

**Range Use, Habitat Selection, and the Influence of Natural
and Human Disturbance on Wood Bison (*Bison bison*
athabasca) in the Ronald Lake Area of Northeastern Alberta**



[Photo: S. Nielsen]

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EXECUTIVE SUMMARY

Many populations of threatened and endangered species exist in landscapes managed for multiple uses, creating conservation challenges. In Alberta, populations of wood bison (*Bison bison athabasca*), a species federally listed as *Threatened*, occur both within and outside of protected areas. Recently, the wood bison of the Ronald Lake area have become a management focus due to their unique genetic structure, potential disease-free status and importance to local First Nations and Métis groups, and their proximity to proposed oil sands development. Since 2010, increasing effort has been made to improve understanding of the herd's ecology to better inform regulatory and management decisions potentially affecting the herd's long-term viability, and in March 2016 this population received *Subject Animal* status under the Wildlife Act. In 2013, global positioning system (GPS) radio-collars were deployed on a sample of female bison ($n = 12$) to examine space use and habitat selection, information that is fundamental to effective wildlife management. Initial analyses of these data identified meadow marsh, graminoid fens, upland pine and aspen forests as important land cover types for females across all seasons. These analyses also identified distinct seasonal ranges, including a discrete calving area used by all collared females.

To further augment understanding of the spatial ecology of Ronald Lake bison, additional GPS collars were deployed on females ($n = 11$) and males ($n = 5$) in 2014. In this report, we compiled GPS collar data collected in 2013, 2014, and 2015 to assess potential inter-annual and gender-specific variation in space use and habitat selection. We further focused on evaluating how recent forest fires (≤ 10 years old) and anthropogenic disturbance affected bison spatial behaviour. To specifically inform landscape-level planning in the region, we used these analyses to generate predictive seasonal maps of bison habitat selection.

Over the two and a half year monitoring period, Ronald Lake bison demonstrated relatively high fidelity to seasonal ranges, particularly by females to the calving area identified in Tan *et al.* (2015). Within these ranges, however, males and females differed in their patterns of habitat selection. Females showed high selection for meadow marshes across all seasons while males were more variable and season-dependent in their selection of land cover types. These differences may be due to gender-specific differences in forage requirements and/or behavioural segregation of forage resources to minimize inter-gender competition.

Recent forest fires had variable influence on bison selection of land cover types with weak overall trends evident. In general, selection for burnt areas was strongest during the spring, areas with higher severity burns were weakly selected over lower severity burns, and selection of burnt areas was stronger by males than females. The dominant fire disturbance within the Ronald Lake range was the 2011 Richardson Fire; thus, most inferences on bison response to fire are in relation to this specific fire and bison responses immediately post-fire (≤ 2 years old) are unknown. Because bison responses are likely strongest in the first 1-2 years post-fire, the

weak and variable response of bison to burnt areas reported here may be due to variations in successional trajectories within the Richardson Fire.

Bison demonstrated more distinct responses to anthropogenic disturbances, which were primarily linear features such as roads, seismic lines and pipelines. In general, both genders selected for anthropogenic disturbance across all seasons except for females in winter. The positive response of bison to these features may indicate their use as travel corridors, or bison may be selecting these features as feeding patches if the created forest gaps contain potentially higher forage abundances than the surrounding forest. We further assessed how disturbance age and human activity on disturbance features affected bison response. Effects of disturbance age were more pronounced for males as they demonstrated a stronger selection for more recent disturbances (≥ 2006). Evaluating bison response to human activity was restricted to females during the winter of 2014. Human activity during the winter significantly impacted female responses to disturbance with the odds of a female selecting an active disturbance feature being 29 times lower than the odds of selecting an inactive disturbance feature. With human activity projected to increase within bison range, further analyses evaluating the potential zone of influence surrounding human activity may be warranted.

Understanding a species' spatial distribution and the potential mechanisms affecting spatial behaviour are integral to wildlife management and conservation. These results build upon existing knowledge of the spatial ecology of Ronald Lake wood bison to further inform management strategies for this herd. We are confident that these results provide a foundation for discussing further avenues of investigation to better understand the behaviour and demography of Ronald Lake bison.

ACKNOWLEDGEMENTS

We would like to thank Teck Resources Limited for funding this study as part of the Ronald Lake Wood Bison Technical Committee managed by the Alberta Environment and Parks (AEP). AEP provided GPS location data from Ronald Lake bison and information on land use in the region. Teck Resources and Royal Dutch Shell provided spatial and temporal information on disturbances. Discussions from Technical Committee members including representatives from industry, government, First Nations, Métis, and trappers were valuable in better understanding the issues and ecology surrounding the Ronald Lake wood bison herd. We are grateful to Ducks Unlimited Canada and affiliated partner organizations for granting permission to use the Enhanced Wetland Classification for our analyses.

TABLE OF CONTENTS

Executive Summary.....	i
Acknowledgements.....	iii
Introduction	1
Study Area.....	2
Methods.....	5
Bison Spatial Data	5
Defining Seasons.....	5
Evaluating Variation in Bison Movement Rates.....	6
Estimating Bison Annual and Seasonal Home Range Size and Cumulative Space Use.....	6
Evaluating Habitat Selection by Bison: General Framework	8
Land Cover Data	11
Natural Disturbance Data	11
Anthropogenic Disturbance Data	11
Resource Selection: Statistical Analyses	17
Results.....	18
Bison Movement Rates	18
Bison Annual and Seasonal Home Ranges and Cumulative Space Use	21
Seasonal Habitat Selection by Bison	25
Spring	25
Calving.....	28
Summer / Fall.....	30
Winter	33
RSF Model Validation.....	37
Discussion.....	38
Response to Land Cover.....	38
Response to Fire.....	39
Response to Anthropogenic Disturbance	40
Future Considerations.....	41
Literature Cited	43
Appendix 1: Summary Statistics of GPS Radio-collar Fix Rates.....	50
Appendix 2: Movement Behaviour of Female Wood Bison during May and June, 2013 - 2015.....	51
Appendix 3: Sensitivity of Home Range Estimator to Monitoring Time	58

Appendix 4: Random Point Sensitivity Analysis	59
Appendix 5: Seasonal Ranges of Ronald Lake Wood Bison	60
Appendix 6: Predictive Maps of Seasonal Habitat Selection by Male and Female Wood Bison	64

LIST OF FIGURES (EXCLUDES APPENDICES)

