & Torchiano, 2016). In addition to penning status, we tested if reproductive status of caribou – i.e., if there was a calf with the female at the time of release – affected home range size using a permutation test.

Lastly, we examined if penning affected habitat use via two analyses related to habitat quality and elevation. Using an existing habitat model (Apps et al., 2001) we first examined if the average seasonal habitat quality affected home range size. Using GIS software, we extracted the average values of a resource selection function (i.e., the RSF score) of each home range polygon (derived from the AKDE analyses described above). We evaluated if penned and unpenned animals had access to the similar types of habitat, by first using a mixed-effects model with the mean RSF score as the response variable and penning status and season as interacting predictors and animal identity as a random intercept. We then used a linear model to analyze if the seasonal-specific RSF score affects home range size, along with interacting effects of penning and season. Second, we examined how penning affected seasonal use of elevation. In this landscape, elevation is an important driver of access to resources and risk of predation, mediated by disturbance from roads, elevational gradients in snowfall, and forestry (Wittmer et al., 2007; Serrouya, McLellan, et al., 2017). We used a mixed-effects model with the median seasonal elevation for each individual as the response variable and season and penning status as interacting predictors. Animal identity as a random intercept. Only data from an animals' first release was used in this analysis.

Results

We found that the first two dimensions of a PCA explained 75.2% of the variance in caribou movement metrics. The first dimension ('range dimension') explained 53.1% of the variance, and was governed primarily by the four metrics that described movement range (i.e., τ_p, home-range area, and median/maximum displacements). The second dimension ('mode dimension') explained 22.1% of the variance, and was governed primarily by the two metrics that described movement mode (i.e., τ_v, speed). Caribou with greater values across the range dimension tended to move across larger areas, and those with greater values across the mode dimension tended to move more slowly and with longer directional persistence. When projecting the data into the reduced dimension space of these two dimensions, we found that most of the separation between penned and unpenned animals occurred along the mode dimension, with little separation along the range dimension (Fig. 1). In other words, penned and unpenned animals used areas of comparable magnitudes, but movement range within these areas were different.

Home-range metrics

Overall, we found few differences in movement-range metrics between penned and unpenned caribou. While a permutation test revealed that the home-range centres of penned caribou tended to be closer to the maternal pen than those of unpenned caribou ($F_{[1,65]}$ =134.4, $p < 0.001$; Fig. 2a,b), we found no evidence that home-range sizes differed between penned and unpenned animals ($\bar{x}$ = 1052.2 km^2 , 95% CIs 653.3 – 1451.1 km^2, $\bar{x}$ = 1314.6 km^2, 95% CIs 744.1 – 1885.1km^2, respectively, $p = 0.46$; Fig. 3). There was also no evidence that median, nor maximum displacements differed between groups ($F_{[1,62]} < 0.01$, $p = 0.95$; $F_{[1,62]} = 0.55$, $p = 0.46$, respectively). In other words, beyond the difference in mean location, there was no evidence of any differences in the range of movement exhibited by penned and unpenned animals. When calculating the MDs between individual home ranges, capture locations, and the maternal pen, we found that the home ranges of penned animals had 96.7% lower MDs to the pen on average as compared to unpenned animals ($F_{[1,61]} = 25.1$, $p < 0.001$). Penned animals also had 3678.8% larger MDs from their capture locations on average as compared to unpenned animals ($F_{[1,61]}$ = 11.8, $p < 0.005$). In addition, penned animals had, on average, 75.2% larger MDs from the pen than unpenned animals had from their capture locations ($F_{[1,61]} = 6.28$, $p = 0.015$), but with no significant difference between how far penned animals were from their capture locations vs. unpenned animals from the pen ($F_{[1,61]} = 2.45$, $p = 0.123$). Finally, displacement distances over time showed no evidence of penned animals tending to return to their release location (Fig. S6).

Collectively, these results indicate a tendency for penned animals to establish their home ranges in the vicinity of the maternal pen.

For the nine caribou that were held in the maternity pen over multiple breeding seasons, we found that home range areas were significantly smaller in subsequent captures ($p<0.0001$; Fig. 4). These individuals had an average home range area of 2054.4 km^2 (95% CI: 1031.4 – 3077.5 km^2) at first capture, with a reduction to a mean home range area of 842 km^2 (95% CI: 1031.4 – 3077.5 km^2) after their second release. A permutation test revealed no relationship between caribou home range size and whether or not the animals had a calf at the time of release ($F_{[1,40]} = 0.526$, $p = 0.47$; Fig. S7)

Movement-mode metrics

When comparing the two movement mode metrics, we found that penned animals tended to move faster than unpenned animals ($\bar{x}$ = 9.13 km/day, 95% CIs 5.39 – 12.87 km/day, $\bar{x}$ = 3.46 km/day, 95% CIs 2.69 – 4.24 km/day, respectively, $F_{[1,45]} = 8.29$, $p = 0.006$; Fig. 4), and exhibited less directional persistence ($F_{[1,44]} = 19.95$, $p < 0.001$).

Habitat use

Home range area tended to decline with the average RSF score in each home range (Table 1; Figure 6). We also found average RSF score varied by season, with spring being slightly higher and late winter being slightly lower quality compared to the RSF scores in other seasons. We did not find an effect of penning status on habitat quality in the home range (Table 1). Caribou use of elevation varied by season and this effect was mediated by penning status (Table 2; Figure 8). On average, penned animals were 150-m lower than unpenned caribou, but there was a strong effect of season with the largest differences observed in spring when penned animals were ~500-m lower in elevation (Figure 8).

Discussion

Caribou – particularly the Southern Mountain herds – are one of Canada's most endangered terrestrial mammals and there are substantial efforts focused on stabilizing and restoring their populations (Hebblewhite, 2017; Serrouya et al., 2019). Maternity penning is one such effort, where it has been shown that by separating caribou and predators for the early period of the calves' life, annual survival can be higher and help contribute towards population growth (Adams, Singer, & Dale, 1995; Adams et al., 2019). Our goal in this study was to determine whether maternal penning might have an impact on the movement of caribou post release. Contrary to our hypothesis, we found that, following release from the maternity pen, caribou interacted with novel terrain in broadly similar ways as animals that were never translocated. Penned caribou tended to move in a less directed manner and had smaller home ranges after subsequent releases, but, on the whole, there were few differences in the movement of penned and unpenned individuals. In terms of habitat use, penned and unpenned caribou used habitat of similar quality, and both groups exhibited seasonal patterns in elevation, however, penned animals spent more time at lower elevation during spring and early winter. Given that predators spend more time at low elevation during those seasons, this behavior by penned caribou could have negative implications for their survival.

Caribou in the deep snow zones of British Columbia's interior rainforest have some of the largest home ranges for their body size, with allometric equations predicting areas less than half of the size we observed here (Noonan et al 2020). Preserving the unique movement ecology of this species is therefore an important part of their conservation. We found that translocated animals established their home ranges in and around the maternal pen from which they were released, with no evidence of any 'homing' behaviour. Encouragingly, we also found that penned and unpenned caribou had similar-sized home ranges, and there was no effect of penning on maximum or median displacements. Similarly, habitat quality within home ranges was similar for penned and unpenned caribou. Taken together, our findings indicate that the characteristics of the release location are likely to be the biggest determinant of space use for penned caribou.

While we found some evidence that penned animals had smaller home ranges after subsequent recaptures, we could not distinguish the extent to which this may have been driven by the effect of maternity pens versus natural behavioural changes. For instance, this reduction in home range size likely reflects some level of increasing efficiency in space use as an animals' memory of the landscape improves with time (Van Moorter et al., 2009). In this regard, we did find that, on average, penned animals moved in a less directed manner through the environment, when compared to unpenned animals (Figure 4). This pattern is suggestive of exploratory behaviour as individuals learn to navigate new habitats without the capacity to rely on spatial memory (Schmidt-Koenig & Walcott, 1978; He et al., 2019). Indeed, most individuals had fewer than two years of data however, and we did not have multiple captures on unpenned animals, so it is still unclear how penning per se interacts with memory and learning to influence space use over time. Nonetheless, it is likely that animals released from the maternity pen for the first time will use an area that is about twice as large as animals released from the pen on multiple occasions.

In addition to memory, we expected that resource demands and resource availability to further affect home range size (Lucherini & Lovari, 1996; Relyea, Lawrence, & Demarais, 2000;

Nilsen, Herfindal, & Linnell, 2005; Nathan et al., 2008). Calving can exert high nutritional and energetic demands on ungulates, with nursing mothers typically requiring greater space than non-nursing adult females (Clutton-Brock, Guinness, & Albon, 1983; Parker et al., 1990). However, we found that animals with calves had the same home range size as animals without calves, suggesting that the demands of calving did not significantly influence area requirements. Similarly, long-term data on roe deer showed that home range sizes were comparable for reproductive and non-reproductive females (Saïd et al., 2009). It is possible that the gregarious social structure of caribou may be a more important driver of home range size than reproductive status. For example, more nutritionally-stressed cow-calf dyads may use the same home ranges areas as dry cows to exploit the fitness benefits of herd formation (Hamilton, 1971).

Resource availability – as indexed by the average seasonal RSF score in the home range – was weakly and negatively associated with home range size. This finding supports predictions from ecological theory (Fretwell, 1969) and biogeographic patterns (McNab, 1963), demonstrating that animals in more productive environments have higher densities and smaller ranges. Given that caribou densities are sensitive to resource extraction, our results indicate that habitat loss near the post-translocation release sites will strongly affect caribou movements with potential consequences for maternal penning and captive breeding programs. We predict that larger management neighborhoods will be required in landscapes with greater modification and lower productivity.