Figure 1: The geographical context of the study area, which encompasses the known distribution of radio-collared wood bison in the Ronald Lake herd from March 2013 to August 2015.	4
Figure 2: Comparison of a minimum convex polygon (A) and a utilization distribution (B) for characterizing home range size for an individual bison from the Ronald Lake herd. The 80% and 95% probability contours for the utilization distribution are shown.	8
Figure 3: Scale of resource selection analyzed for wood bison in the Ronald Lake herd of northeastern Alberta. Analyses were conducted at a third-order scale, which compares bison GPS locations (here, bison collar ID 35454) to random locations within an individual's annual home range. Home ranges were delineated using 95% utilization distributions, which were clipped to exclude areas within Wood Buffalo National Park (see main text).	10
Figure 4: The extent of the 2011 Richardson Fire in relation to space use by Ronald Lake wood bison. Space use was modelled using a 95% utilization distribution (UD) estimated with all available bison GPS locations from 2013-2015. The resulting UD was clipped at the border of Wood Buffalo National Park and along the Athabasca River.	15
Figure 5: The extent of anthropogenic disturbance in relation to space use by Ronald Lake wood bison. Space use was modelled using a 95% utilization distribution (UD) estimated with all available bison GPS locations from 2013-2015. The resulting UD was clipped at the border of Wood Buffalo National Park and along the Athabasca River.	16
Figure 6: Mean individual bison step length (in meters) from all data collected to August 21, 2015 for the Ronald Lake herd. Step length is the straight line distance between successive GPS locations, which are recorded every 90 minutes.	19
Figure 7: Mean step length (in meters) per month calculated from all data collected to August 21, 2015 from individual bison in the Ronald Lake herd. Step length is the straight line distance between successive GPS locations, which are recorded every 90 minutes.	20
Figure 8: Estimated annual (A) and cumulative (B) extent of the calving area used by Ronald Lake wood bison in northeast Alberta.	23
Figure 9: Cumulative space use by Ronald Lake wood bison in northeast Alberta from 2013 - 2015. GPS locations followed a crescent-shaped pattern along the east side of the Athabasca River (panel A). A minimum convex polygon (MCP) around these locations provides a more liberal estimate of space use than utilization distributions (UDs), which delineate areas of relatively high bison use (panel B).	24

LIST OF TABLES (EXCLUDES APPENDICES)

Table 1: Classification of land cover types used to model resource selection by wood bison in the Ronald Lake herd of northeastern Alberta. Land cover classification was based on Ducks Unlimited Canada's Enhanced Wetlands Classification data (DU 2012).....	13
Table 2: Metrics of individual bison home range size in the Ronald Lake herd of northeastern Alberta. Minimum convex polygons (MCPs) were estimated annually and across years (All Data MCP) per individual. Utilization distributions (UDs) were estimated using all accumulated data per individual with 80% and 95% probability contour boundaries calculated.	22
Table 3: Selection coefficients (β ; with standard errors [SE] and p-values) from the top resource selection functions estimated during spring for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. For fire interactions (second grouping), coefficients indicate relative selection compared to the coefficients of the given land cover. Anthropogenic disturbance coefficients (third grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.....	26
Table 4: Selection coefficients (β ; with standard errors [SE] and p-values) from the top resource selection functions estimated during calving for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. Anthropogenic disturbance coefficients (second grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.	29
Table 5: Selection coefficients (β ; with standard errors [SE] and p-values) from resource selection functions estimated during summer and fall for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. For fire interactions (second grouping), coefficients indicate relative selection compared to the coefficients of the given land cover. Anthropogenic disturbance coefficients (third grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.	31
Table 6: Selection coefficients (β ; with standard errors [SE] and p-values) from resource selection functions estimated during winter for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. For fire interactions (second grouping), coefficients indicate relative selection compared to the coefficients of the given land cover. Anthropogenic disturbance coefficients (third grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.....	34
Table 7: Selection coefficients (β ; with standard errors [SE] and p-values) from a resource selection function assessing the response of female wood bison of the Ronald Lake herd to human activity levels on anthropogenic disturbance features (e.g., roads, seismic lines and well sites during winter 2013. Coefficients for disturbance effects (in bold) are relative to undisturbed areas.	36

Table 8: Model validation of seasonal resource selection functions estimated for female and male wood bison of the Ronald Lake herd in northeastern Alberta. Listed seasonal values by gender are selection ratios, defined as the proportion of GPS locations falling within an ordinal RSF bin divided by the bin's proportional area. Values > 1 indicate selection while values < 1 indicate avoidance. Predictive performance was evaluated by measuring the strength of correlation (Spearman's correlation coefficient, r_s) between selection ratios and RSF bin rank. Note that validation procedures resulted in the total number of RSF bins varying by season..... 37

1 INTRODUCTION

2 Wood bison are federally listed as *Threatened* under *Schedule 1* of the *Species at Risk Act* due
3 to small population sizes, restricted spatial extent and threats from disease outbreaks
4 (COSEWIC 2013). In Alberta, wood bison were classified as *At Risk* in the 2010 *Wild Species*
5 *General Status Listing* (Government of Alberta 2012a) with populations occurring within and
6 adjacent to Wood Buffalo National Park and in the province's northwest corner where the Hay-
7 Zama population was reintroduced (Mitchell & Gates 2002). Of these populations, only the
8 Hay-Zama herd is listed as *Endangered* under the province's *Wildlife Act* (Government of
9 Alberta 2015). Provincial management of wood bison has focused primarily around controlling
10 disease outbreaks and transmission, a strategy that has resulted in bison receiving no legal
11 protection as wildlife outside of WBNP and the Bison Management Zone surrounding the
12 disease-free Hay-Zama herd (Mitchell & Gates 2002; Government of Alberta 2012b). This
13 strategy is, however, considered a short-term objective as the ultimate goal is to recover and
14 restore healthy bison populations within suitable ranges across the province's northern regions
15 (Government of Alberta 2012b).

16 Recently, the Ronald Lake herd of wood bison south of WBNP has become a conservation focus
17 due to its perceived disease-free status (Shury *et al.* 2015), potentially unique genetic structure
18 (COSEWIC 2013; Ball *et al.*, *in review*), cultural significance to First Nations and Métis, and its
19 location relative to proposed oil sands development (Government of Alberta 2013).
20 Accordingly, concerted effort has been made since 2010 to build upon existing knowledge to
21 better understand the herd's ecology and subsequently inform potential regulatory and
22 management decisions (Powell & Morgan 2010, Government of Alberta 2013, Tan *et al.* 2015).
23 In response to growing harvest pressures and a need for a better understanding of the herd,
24 the herd was granted *Subject Animal* status in March 2016 under the Wildlife Act (in press
25 2016).