Landscape change in mountain caribou herd ranges area has an elevational bias that interacts with caribou movements (MacNearney et al., 2016). Work completed on caribou movement in the 1990s suggest there are two seasonal migrations from high to low elevation areas (Apps et al. 2001, and See Figure S3). One of these movements occurs in the spring when caribou are calving. The other migration occurs in early winter when caribou crater-forage through the snow for low lying plants, until the snow gets too deep and then they move back up to the supported snowpack that lets them feed on arboreal lichen in the subalpine (Apps et al., 2001; Serrouya, McLellan, & Flaa, 2007). In addition to access to forage, use of high-elevation areas may reduce exposure of caribou to predators, particularly near the resource roads that characterize low-elevation sites in this landscape. Roads and other linear features can facilitate wolf movement and likely confer added risk to caribou (Dickie et al., 2017), particularly given that mountain caribou also select forestry roads for ease of travel (Serrouya, Kellner, et al., 2017). Our observations of the low-elevation return of adults to an area near the maternity pen were observed in Alberta as well (Smith & Pittaway, 2011). Further analyses of how landscape change has influenced seasonal use of elevation by caribou should be a priority for future research, particularly given that risk of predation increases at lower elevation (Stotyn, 2008).

While our study exploited available telemetry data to ask an important question to support caribou conservation, we note a number of limitations that affect the strength of our inferences. First, while the telemetered animals occurred in the same area (Figure 1), their collaring schedules were not synchronous (Figures S1 and S2). This means that annual variation in weather, predators, or landscape change was not systematically applied across treatments (penning status). Second, we did not have measures of movement patterns before and after penning for individuals. We also did not translocate unpenned animals to new areas. Ideally, such a design (i.e., before-after-control-impact) would help us separate the potential effects of penning and translocation per se on caribou. While interesting from an ecological perspective, such insights would require the handling of several more individuals and this comes with a risk of injury to telemetered animals, with questionable returns on population growth under the best-case scenario of no injury. Finally, we focused our analyses on the movement ecology of caribou and see this work supporting the restoration of caribou populations. We did not measure direct links between movement metrics and survival or population growth, but there is a clear need for further research on this subject. Ongoing work in British Columbia is taking a closer look at the effects of caribou management strategies on populations (Lamb et al *In Review*).

Conclusion

Maternity penning is an important conservation effort that can help stabilize and restore the populations one of Canada's most endangered terrestrial mammals (Adams et al. 1995, 2019b Hebblewhite 2017, Serrouya et al. 2019, Lamb et al In review). For penning efforts to yield positive conservation outcomes it is critical to ensure that post-penned caribou have access to the resources they need to survive and reproduce. We found that penned animals established home ranges in and around the vicinity of the maternal pen, with few differences in movement behaviour between penned and unpenned individuals. A notable exception is the use of lower elevation areas by penned animals, which may influence their survival. The management neighborhood of penned caribou had an upper limit of close to 10,000 km^2 and an average area that was similar to penned animals (~1200 km^2). For caribou, the best predictor of how they will use the landscape appears to be driven by conditions at the release site. Future plans for maternity pens and captive breeding programs need to carefully choose a location that considers the survival of post-released animals across the expansive home ranges that will form near the release site. Collectively, these home ranges form a neighborhood around the captive release site where managing the distribution of key factors limiting population growth – such as food, predators, and habitat - need to be prioritized. Further work is needed to understand how seasonal shifts in elevation relate to habitat disturbance and survival for these threatened populations.

Author's contributions: *ATF, MJN, and RS co-lead the writing and analysis of the manuscript. CL, RG, KB, RS collated field data collection and acquisition. ATF, MJN, RS conceived the ideas and designed methodology. All authors contributed critically to the drafts and gave final approval for publication.*

Acknowledgements: Support for this research was provided by Revelstoke Rearing Caribou in the Wild and the Canada Research Chairs Program. Bill Beard provided commented on an earlier version of this manuscript. Clayton Apps provided the resource selection function model.

References

Adams, L. G., Farnell, R., Oakley, M. P., Jung, T. S., Larocque, L. L., Lortie, G. M., Mclelland, J., Reid, M. E., Roffler, G. H., & Russell, D. E. (2019). Evaluation of Maternal Penning to Improve Calf Survival in the Chisana Caribou Herd. *Wildl. Monogr.* **204**, 5–46.

Adams, L. G., Singer, F. J., & Dale, B. W. (1995). Caribou calf mortality in Denali national park, Alaska. *J. Wildl. Manage.* 584–594.

Ali, A. H., Kauffman, M. J., Amin, R., Kibara, A., King, J., Mallon, D., Musyoki, C., & Goheen, J. R. (2018). Demographic drivers of a refugee species: large-scale experiments guide strategies for reintroductions of hirola. *Ecol. Appl.* **28**, 275–283.

Apps, C. D., McLellan, B. N., Kinley, T. A., & Flaa, J. P. (2001). Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. *J. Wildl. Manage.*

65–77.

Apps, C. D., McLellan, B. N., Kinley, T. A., Serrouya, R., Seip, D. R., & Wittmer, H. U. (2013). Spatial factors related to mortality and population decline of endangered mountain caribou. *J. Wildl. Manage.* **77**, 1409–1419.

Bradshaw, C. J. A., Ehrlich, P. R., Beattie, A., Ceballos, G., Crist, E., Diamond, J., Dirzo, R., Ehrlich, A. H., Harte, J., Harte, M. E., Pyke, G., Raven, P. H., Ripple, W. J., Saltré, F., Turnbull, C., Wackernagel, M., & Blumstein, D. T. (2021). Underestimating the Challenges of Avoiding a Ghastly Future. *Front. Conserv. Sci.* **1**, 9.

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* **7**, 1124–1132.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci.* 201704949.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1983). The costs of reproduction to red deer hinds. *J. Anim. Ecol.* 367–383.

Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J. Appl. Ecol.* **54**, 253–263.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., Ladage, L., Schlägel, U. E., Tang, W. W., Papastamatiou, Y. P., Forester, J., & Mueller, T. (2013, October 1). Spatial memory and animal movement. *Ecol. Lett.* John Wiley & Sons, Ltd.

Fattebert, J., Robinson, H. S., Balme, G., Slotow, R., & Hunter, L. (2015). Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecol. Appl.* **25**, 1911–1921.

Fleming, C. H., Drescher-Lehman, J., Noonan, M. J., Akre, T. S. B., Brown, D. J., Cochrane, M. M., Dejid, N., DeNicola, V., DePerno, C. S., Dunlop, J. N., Gould, N. P., Hollins, J., Ishii, H., Kaneko, Y., Kays, R., Killen, S. S., Koeck, B., Lambertucci, S. A., LaPoint, S. D., Medici, E. P., Meyburg, B. U., Miller, T. A., Moen, R. A., Mueller, T., Pfeier, T., Pike, K. N., Roulin, A., Sa, K., Séchaud, R., Scharf, A. K., Shephard, J. M., Stabach, J. A., Stein, K., Tonra, C. M., Yamazaki, K., Fagan, W. F., & Calabrese, J. M. (2020). A comprehensive framework for handling location error in animal tracking data. *bioRxiv*.

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., Calabrese, J. M., & Cooch, E. G. (2015). Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator. *Ecology* **96**, 1182–1188.

Fleming, C. H., Sheldon, D., Fagan, W. F., Leimgruber, P., Mueller, T., Nandintsetseg, D., Noonan, M. J., Olson, K. A., Setyawan, E., Sianipar, A., & Calabrese, J. M. (2018). Correcting for missing and irregular data in home-range estimation. *Ecol. Appl.* **28**, 1003–1010.

Fleming, Christen H., & Calabrese, J. M. (2017). A new kernel density estimator for accurate home-range and species-range area estimation. *Methods Ecol. Evol.* **8**, 571–579.

Fleming, Christen H., Noonan, M. J., Medici, E. P., & Calabrese, J. M. (2019). Overcoming the challenge of small effective sample sizes in home-range estimation. *Methods Ecol. Evol.* **10**, 1679–1689.

Ford, A. T., & Fahrig, L. (2008). Movement patterns of eastern chipmunks (Tamias striatus) near roads. *J. Mammal.* **89**, 895–903.

Fraser, D. J. (2008). How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evol. Appl.* **0**, 080602014503553-???

Fretwell, S. D. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**, 45–52.

Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T., & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 19114–19119.

Hamilton, W. D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311.

Hare, K. M., Schumann, N., Hoskins, A. J., Daugherty, C. H., Towns, D. R., & Chapple, D. G. (2020). Predictors of translocation success of captive-reared lizards: implications for their captive management. *Anim. Conserv.* **23**, 320–329.

He, K., Dai, Q., Foss-Grant, A., Gurarie, E., Fagan, W. F., Lewis, M. A., Qing, J., Huang, F., Yang, X., Gu, X., Huang, Y., Zhang, H., Li, D., Zhou, X., & Yang, Z. (2019). Movement and activity of reintroduced giant pandas. *Ursus* **29**, 163–174.

Hebblewhite, M. Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. , 206 Biological Conservation 102–111 (2017). Elsevier Ltd.

Hijmans, R. J. (2016). geosphere: Spherical Trigonometry.