26 Effective wildlife conservation and management fundamentally depends on identifying and
27 protecting a species' habitat (Kerr & Deguise 2004). This critical step is particularly relevant for
28 populations residing in multiple-use landscapes, such as the Ronald Lake herd, where spatially-
29 explicit predictions (i.e., maps) of a species' distribution and habitat requirements are necessary
30 to inform landscape-level planning that seeks to balance wildlife conservation with social and
31 economic interests (Nielsen *et al.* 2009; Schneider *et al.* 2011). Inherent to this process is
32 understanding the potential influence of anthropogenic disturbance on patterns of habitat
33 selection and space use as animals respond to new, and perhaps novel, environmental stimuli
34 (Sih 2013). Moreover, developed spatial predictions should reflect seasonal changes in an
35 animal's behaviour (Nielsen *et al.* 2010).

36 In 2013, radio-collars with global positioning systems (GPS) were deployed on a sample of
37 female wood bison in the Ronald Lake herd to ultimately develop spatial predictions of the

herd's seasonal space use and habitat selection. Tan *et al.* (2015) provided a preliminary analysis using data from the first year post-deployment. Key findings included the identification of a discrete calving area, relatively synchronous migratory behaviour to and from this area, and a high degree of overlap among individual home ranges, indicating potential core areas of use by bison both seasonally and annually. The analysis also provided an initial evaluation of bison response to natural and anthropogenic disturbance. Based on these results, Tan *et al.* (2015) suggested continued monitoring of the herd to assess multi-year and gender-specific variation in space use and habitat selection. Further, they recommended additional analyses of bison response to disturbance, in particular evaluating the effects of disturbance intensity (e.g., fire severity), disturbance age, and human activity levels on disturbance features. To that end, additional collars were deployed in 2014 on both male and female bison to better understand bison spatial ecology and augment predictions and inferences developed during the study's first year.

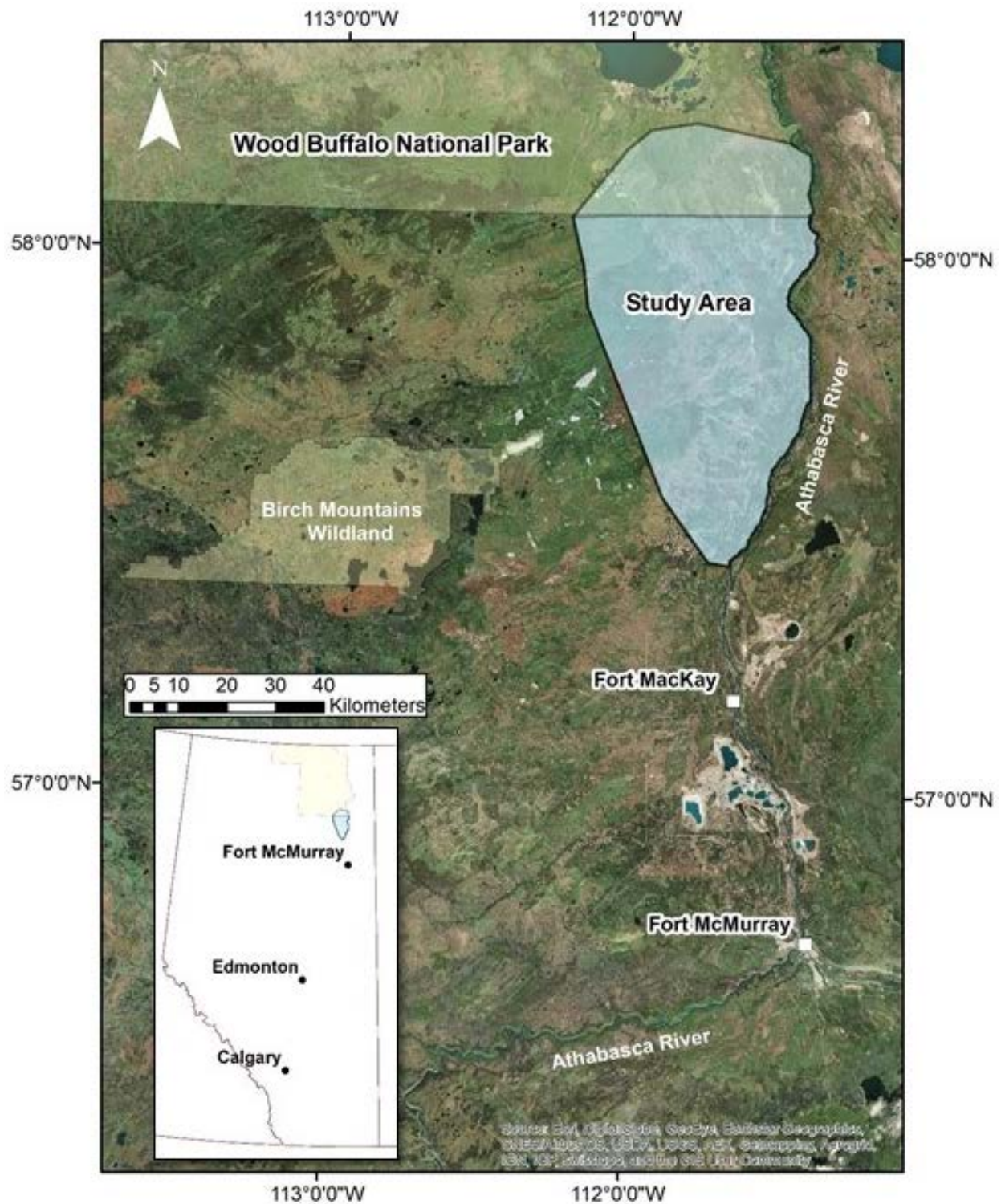
In this report, we update the results of Tan *et al.* (2015) using additional data collected in 2014 and 2015. Our primary objectives were to *i*) evaluate the spatial distribution and movements of male and female bison both seasonally and annually; *ii*) understand seasonal patterns of habitat selection of both genders; and *iii*) determine how the timing, type and intensity of disturbance affects seasonal- and gender-specific selection of habitat. We anticipate that outcomes from these current analyses will further enhance bison management strategies and directly inform landscape-level planning aimed at balancing bison conservation with First Nations, Métis, and stakeholder interests within the range of the Ronald Lake bison herd.