Hofman, M. P. G., Hayward, M. W., Heim, M., Marchand, P., Rolandsen, C. M., Mattisson, J., Urbano, F., Heurich, M., Mysterud, A., Melzheimer, J., Morellet, N., Voigt, U., Allen, B. L., Gehr, B., Rouco, C., Ullmann, W., Holand, Jørgensen, N. H., Steinheim, G., Cagnacci, F., Kroeschel, M., Kaczensky, P., Buuveibaatar, B., Payne, J. C., Palmegiani, I., Jerina, K., Kjellander, P., Johansson, LaPoint, S., Bayrakcismith, R., Linnell, J. D. C., Zaccaroni, M., Jorge, M. L. S., Oshima, J. E. F., Songhurst, A., Fischer, C., Mc Bride, R. T., Thompson, J. J., Streif, S., Sandfort, R., Bonenfant, C., Drouilly, M., Klapproth, M., Zinner, D., Yarnell, R., Stronza, A., Wilmott, L., Meisingset, E., Thaker, M., Vanak, A. T., Nicoloso, S., Graeber, R., Said, S., Boudreau, M. R., Devlin, A., Hoogesteijn, R., May-Junior, J. A., Nifong, J. C., Odden, J., Quigley, H. B., Tortato, F., Parker, D. M., Caso, A., Perrine, J., Tellaeche, C., Zieba, F., Zwijacz-Kozica, T., Appel, C. L., Axsom, I., Bean, W. T., Cristescu, B., Périquet, S., Teichman, K. J., Karpanty, S., Licoppe, A., Menges, V., Black, K., Scheppers, T. L., Schai-Braun, S. C., Azevedo, F. C., Lemos, F. G., Payne, A., Swanepoel, L. H., Weckworth, B. V., Berger, A., Bertassoni, A., McCulloch, G., Šustr, P., Athreya, V., Bockmuhl, D., Casaer, J., Ekori, A., Melovski, D., Richard-Hansen, C., Van De Vyver, D., Reyna-Hurtado, R., Robardet, E., … Balkenhol, N. (2019). Right on track? Performance of satellite telemetry in terrestrial wildlife research. *PLoS One* **14**, e0216223.

Ishii, H., Yamazaki, K., Noonan, M. J., Buesching, C. D., Newman, C., & Kaneko, Y. (2019). Testing cellular phone-enhanced GPS tracking technology for urban carnivores. *Anim. Biotelemetry* **7**.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., Mcwhirter, D. E., Miyasaki, H. M., Monteith, K. L., & Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals **1025**, 1023–1025.

Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T. M., Bertzky, B., Butchart, S. H. M., Stuart, S. N., Badman, T., & others. (2013). Protected areas and effective biodiversity conservation. *Science (80-.).* **342**, 803–805.

Lucherini, M., & Lovari, S. (1996). Habitat richness affects home range size in the red fox Vulpes vulpes. *Behav. Processes* **36**, 103–105.

MacNearney, D., Pigeon, K., Stenhouse, G., Nijland, W., Coops, N. C., & Finnegan, L. (2016). Heading for the hills? Evaluating spatial distribution of woodland caribou in response to a growing anthropogenic disturbance footprint. *Ecol. Evol.* **6**, 6484–6509.

Mahalanobis, P. C. (1936). On the generalized distance in statistics. National Institute of Science of India.

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.* **97**, 133–140.

Mertes, K., Stabach, J. A., Songer, M., Wacher, T., Newby, J., Chuven, J., Al Dhaheri, S., Leimgruber, P., & Monfort, S. (2019). Management Background and Release Conditions Structure Post-release Movements in Reintroduced Ungulates. *Front. Ecol. Evol.* **7**.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008, December 9). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. U. S. A.*

Nilsen, E. B., Herfindal, I., & Linnell, J. D. C. (2005). Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Ecoscience* **12**, 68–75.

Noonan, M. J., Fleming, C. H., Akre, T. S., Drescher-Lehman, J., Gurarie, E., Harrison, A. L., Kays, R., & Calabrese, J. M. (2019). Scale-insensitive estimation of speed and distance traveled from animal tracking data. *Mov. Ecol.* **7**, 35.

Noonan, M. J., Tucker, M. A., Fleming, C. H., Akre, T. S., Alberts, S. C., Ali, A. H., Altmann, J., Antunes, P. C., Belant, J. L., Beyer, D., Blaum, N., Böhning-Gaese, K., Cullen, L., de Paula, R. C., Dekker, J., Drescher-Lehman, J., Farwig, N., Fichtel, C., Fischer, C., Ford, A. T., Goheen, J. R., Janssen, R., Jeltsch, F., Kauffman, M., Kappeler, P. M., Koch, F., LaPoint, S., Markham, A. C., Medici, E. P., Morato, R. G., Nathan, R., Oliveira-Santos, L. G. R., Olson, K. A., Patterson, B. D., Paviolo, A., Ramalho, E. E., Rösner, S., Schabo, D.

G., Selva, N., Sergiel, A., Xavier da Silva, M., Spiegel, O., Thompson, P., Ullmann, W., Zięba, F., Zwijacz-Kozica, T., Fagan, W. F., Mueller, T., & Calabrese, J. M. (2019). A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecol. Monogr.* **89**, e01344.

Parker, K. L., White, R. G., Gillingham, M. P., & Holleman, D. F. (1990). Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. *Can. J. Zool.* **68**, 106–114.

Relyea, R. A., Lawrence, R. K., & Demarais, S. (2000). Home range of desert mule deer: testing the body-size and habitat-productivity hypotheses. *J. Wildl. Manage.* 146–153.

Saïd, S., Gaillard, J.-M., Widmer, O., Débias, F., Bourgoin, G., Delorme, D., & Roux, C. (2009). What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos* **118**, 1299–1306.

Schmidt-Koenig, K., & Walcott, C. (1978). Tracks of pigeons homing with frosted lenses. *Anim. Behav.* **26**, 480–486.

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007, April). Developing the science of reintroduction biology. *Conserv. Biol.*

Serrouya, R., Kellner, A., Pavan, G., Lewis, D. W., DeMars, C. A., & McLellan, B. N. (2017). Time vs. distance: Alternate metrics of animal resource selection provide opposing inference. *Ecosphere* **8**, e01730.

Serrouya, R., McLellan, B. N., & Flaa, J. P. (2007). Scale-dependent microhabitat selection by threatened mountain caribou (Rangifer tarandus caribou) in cedar–hemlock forests during winter. *Can. J. For. Res.* **37**, 1082–1092.

Serrouya, R., McLellan, B. N., van Oort, H., Mowat, G., & Boutin, S. (2017). Experimental moose reduction lowers wolf density and stops decline of endangered caribou. *PeerJ* **5**, e3736.

Serrouya, R., Seip, D. R., Hervieux, D., McLellan, B. N., McNay, R. S., Steenweg, R., Heard, D. C., Hebblewhite, M., Gillingham, M., & Boutin, S. (2019). Saving endangered species using adaptive management. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 6181–6186.

Smith, K. G., & Pittaway, L. (2011). Little Smoky Woodland Caribou Calf Survival Enhancement Project. *Rangifer* 97–102.

Stotyn, S. A. (2008). Ecological interactions of mountain caribou, wolves and moose in the north Columbia Mountains, British Columbia. University of Alberta Edmonton, Alberta, Canada.

Strasser, H., & Weber, C. (1999). On the Asymptotic Theory of Permutation Statistics.

Struzik, E. (2020). Caribou captive breeding program may come too late to prevent extinction in national parks. *Conversat.*

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature* **546**, 73–81.

Tribe, A., & Booth, R. (2003). Assessing the role of zoos in wildlife conservation. *Hum. Dimens. Wildl.* **8**, 65–74.

Van Dierendonck, M. C., & Wallis De Vries, M. F. (1996). Ungulate reintroductions: Experiences with the takhi or Przewalski horse (Equus ferus przewalskii) in Mongolia. *Conserv. Biol.* Blackwell Publishing Inc.

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S., & Gaillard, J. M. (2009). Memory keeps you at home: A mechanistic model for home range emergence. *Oikos* **118**, 641–652.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor. *J. Stat. Softw.* **36**, 1–

48.

Wheeler, B., Torchiano, M., & Torchiano, M. M. (2016). Package 'lmPerm.' *R Packag. version* 1.

Williams, B. K., & Johnson, F. A. (1995). Adaptive management and the regulation of waterfowl harvests. *Wildl. Soc. Bull.* **23**, 430–436.

Wittmer, H. U., McLellan, B. N., Serrouya, R., & Apps, C. D. (2007). Changes in landscape composition influence the decline of a threatened woodland caribou population. *J. Anim. Ecol.* **76**, 568–579.

Witzenberger, K. A., & Hochkirch, A. (2011). Ex situ conservation genetics: a review of molecular studies on the genetic consequences of captive breeding programmes for endangered animal species. *Biodivers. Conserv.* **20**, 1843–1861.

Wright, C. A., Adams, I. T., Stent, P., & Ford, A. T. (2020). Comparing Survival and Movements of Non-Urban and Urban Translocated Mule Deer. *J. Wildl. Manage.* **84**, 1457–1472.