STUDY AREA

The study area is north of the community of Fort MacKay, Alberta and straddles the boundary of the southeastern portion of Wood Buffalo National Park (Fig. 1). We delineated boundaries of the study area to encompass the distribution of all bison GPS locations recorded from 2013-2015. These boundaries, however, should not be interpreted as barriers to bison movement. The area is bounded to the east by the Athabasca River and is east of Birch Mountains Wildland. The area is situated within the Boreal Plains ecoregion and, at a finer regional scale, is predominantly comprised of the Athabasca Plains subregion in the eastern half and the Central Mixedwoods subregion in the west (Natural Regions Committee 2006). Elevation ranges from 240 -300 m above sea level and the climate is northern continental characterized by short, relatively warm summers (mean July temperature: 16.6 °C) and long, cold winters (mean January temperature: -19.8 °C; Natural Regions Committee 2006). The landscape is a mosaic of upland forests, low-lying peatlands (i.e., fens and bogs), marshes and other riparian areas. In the eastern portion, upland conifer forests are dominated by jack pine (*Pinus banksiana*) while white spruce (*Picea glauca*) is the leading species in western stands. Low-lying peatlands are dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Common deciduous tree species include trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and, in more mesic areas, paper birch (*Betula papyrifera*). Forest fire is

1 the dominant form of natural disturbance with a mean interval of c.a. 40 years for jack pine and
2 aspen forests and c.a. 80 years for spruce forests (Larsen 1997). Anthropogenic disturbances
3 from petroleum development and forest harvesting are also present in the study area with the
4 greatest concentrations occurring in the southern portions (petroleum development) and along
5 the Athabasca River (forest harvesting).

6



1
2 Figure 1: The geographical context of the study area, which encompasses the known
3 distribution of radio-collared wood bison in the Ronald Lake herd from March 2013 to August
4 2015. Note that background imagery in all figures predates the study's timeframe.

METHODS

Bison Spatial Data

We used location data collected from 28 wood bison fitted with GPS radio-collars, a number representing c.a. 15% of the most recent minimum population count for the Ronald Lake herd (Government of Alberta 2013). The initial sample of collars was deployed in late March 2013 on 12 females. In March 2014, 16 additional collars were deployed on both male ($n = 5$) and female bison ($n = 11$) to better understand individual and gender-specific variation in space use patterns within the herd. All collars were programmed to acquire one GPS location (or fix) every 90 minutes, which equated to an expected collar lifespan of two years. For this report, we include data collected up to August 21, 2015.

Prior to analyses, we used the following procedures to screen raw GPS location data for potential errors. First, we removed the initial two weeks of GPS locations post-capture to reduce the effects of captured-related behavioural alterations (Morellet *et al.* 2009). Second, we removed all locations with low positional accuracy, defined here as two-dimensional GPS locations (or fixes) with positional dilution of precision values > 5 (Lewis *et al.* 2007). Third, we used the methods of Bjørneraas *et al.* (2010) to exclude outlying locations that were beyond the range of possible bison movement within the 90 min fix acquisition interval. Finally, we specified a regular sampling interval across all bison by removing GPS locations that fell outside of the normal sampling interval (every 90 minutes), a procedure necessitated by a few collars having periods of aberrant fix acquisition (e.g., recording fixes every minute for a 30 minute period).

These data screening procedures eliminated two bison from further analyses. One female (collar ID 33922) died approximately three days after collar deployment. This collar was subsequently redeployed on another animal. To distinguish between these animals, the animal with the redeployed collar was assigned an ID of 33924. For the second excluded animal, the collar stopped transmitting less than two weeks after deployment.

The final screened data set comprised 26 individual bison. The mean per collar fix rate was 92% (range: 54 – 100%; Appendix 1) and mean fix rates between males ($\bar{x} = 0.96$) and females ($\bar{x} = 0.92$) did not differ ($p = 0.19$ from a two-sided t -test). The mean data collection interval per collar was 507 days (min: 38, max: 868). Seven bison had data sets that spanned greater than two full years. Two individuals, both males, had monitoring periods of < 3 months, presumably due to collar failures.

Defining Seasons

To evaluate seasonal changes in space use and habitat selection by bison, we first established biologically relevant seasons following a similar approach as outlined in the Preliminary Summary Report (Tan *et al.* 2015). We identified the calving season by assessing movement

behaviour of female bison during May and June (Appendix 2). As previously reported (Tan *et al.* 2015), female bison appear to congregate in a defined calving area in the northwest portion of the study area. We estimated the extent of this area (see *Estimating Bison Annual and Seasonal Home Range Size* below) then defined the start of the calving season as the date that the last collared female “settled” in this area (2013: 5 June; 2014: 8 June; 2015: 29 May) and the end of calving when the last collared female left this area (2013: 28 June; 2014: 25 June; 2015: 23 June). The summer / fall season extended from after calving to the first day of continuous snow on the ground as determined by data from Environment Canada’s meteorological office in Fort McMurray. Because these data were missing for 2013, we used November 1 (2014: 6 November; 2015: NA as existing bison GPS data do not extend past August 2015). Winter encompassed the period with contiguous snow cover (1 November 2013 – 18 April 2014; 7 November 2014 – 7 April 2015). Spring extended from the last day with contiguous snow cover to calving (2013: 25 April – 4 June; 2014: 19 April – 7 June; 2015: 8 April – 28 May).

Evaluating Variation in Bison Movement Rates

We calculated summary statistics of movement rates to assess for seasonal and gender-specific differences in bison movement behaviour. To do so, we used the ‘ltraj’ function from the statistical package ‘adehabitatLT’ (Calenge 2006) within the statistical computing environment R (version 3.1.2; R Core Team 2014). This function creates a regular time-series of movement data for each individual animal by inserting a record for every 90 minute sampling interval, assigning a missed value (i.e., NA) to records removed by our screening procedures or due to missed GPS fixes by the radio-collars. From these individual time-series, we calculated average movement rates per month and across all available data. Movement rates are described in terms of step length, which is the Euclidean distance between successive GPS locations (i.e., the distance moved in 90 minutes), and in all calculations we used only step lengths with starting and ending GPS locations (i.e., steps initiated or ending at a missing value were excluded). For movement rates calculated using all available data, we used a two-sided *t*-test to assess whether movement rates differed between male ($n = 5$) and female bison ($n = 21$).

Estimating Bison Annual and Seasonal Home Range Size and Cumulative Space Use

We estimated the size of bison home ranges using two metrics, the 100% minimum convex polygon (MCP) and the utilization distribution (UD). MCP is defined as the smallest polygon encompassing all recorded GPS locations (Hayne 1949). We developed seasonal, annual and cumulative MCPs for each individual bison. For annual MCPs, we used one year of data starting from the first GPS location (Year 1 MCP), which due to our data screening procedures resulted in the sampling year starting in mid-April. For animals having multi-year data sets, we calculated a second annual MCP using data from the second contiguous year (Year 2 MCP). Cumulative MCPs used all data collected for each animal. For the subset of animals having two

1 annual MCPs, we calculated the percent overlap of the Year 2 MCP with the Year 1 MCP. We
2 further estimated population-level seasonal MCPs by year using all GPS locations falling within
3 the seasonal periods defined above. To specifically identify the calving area used annually by
4 female bison, we used data starting when the last female had completed her migration and all
5 females were therefore highly aggregated in the northwest portion of the study area. We
6 pooled these locations across years to create a cumulative MCP of bison space use during
7 calving.

8 While conceptually straightforward, a main drawback to MCPs is that they can encompass large
9 areas that are devoid of animal locations, which may be problematic when evaluating
10 distributional changes and for defining resource availability in habitat selection analyses
11 (Worton 1987; Burgman & Fox 2003; Barg *et al.* 2005; Beyer *et al.* 2010). This problem is
12 illustrated by many Ronald Lake bison, which have a crescent-shaped distribution of GPS
13 locations (Fig. 2). We therefore estimated UD as an alternative metric of home range size.
14 UDs typically use non-parametric procedures such as kernel functions to estimate a probability
15 density function (PDF) that describes an animal's relative use of space (Worton 1989). We
16 estimated UDs using the 'adehabitatHR' package (Calenge 2006) in R, specifying the "reference
17 bandwidth" as the smoothing parameter or grain over which an animal's space use is measured
18 (Worton 1989). We used the 80% and 95% probability contours to define UD boundaries with
19 the former providing a better estimate of potential core areas for non-territorial ungulate
20 species such as bison (Börger *et al.* 2006). UD estimates of home range size were calculated
21 using all available data for each individual bison.

22 To quantify cumulative space use by Ronald Lake bison, we also constructed a population-level
23 100% MCP and 80% and 95% UDs using all available data across all years.

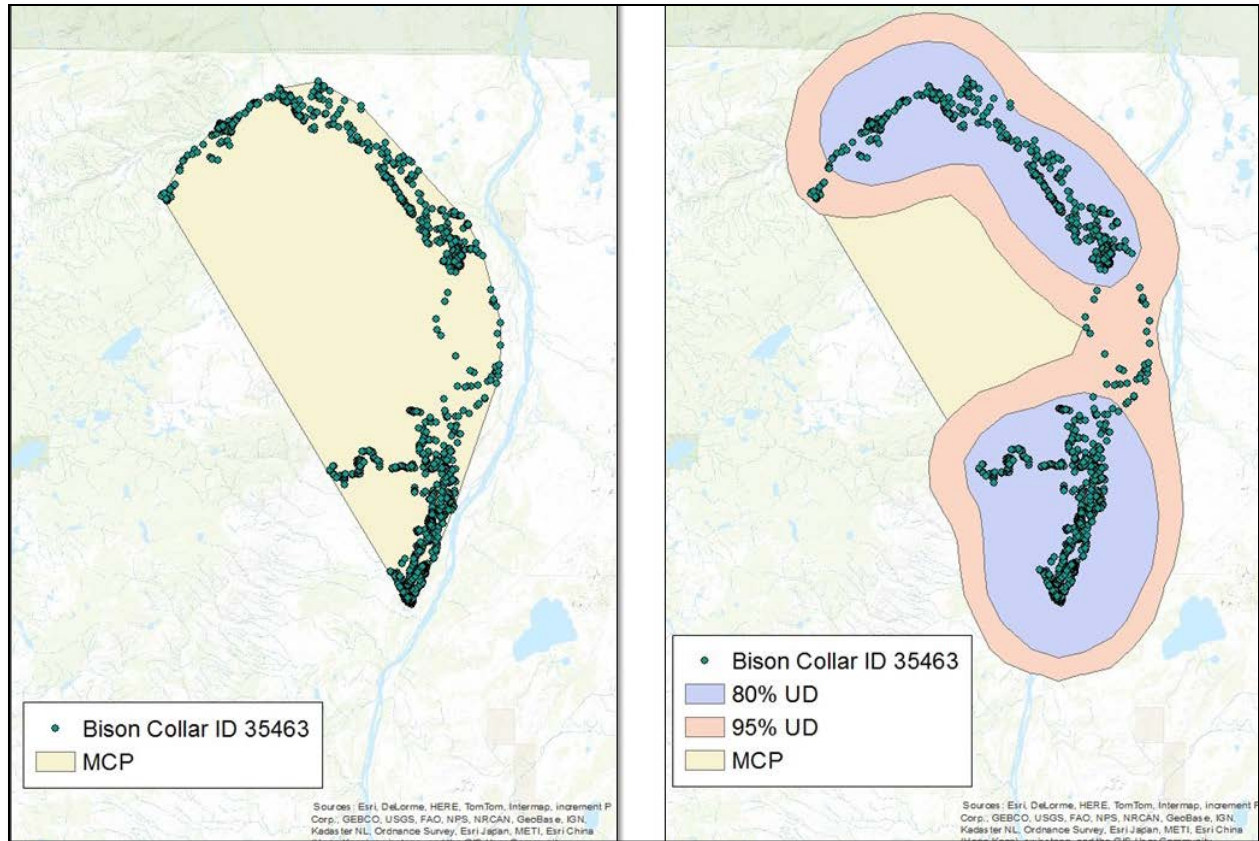


Figure 2: Comparison of a minimum convex polygon (A) and a utilization distribution (B) for characterizing home range size for an individual bison (animal collar ID 35463) from the Ronald Lake herd. The 80% and 95% probability contours for the utilization distribution are shown.