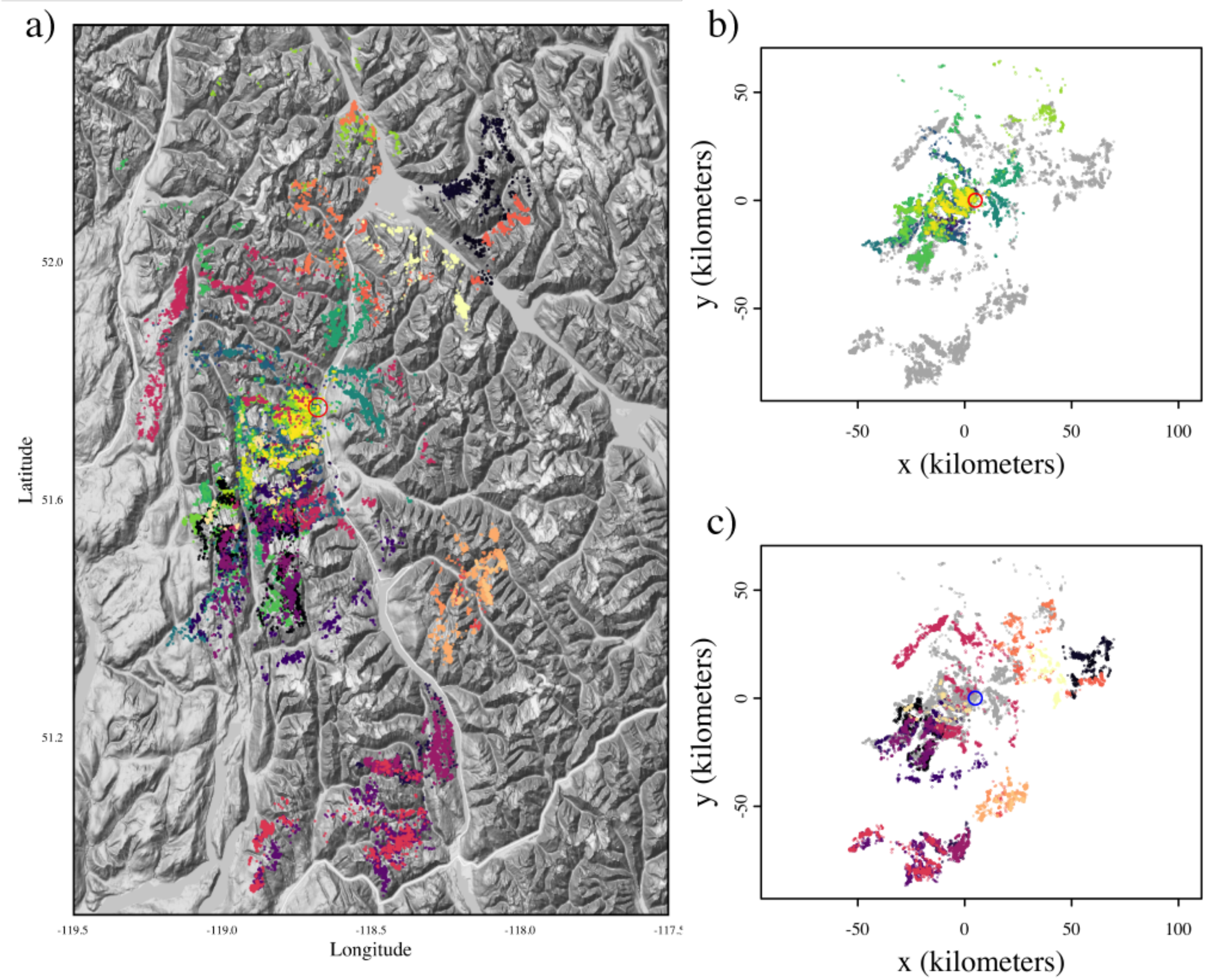


Figure 1. Distribution of penned and unpenned caribou near the Lake Revelstoke Valley of British Columbia, Canada. In a) all of the individual tracking data are overlayed on a satellite image. The location of the maternity pen is shown via the red circle at Long: -118.6784, Lat: 51.75512, and the colours correspond to different individuals. In b) each penned individual is shown in a unique colour, whereas the unpenned animals are grey. In c) unpenned individuals are shown in unique colours, whereas penned animals are grey. The red and blue circles in b) and c) show the location of the maternal pen.

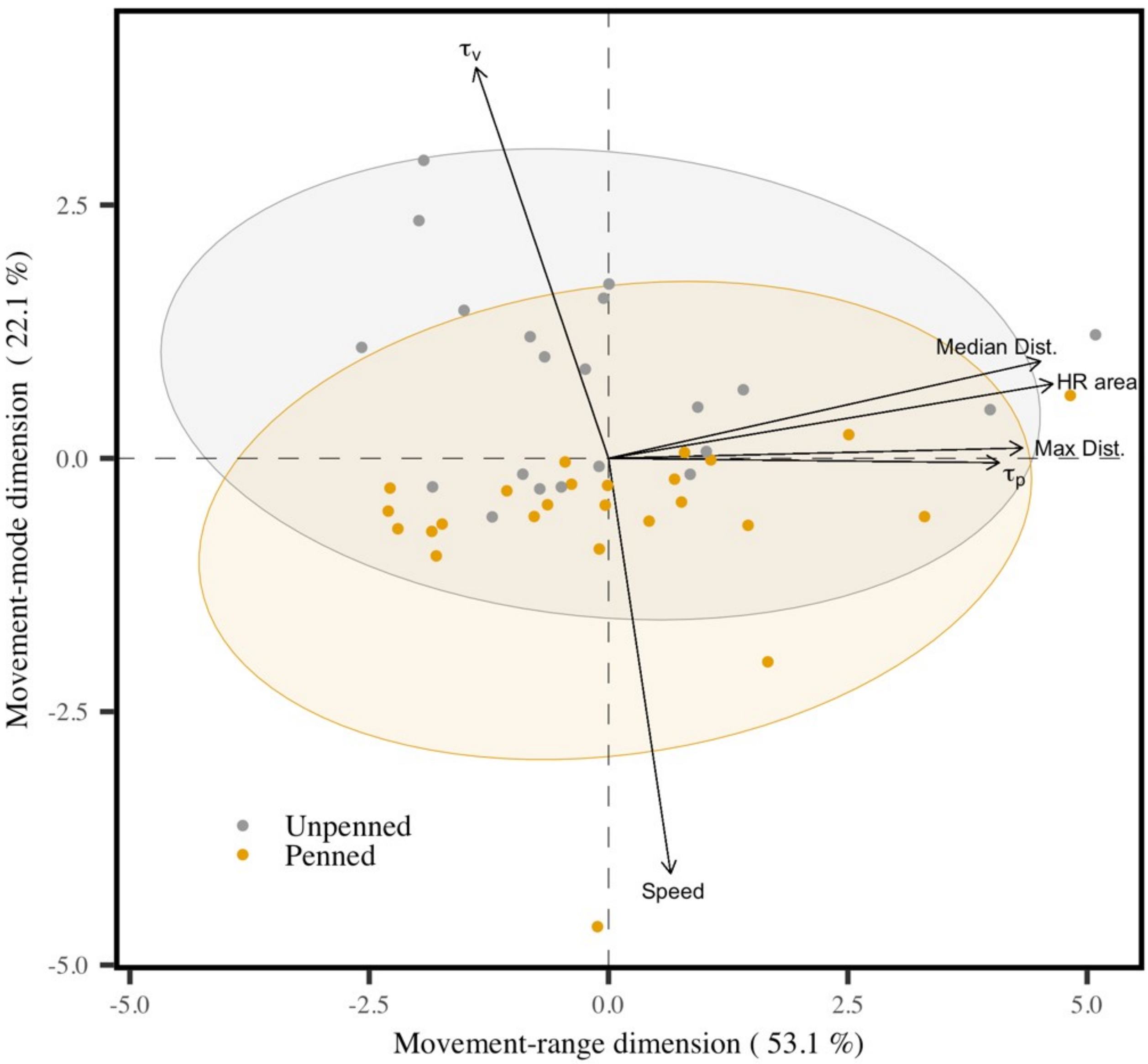


Figure 2 Scatter plot depicting the first two dimensions of a principal component analysis (PCA) across the movement metrics for penned and unpenned caribou. Ellipses depict the means and covariances of the first two dimensions of the PCA for each group. Note how most of the separation is along the movement-mode dimension.