Evaluating Habitat Selection by Bison: General Framework

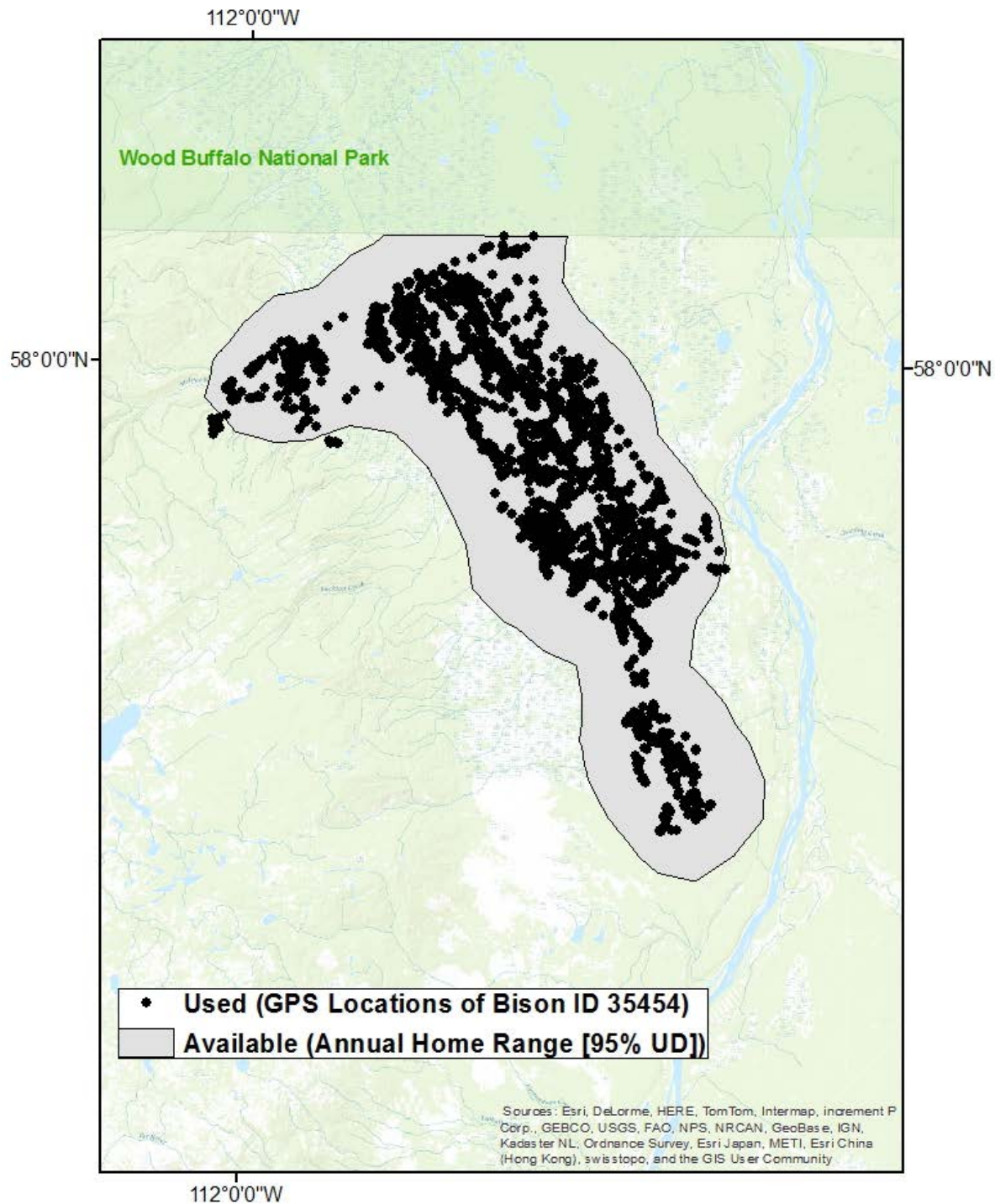
We evaluated seasonal selection of habitat by bison using a framework similar to the one outlined in the project's Preliminary Summary Report (Tan *et al.* 2015). Briefly, we evaluated habitat selection by estimating resource selection functions (RSFs), a modelling approach that compares environmental attributes (or resources) associated with "used" locations (e.g., GPS locations) to environmental attributes of unused or available locations generated within the spatial scale of interest (Manly *et al.* 2002). Here, we compared bison GPS locations to available locations randomly sampled within individual annual home ranges (i.e., 3rd order selection; Fig. 3; Johnson 1980). Environmental attributes used to discriminate between bison GPS and available locations consisted of data representing land cover type, natural disturbance (recent forest fires) and anthropogenic disturbance.

For RSF analyses, we characterized annual home ranges of bison using 95% UD. Because land cover data used to assess resource selection does not extend into Wood Buffalo National Park (WBNP), we clipped UDs to the park boundary and excluded all GPS locations within WBNP

1 from further analyses (Fig. 3). We further clipped the eastern extent of UD_s to the Athabasca
2 River as no bison GPS locations are located east of the river, indicating that the river may form a
3 geographic barrier to movement. We calculated individual annual UD_s starting from the first
4 GPS location (c.a. mid-April) and animals with data spanning multiple years had multiple UD_s.
5 GPS (or used) locations within a given sampling year were compared to random points sampled
6 within the annual UD calculated over that same time frame. This sample-year framework
7 resulted in many animals having fragments of data consisting of < 1 year of monitoring.
8 Because estimates of home range size are sensitive to monitoring time (Börger *et al.* 2006), we
9 conducted a sensitivity analysis to determine the amount of time (in months) required for
10 estimates of annual home range size to stabilize. To identify this asymptote, we used piece-
11 wise (or break point) linear regression on a subset of animals ($n = 16$) having a full year of data.
12 This type of analysis evaluates for a break in the linear relationship between monitoring time
13 and home range size and we specified a model where the slope is equal to zero after the break
14 point (i.e., an asymptote). We pooled data across animals and sampling years. Model output
15 suggested that home range size reached an asymptote after 3.5 months of monitoring (break
16 point = 3.5, SE = 0.2, $p < 0.001$, Appendix 3). Therefore, for a given sampling year, we excluded
17 from further analyses those animals with < 3.5 months of data (2014: $n = 3$; 2015: $n = 5$).

18 Within each UD, we generated random points to sample resources available to individual bison.
19 Because insufficient sampling of availability can lead to biased estimates of resource selection
20 (Northrup *et al.* 2013; Benson 2013), we conducted a sensitivity analysis to determine the
21 number of random points needed to adequately characterize availability within annual UD_s
22 (Appendix 4). Using data from the summer / fall season (see below), we performed repeated
23 RSF analyses, plotting parameter estimates of land cover covariates against the number of
24 random points used (range: 200 – 20,000 per UD). Based on this analysis, parameter estimates
25 stabilized at 5000 random points per UD and we used this number in all subsequent analyses.

26



1

2 Figure 3: Scale of resource selection analyzed for wood bison in the Ronald Lake herd of

3 northeastern Alberta. Analyses were conducted at a third-order scale, which compares bison

4 GPS locations (here, bison collar ID 35454) to random locations within an individual's annual

5 home range. Home ranges were delineated using 95% utilization distributions, which were

6 'clipped' to exclude areas within Wood Buffalo National Park (see main text).

1 *Land Cover Data*

2 We used Enhanced Wetlands Classification (EWC) data from Ducks Unlimited Canada to
3 characterize land cover (30-m pixel resolution from 2010 satellite imagery; DUC 2011). These
4 data constitute 29 land cover classes, which for our analyses were reduced to 22 as we
5 combined classes with small extents (e.g., Mudflats [$<0.02\%$]) with other biologically similar
6 classes and one class – Agriculture – did not occur in any bison UD (Table 1). Note that Alberta
7 Vegetation Inventory data, which covers $< 50\%$ of our study area (Tan *et al.* 2015), was
8 unavailable for this analysis and that EWC data at the time of this analysis did not include Wood
9 Buffalo National Park.

10 *Natural Disturbance Data*

11 The dominant form of natural disturbance in northern boreal forests is fire (Larsen 1997). To
12 assess bison response to fire, we obtained data representing historic wildlife fire perimeters up
13 to 2014 (Government of Alberta 2014). Within the study area, fire data extended back to 1946;
14 however, for our analyses we only considered fires occurring within the last 10 years because
15 as grazers, bison response to fire should be strongest in early successional stages post-fire (i.e.,
16 when grass and forb abundance is relatively high). Moreover, prior to 2006, there is a gap of
17 c.a. 25 years without fire and areas burnt >30 years ago will likely have recovered to mature
18 forest (Johnstone *et al.* 2010). Within the past 10 years, the largest fire in the study area was
19 the 2011 Richardson Fire, which burned c.a. 59% of the area encompassed by the population-
20 level 95% UD constructed using all available bison GPS data (Fig. 4). Polygons from two other
21 smaller fires (2006 and 2008) were also present in the study area but collectively represented $<$
22 25 ha.

23 Fire severity can affect the successional trajectory and composition of the plant community
24 post-fire (Johnstone *et al.* 2010) and consequently may influence bison selection of burnt areas.
25 We therefore modelled fire in terms of severity using the attribute data associated with each
26 fire polygon (1 – 5 scale in ascending severity). Because some severity categories had low
27 representation in the study area (e.g., $< 7\%$ for category 4), we collapsed the original severity
28 index into a three category variable: 0 = unburned; 1 = low severity burn (original fire severity
29 categories 1-3); 2 = high severity burn (original fire severity categories 4-5). We used this
30 variable to evaluate how fire modified bison selection of various land cover types. To assess
31 this interaction with adequate sample sizes, we considered only those burnt land cover classes
32 that contained GPS locations from > 5 individual bison per season or an availability (or spatial
33 extent) of $\geq 1\%$ cover. Burnt land covers not meeting these criteria were excluded because low
34 availability would confound any inferences on bison behavioural avoidance of these areas.
35 Further, we excluded analysis of fire responses during the calving season as the Richardson Fire
36 did not extend into the calving area in the northwest part of the bison range.

37 *Anthropogenic Disturbance Data*

38 We modelled bison response to anthropogenic disturbance using data representing linear
39 features (e.g., roads, pipelines and seismic lines) and industrial sites (e.g., well sites, camps, and

log decks). Recent disturbance data (≥ 2006) were provided by Royal Dutch Shell PLC, Teck Resources Limited, and SilverWillow Energy Corporation while older linear feature data (≤ 2005) were provided by the Government of Alberta. We combined all data sources to create a parsimonious disturbance layer while retaining attributes describing relative disturbance age (≤ 2005 versus ≥ 2006). Note that the DU land cover data also included an “Anthropogenic” class, but this class did not include linear disturbances, nor disturbances since 2010. Consequently, we focused on the cumulative data provided by our industry partners to infer bison response to anthropogenic disturbance. We attempted to also evaluate bison responses to cutblocks, the other dominant form of anthropogenic disturbance in the study area, but the data available or obtained were ambiguous as to whether a potential cutblock had been harvested and, if so, harvest date. Further, older cutblock polygons overlaid on the DU data did not match up with the DU class “Cutblock”. We therefore advise caution when inferring bison response to cutblocks from our analysis and suggest that adequately assessing this response will require higher quality data.

Anthropogenic disturbances were distributed throughout the study area although the highest densities were restricted to the southern half of the study area (Fig. 5). To evaluate bison responses to anthropogenic disturbances, we compared the proportion of bison GPS locations falling within the disturbance footprint to the proportion of available locations within the disturbance footprint. To account for potential GPS measurement error, we buffered all disturbances by 20 m (McKenzie *et al.* 2009); thus, locations falling within this buffered distance were considered to be within the footprint. We assessed season-specific bison responses to disturbance with and without the effects of disturbance age. We also assessed whether the level of human activity on a disturbance feature affected bison responses. This analysis was conducted using 2013-14 winter data when activity levels (binary variable: active / non-active) were known on post-2005 disturbance features within Teck’s oil sands lease area.

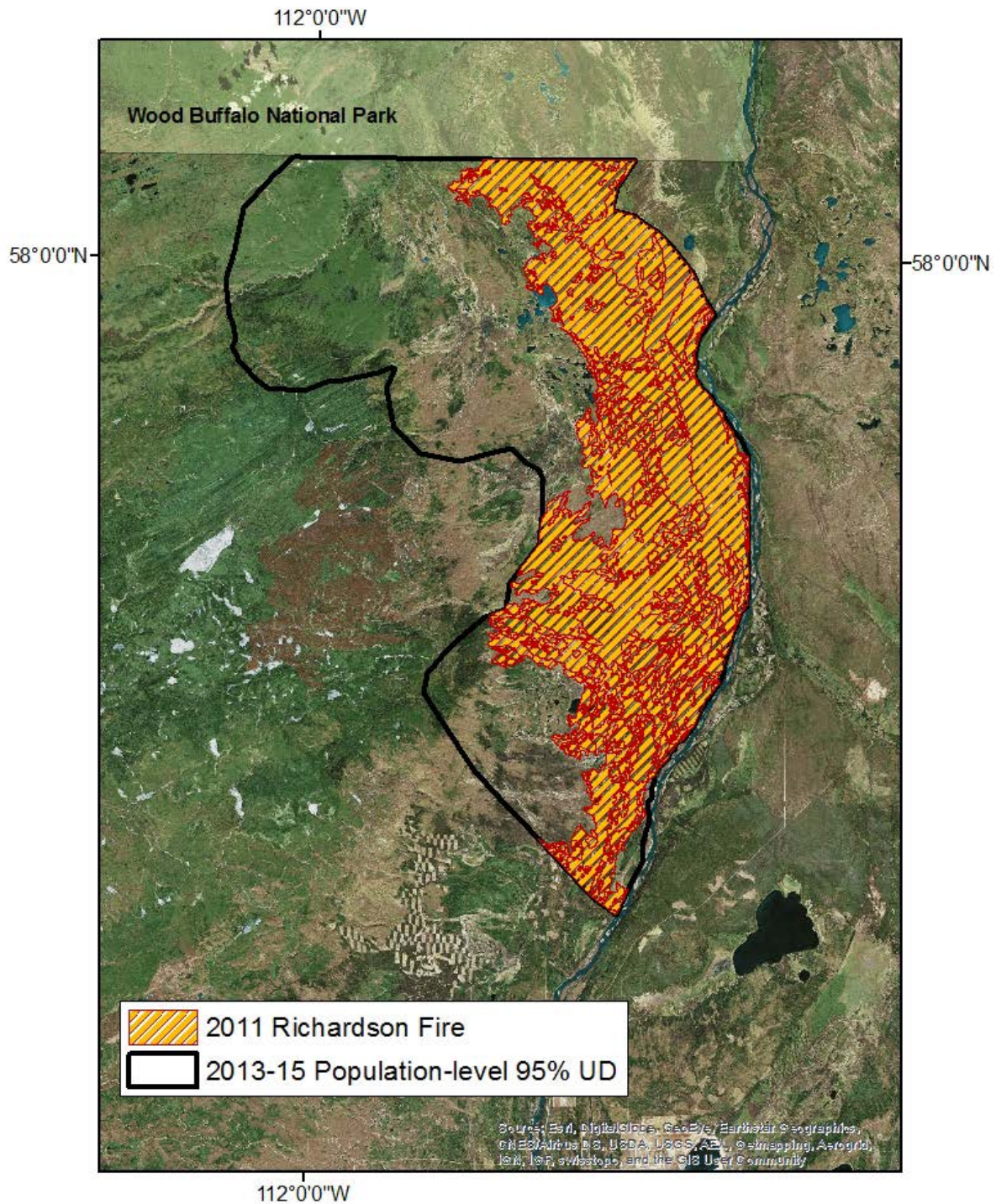
1 Table 1: Classification of land cover types used to model resource selection by wood bison in
2 the Ronald Lake herd of northeastern Alberta. Land cover classification was based on Ducks
3 Unlimited Canada's Enhanced Wetlands Classification data (DU 2012).