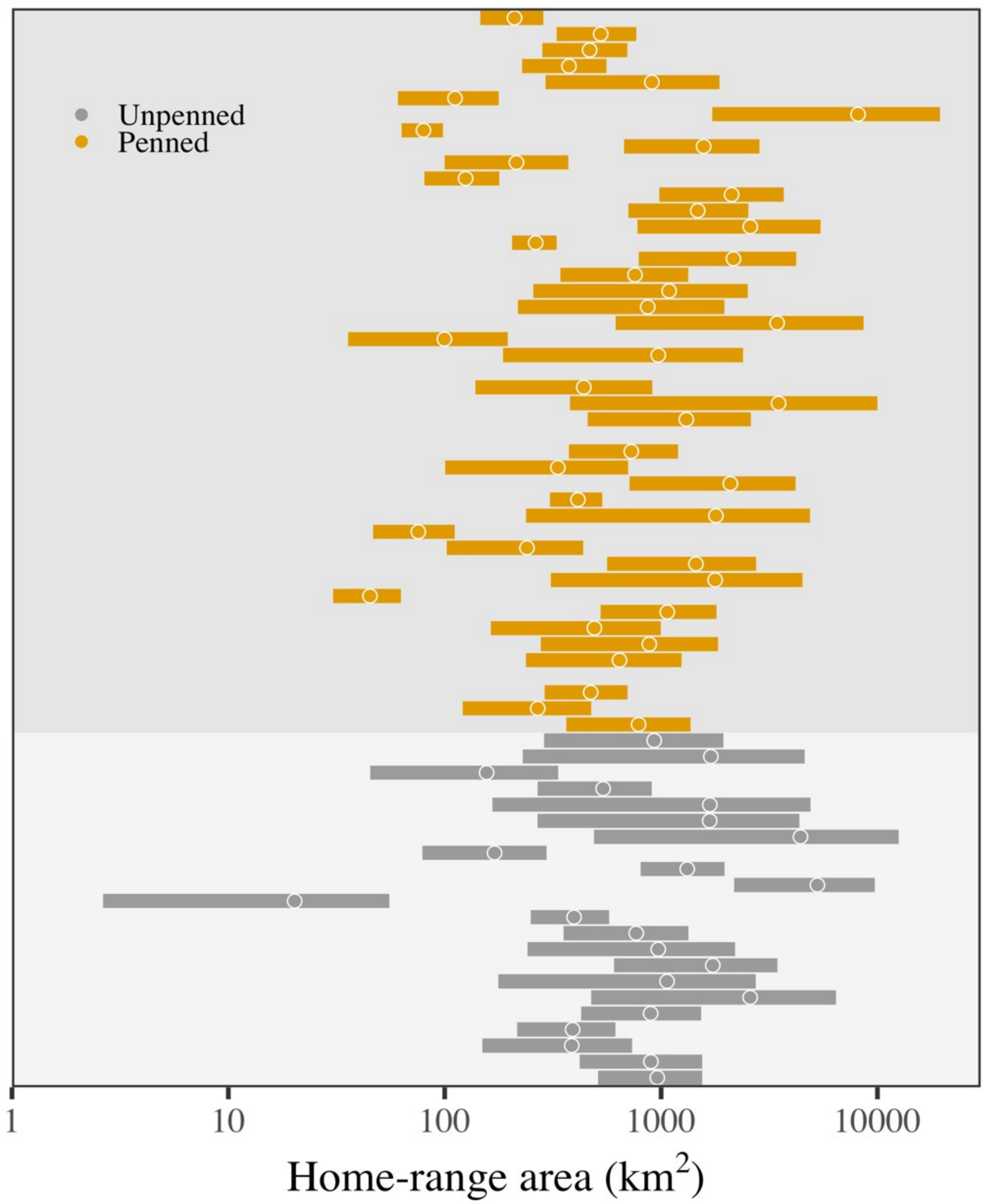
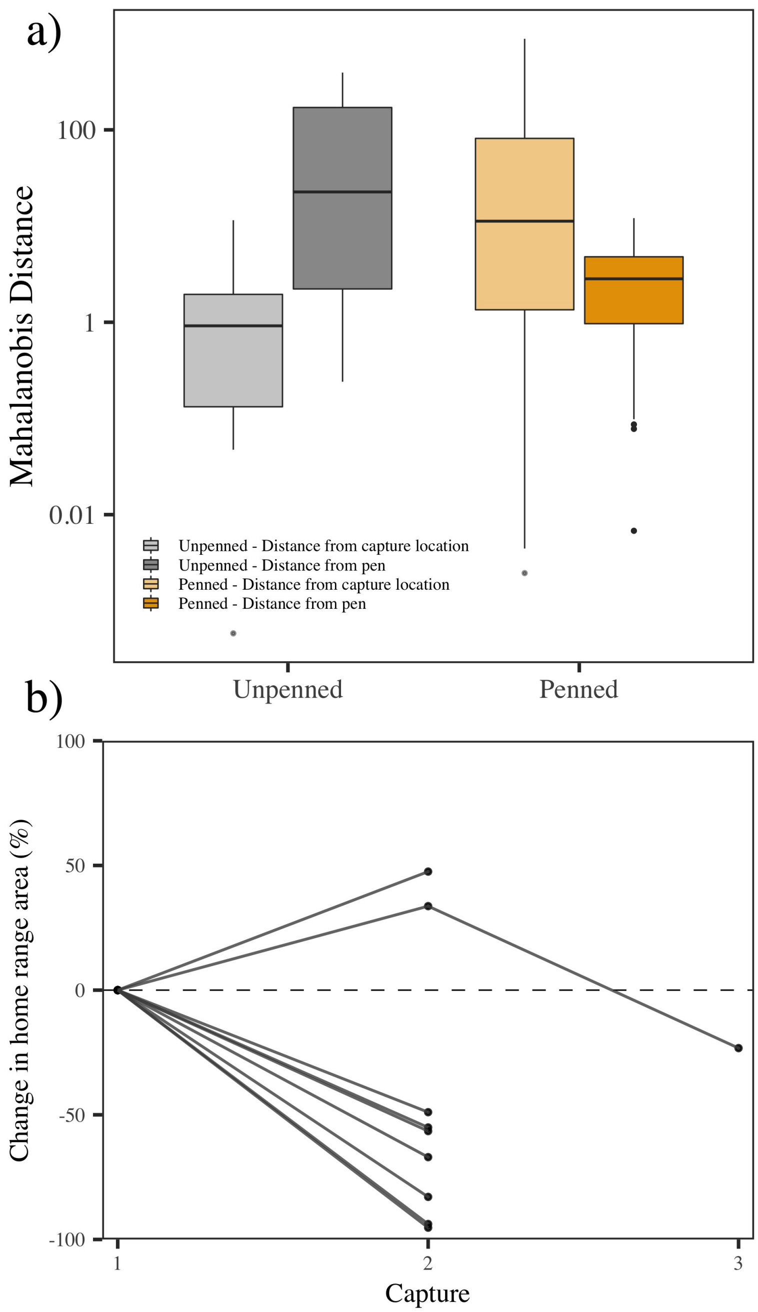


Figure 3.The individual home-range area estimates +/- 95% confidence intervals for penned and unpenned caribou. The circles depict the point estimates, and the bars the width of the 95% confidence intervals.



649

Figure 4 Panel a) shows the Mahalanobis Distances between each animal's home range and it's capture location or the maternal pen. In b) a scatterplot depicting the change in home range area over time for those caribou that were held in the maternal pen for multiple breeding seasons is shown.

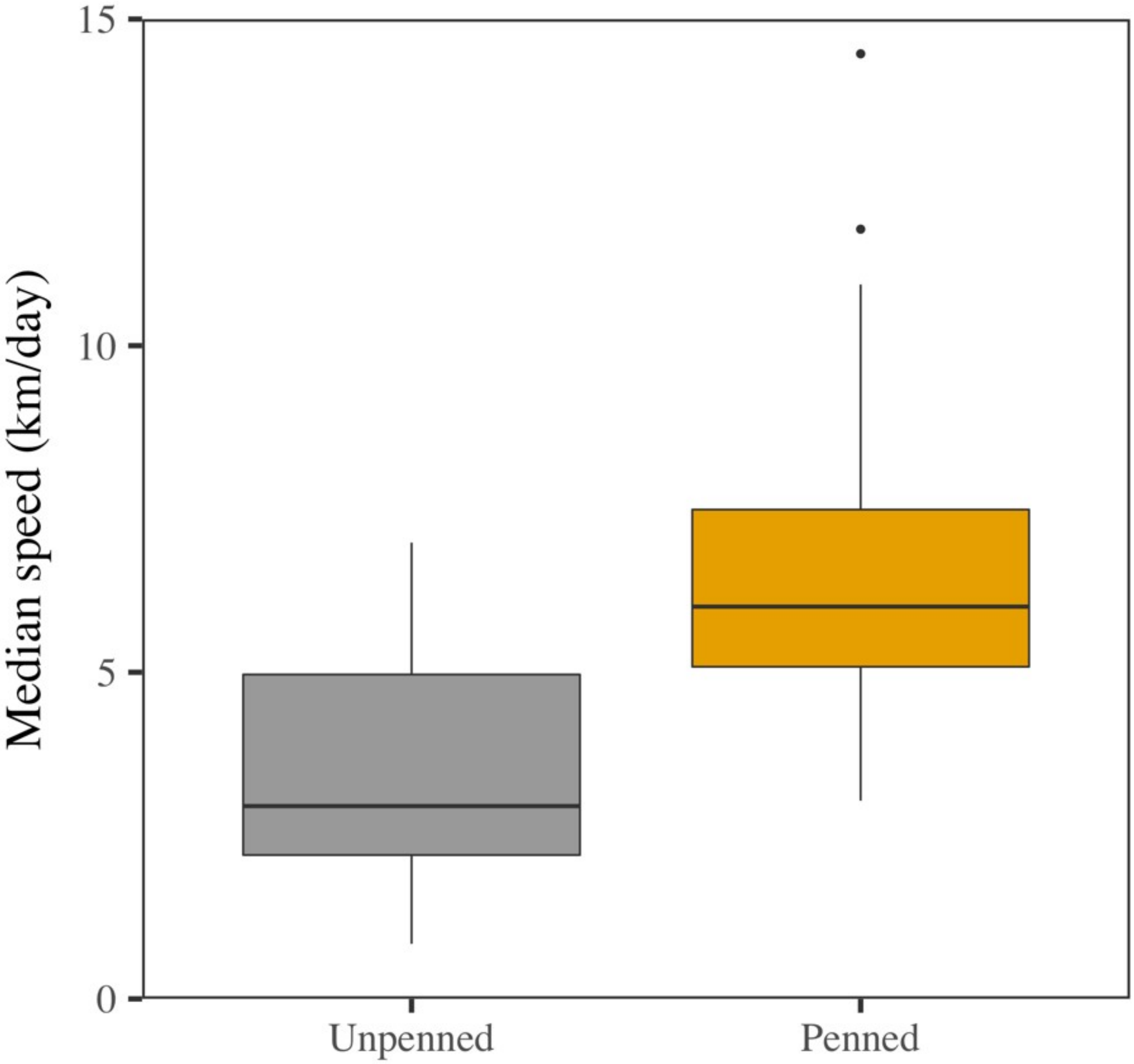


Figure 5 Boxplots depicting the movement speeds of penned and unpenned caribou.

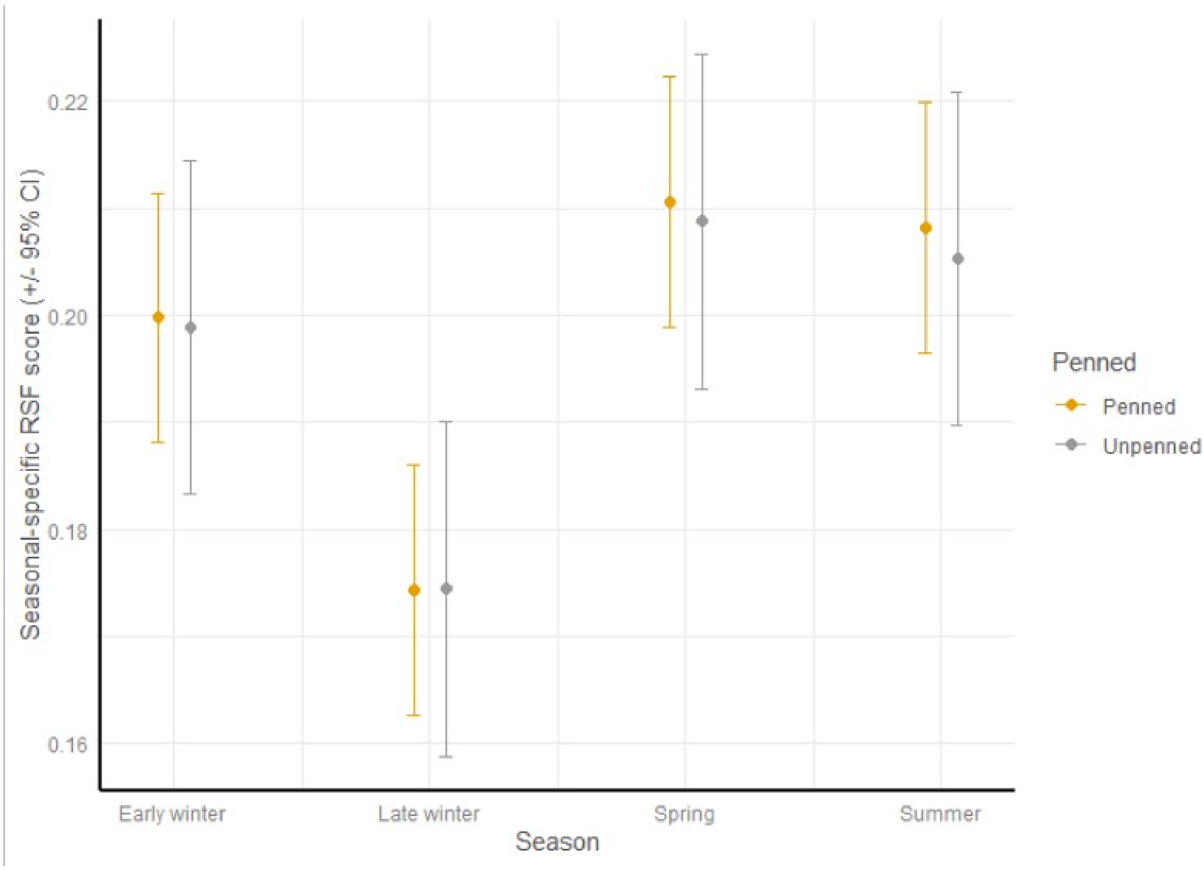


Figure 6. Predicted habitat quality (i.e., the seasonal-specific resource selection function (RSF) score) for penned and unpenned animals, after controlling for individual-level random effects. Habitat quality was similar at the home range scale across seasons, but late winter tended to have lower quality than other seasons (see Table 1).

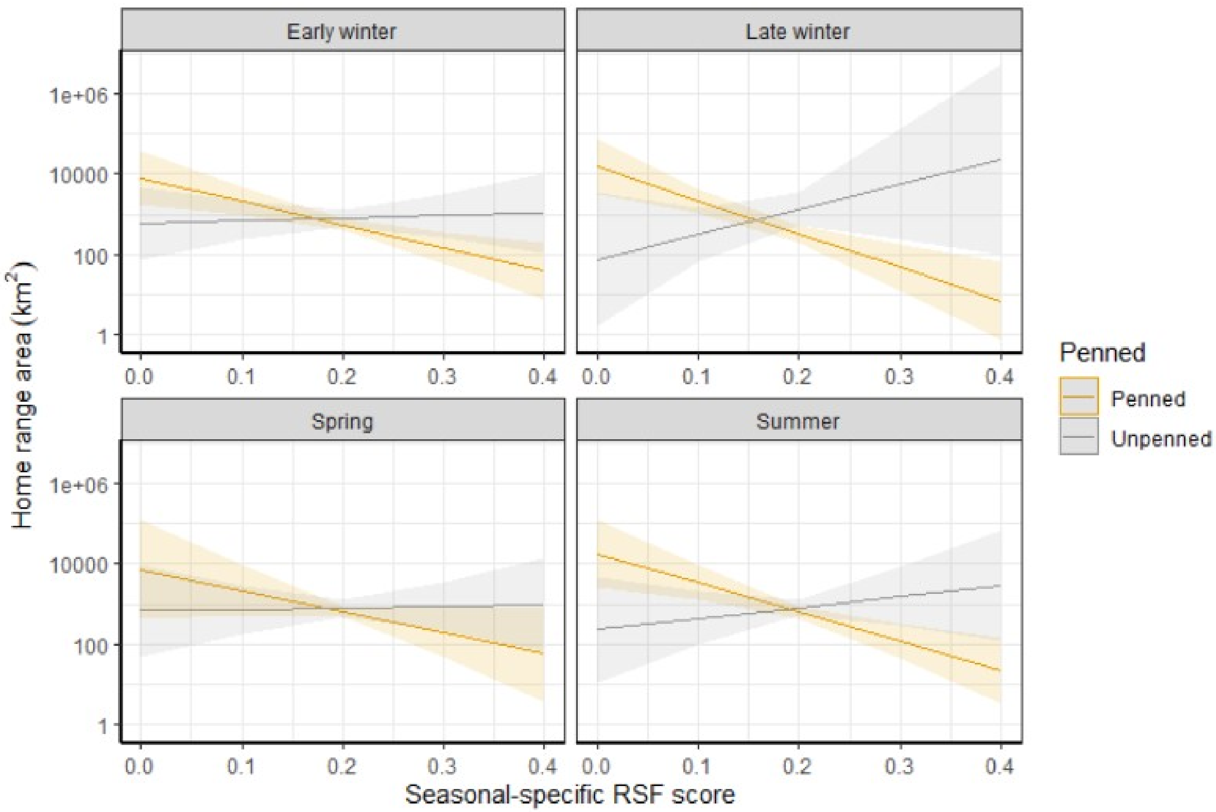


Figure 7. The predicted effect of average habitat quality (i.e., the home range average, seasonal-specific resource selection function (RSF) score) on home range size for penned and unpenned caribou. A single home range was used for each animal for all seasons (see Table 1). Shaded areas represent the 95th confidence intervals of the prediction

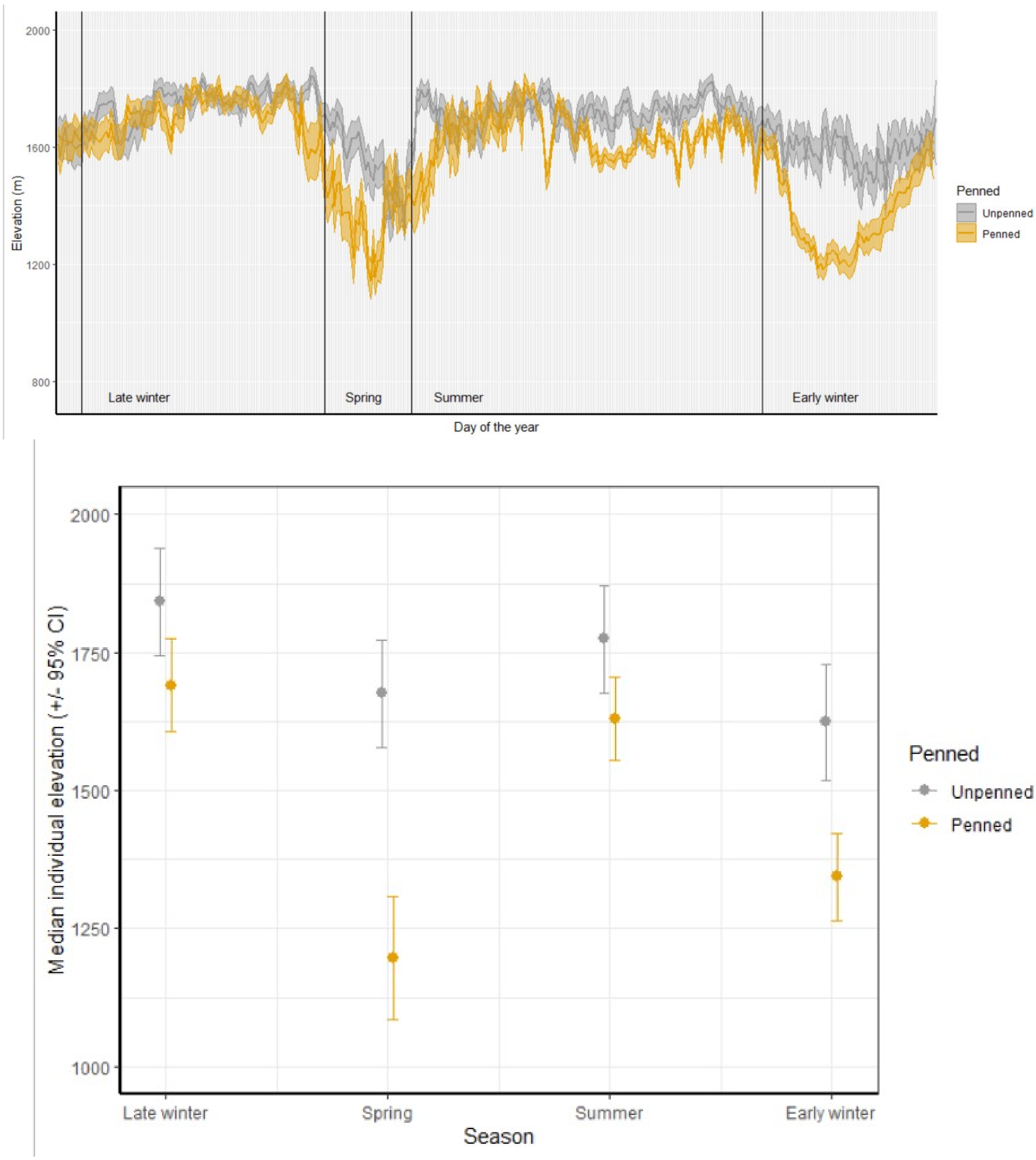


Figure 8. Seasonal use of elevation for penned and unpenned caribou, with (top) showing raw data pooled across individuals per day of the year and (bottom) predicted marginal effects of median seasonal elevation use (see Table 2).

Table 1. Summary of a linear mixed effect model predicting the effects of penning status and season on habitat quality at the home range scale (based on the Apps 2007 RSF).

	Predictors		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.20	0.19 – 0.21	**<0.001**
Penned [vs Unpenned]	-0.00	-0.02 – 0.02	0.920
Season [Late winter]	-0.03	-0.03 – -0.02	**<0.001**
Season [Spring]	0.01	0.00 – 0.02	**0.025**
Season [Early winter]	0.01	-0.00 – 0.02	0.080
Home range area	-0.08	-0.13 – -0.03	**0.003**
Penning x Late winter	0.00	-0.02 – 0.02	0.899
Penning x Spring	-0.00	-0.02 – 0.02	0.912
Penning x Summer	-0.00	-0.02 – 0.01	0.807
Random Effects			
σ^2	0.00		
$\tau_{00\ ID}$	0.00		
ICC	0.57		
N_{ID}	64		
Observations	256		
Marginal R^2 / Conditional R^2	0.211 / 0.664		

Table 2. Summary of a linear mixed effect model predicting the effects of penning status and season on elevation.

	Elevation		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1841.66	1743.85 – 1939.47	**<0.001**
Penned [Penned]	-150.82	-279.61 – -22.03	**0.022**
Spring vs Late winter	-166.05	-283.22 – -48.89	**0.005**
Summer vs Late winter	-67.27	-184.44 – 49.89	0.260
Early winter vs Late winter	-217.57	-339.76 – -95.37	**<0.001**
Penned x Spring	-328.22	-498.92 – -157.52	**<0.001**
Penned x Summer	5.91	-146.44 – 158.26	0.939
Penned x Early winter	-130.18	-286.99 – 26.64	0.104
Random Effects			
σ^2	37050.82		
$\tau_{00\ ID}$	15571.56		
ICC	0.30		
N_{ID}	58		
Observations	192		
Marginal R^2 / Conditional R^2	0.406 / 0.582		

Supplemental information.

Figure S1. Data operability for unpenned caribou in the study.

Figure S2. Data operability for penned caribou in the study.

Figure S3. Seasonal cutoff dates based on Apps 2007, with end dates as: 11 January (EW), 22 April (LW), 28 May (SP), and 21 Oct (SU), taken from Apps 2007

Figure S4. Distribution of RSF scores (Apps et al 2007) by season and penning status for all GPS relocations.

Figure S5. Home range size for caribou with and without a calf at the time of release.

Figure S6. Displacement distances over time from both the pen, and each animal's capture/release location.

Figure S7. Box plot showing the home range area of caribou release with and without a calf.

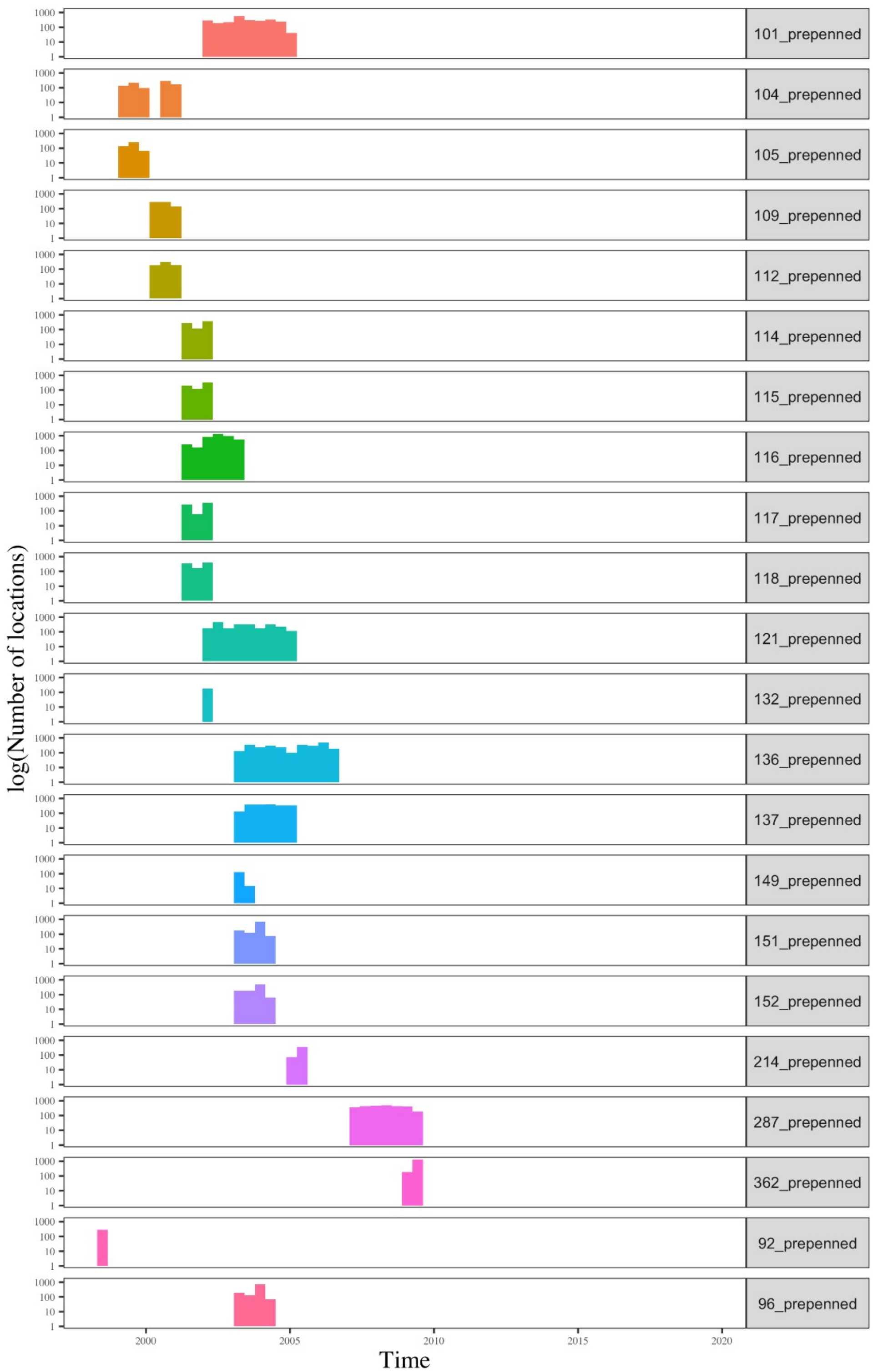


Figure S1. GPS collar operability for unpenned caribou.

Figure S2. GPS collar operability for penned and released caribou.

Figure S3. Seasonal cutoff dates based on Apps et al. (2001) with end dates as: 11 January (EW), 22 April (LW), 28 May (SP), and 21 Oct (SU).

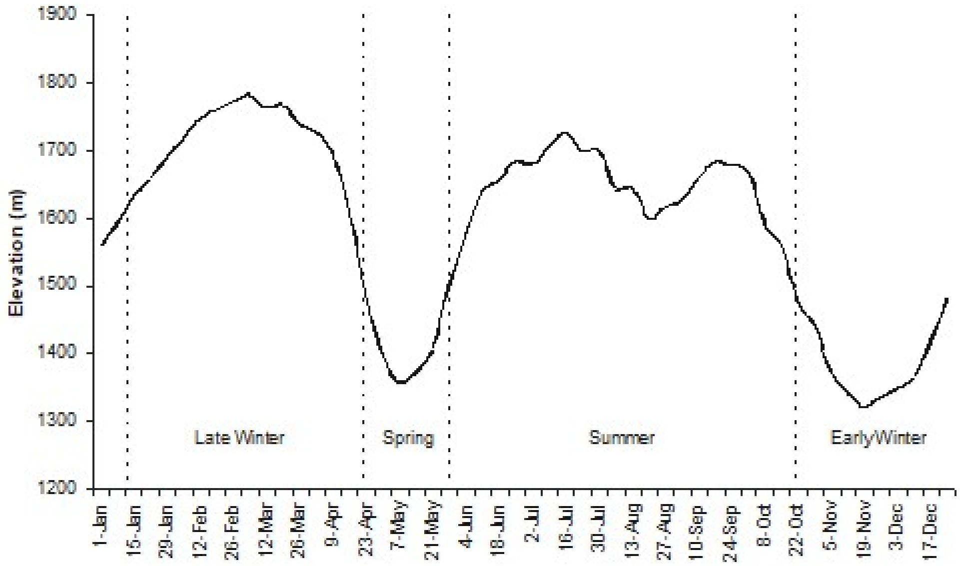


Figure 3. Running 3-week mean elevations used by radiocollared mountain caribou, 1992 – 2006, in the North Columbia Mountains ecoregion and environs, British Columbia. Vertical lines indicate multi-year seasonal cutpoints defined by Apps et al. (2001).

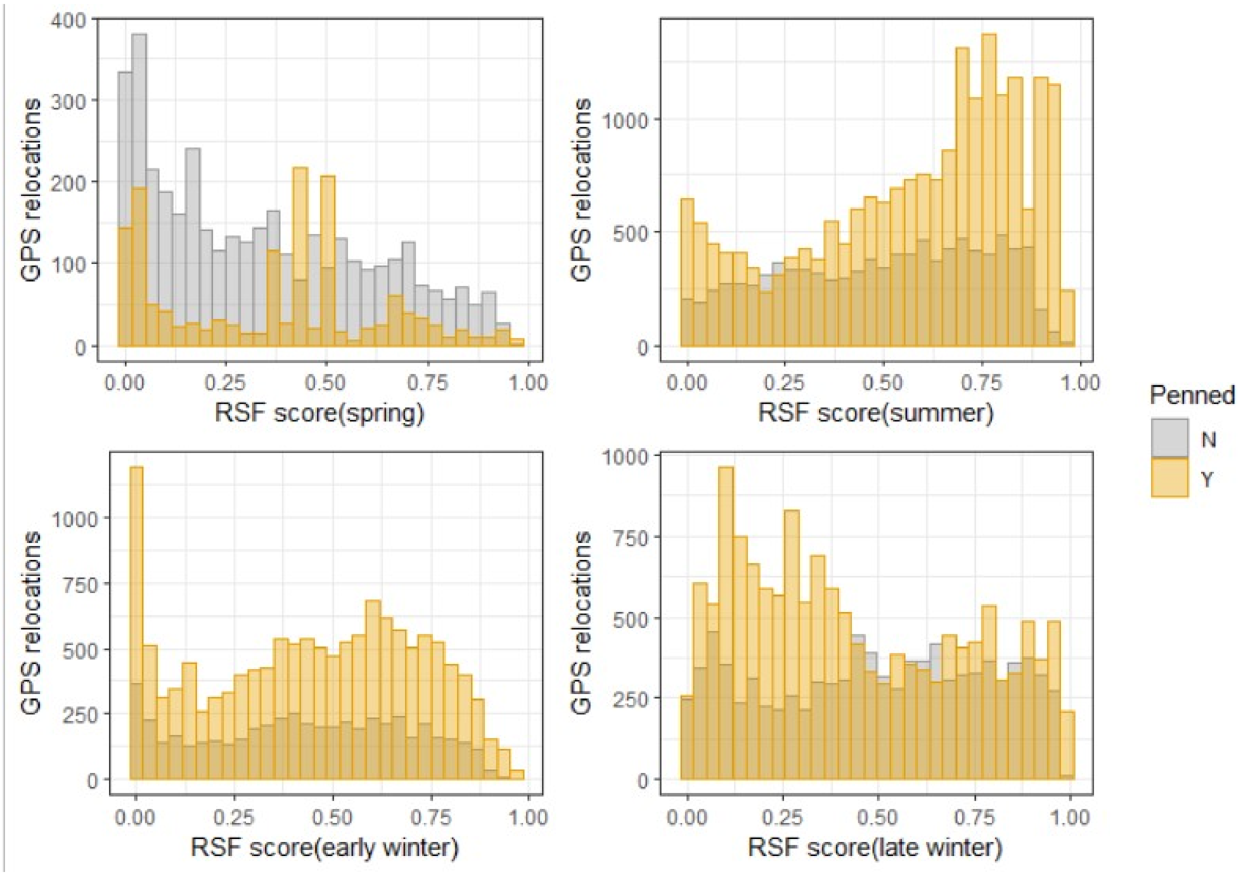


Figure S4. Distribution of RSF scores (Apps 2007) by season and penning status for all GPS relocations.

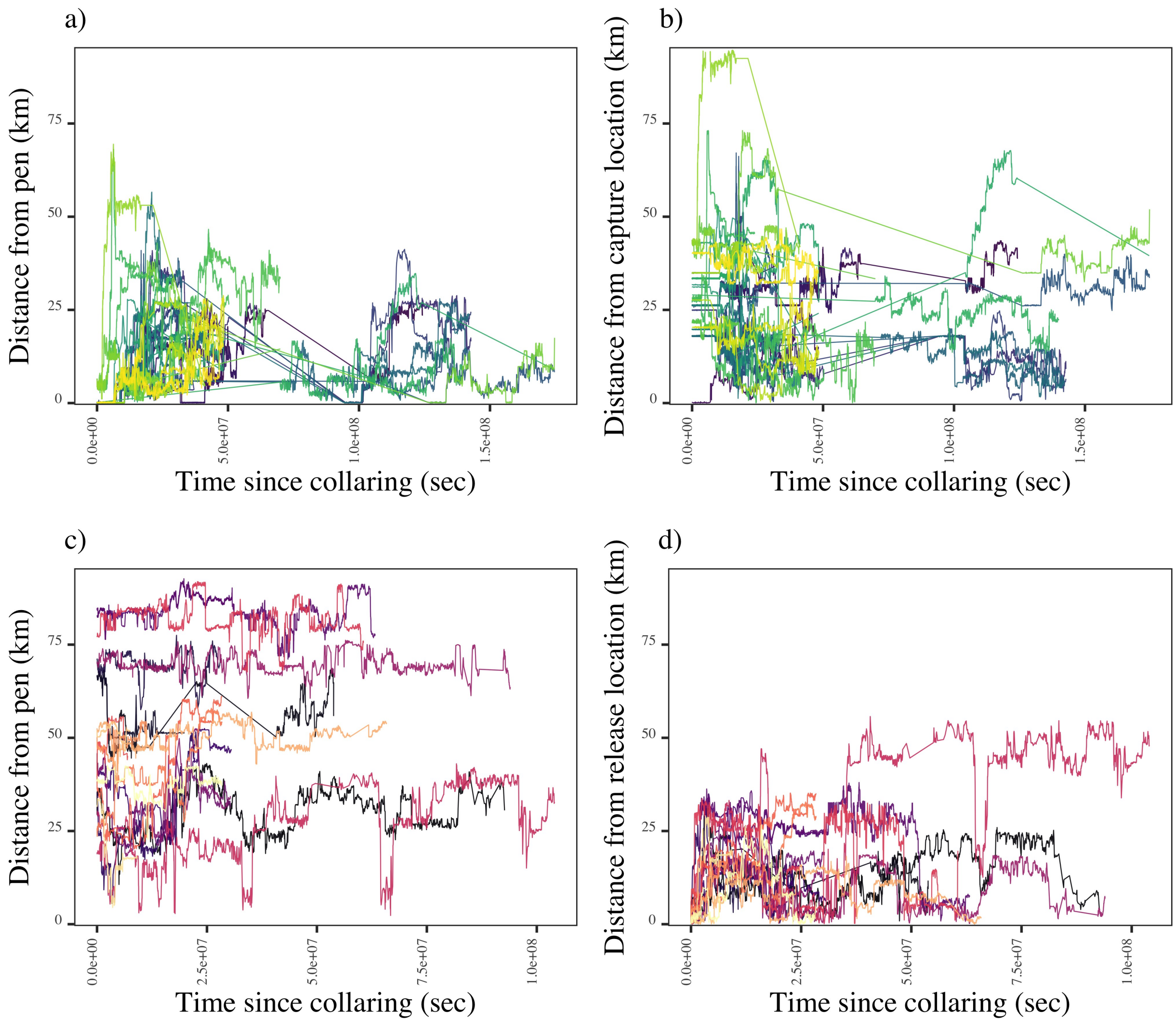


Figure S6. Figure depicting the displacement distances over time from both the pen, and each animal's capture/release location. The top row, panels a) and b), show displacement distances for penned animals, whereas the bottom row, panels c) and d), show displacement distances for unpenned animals. In all panels each colour corresponds to a unique animal.

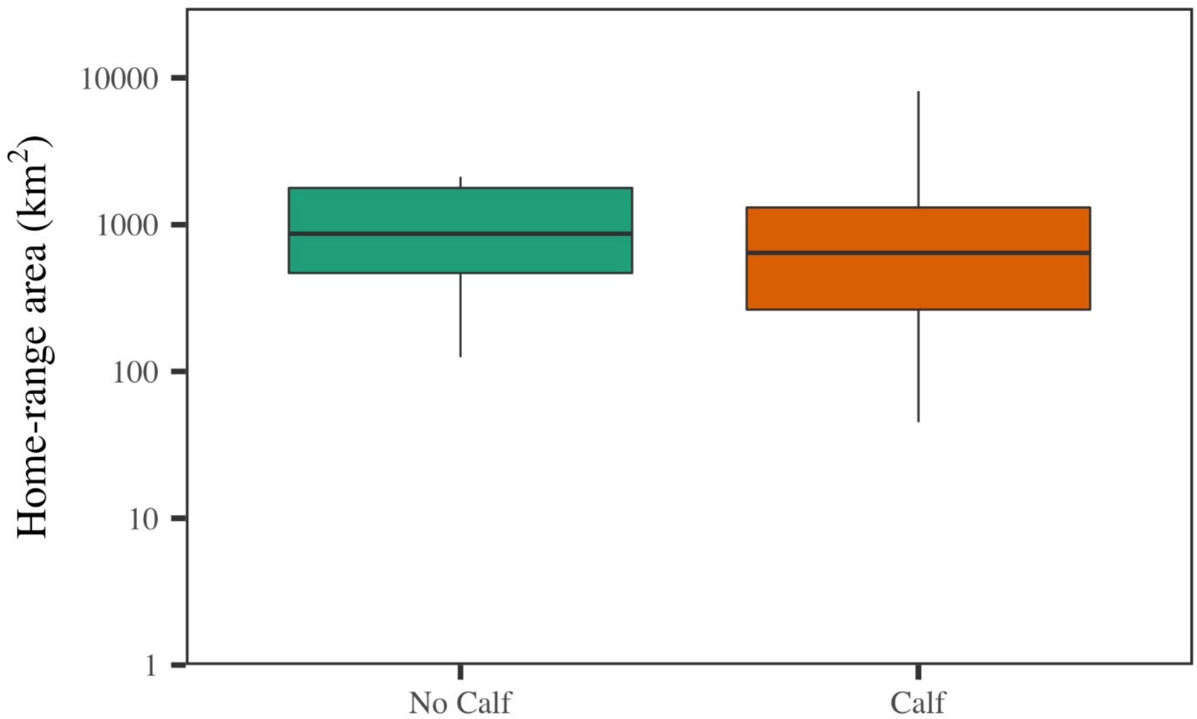


Figure S7. Box plot showing the home range area of caribou release with ($\bar{x}$ = 1140.0 km^2, n = 33) and without ($\bar{x}$ = 1081.2 km^2, n = 9) a calf. A permutation test revealed no relationship between caribou home range size and whether or not the animals had a calf at the time of release ($F_{[1,40]}$ = 0.526, p = 0.47).