Land cover	EWC Class	Description
Open Water	Open Water	Includes lakes, ponds, rivers and other water bodies. Aquatic and above surface vegetation each < 25%. Areal coverage: ~1%
Aquatic Bed	Aquatic Bed, Mudflats	Transitional between open water and emergent marsh. Aquatic vegetation > 25% (except Mudflats <25%). Above surface vegetation <25%. Areal coverage: <1%
Emergent Marsh	Emergent Marsh	Aquatic vegetation <25%. Above surface vegetation >25%. Saturated to permanently flooded. Common plant species: <i>Typha</i> spp., <i>Scirpus</i> spp, and <i>Juncus</i> spp. Areal coverage: <1%
Meadow Marsh	Meadow Marsh	Above surface vegetation >25%. Saturated to mesic-dry. Seasonally flooded. Common plant species: broadleaf sedges, bluejoint grass. Areal coverage: ~ 1%
Graminoid Rich Fen	Graminoid Rich Fen	Rich fen indicators: buckbean and wire sedge. Sphagnum <20%. Tree / shrub cover < 25%. Areal coverage: ~ 1%
Graminoid Poor Fen	Graminoid Poor Fen	Some fen indicators but Sphagnum > 20%. Tree cover < 25%. Areal coverage: ~ 1%
Shrubby Rich Fen	Shrubby Rich Fen	Fen indicators. Shrubs < 2m and shrub cover >25%. Tree cover <25%. Areal coverage: ~2%
Shrubby Poor Fen	Shrubby Poor Fen	Sphagnum > 20%. Shrubs < 2m and shrub cover >25%. Tree cover <25%. Areal coverage: ~ 1%
Treed Rich Fen	Treed Rich Fen	Fen indicators. Tree cover >25% but <60%. Sphagnum <20%. Areal coverage:~ 7%
Treed Poor Fen	Treed Poor Fen	Tree cover >25% but <60%. Dominant tree species: tamarack and black spruce. Sphagnum >20%. Areal coverage: ~ 7%
Shrubby Bog	Shrubby Bog, Open Bog	Open and shrubby bogs. Tree cover <25%/ Sphagnum >20%. Areal coverage: < 1%
Treed bog	Treed Bog	Black spruce and Spagnum moss dominated bogs with no hydrodynamic flow. Tree cover >20% but <60%. Areal coverage: ~1%
Shrub Swamp	Shrub Swamp	Mineral soils. Saturated to seasonally flooded. Tree cover <25%. Common shrubs: speckled alder and tall willow. Areal coverage: ~ 5%
Hardwood Swamp	Hardwood Swamp	Mineral soils. Saturated to seasonally flooded. Tree cover >25%. Dominant tree species: paper birch and balsam poplar. Areal

Land cover	EWC Class	Description
		coverage: ~ 2%
Mixedwood Swamp	Mixedwood Swamp	Mineral soils. Saturated to seasonally flooded. Tree cover >25%. Mix of tree species: tamarack, paper birch and black spruce. Areal coverage: ~ 2%
Tamarack Swamp	Tamarack Swamp	Mineral soils. Saturated to seasonally flooded. Tree cover >25%. Tamarack >75% of tree species. Areal coverage: ~ 1%
Conifer Swamp	Conifer Swamp	Transitional between peatlands and upland. Black spruce dominant with tree heights > 10m. Areal coverage: ~ 5%
Upland Conifer	Upland Conifer	Tree cover >25% and ≥ 80% are conifer. Common tree species: white spruce, black spruce, balsam fir, jack pine. Areal coverage: ~ 14%
Upland Deciduous	Upland deciduous	Mineral soils with tree cover >25% and >25% deciduous trees. Dominant tree species: aspen, balsam poplar, and paper birch. Areal coverage: ~40%
Upland Mixedwood	Upland Mixedwood, Upland Other	Mineral soils with tree cover >25% and >25% deciduous trees. Mix of conifer and deciduous trees with no dominant species. Areal coverage: ~ 4%
Cutblock	Cutblock	Cutblocks of varying seral stage. Classified as cutblock if boundary was still distinct at classification. Areal coverage: < 1%
Anthropogenic	Anthropogenic, Cloud, Cloud Shadow	Areas of >50% urban development. Includes original EWC categories Cloud and Cloud Shadow. Areal coverage: < 1%

1

2



1

2 Figure 4: The extent of the 2011 Richardson Fire in relation to space use by Ronald Lake wood
 3 bison. Space use was modelled using a 95% utilization distribution (UD) estimated with all
 4 available bison GPS locations from 2013-2015. The resulting UD was clipped at the border of
 5 Wood Buffalo National Park and along the Athabasca River.

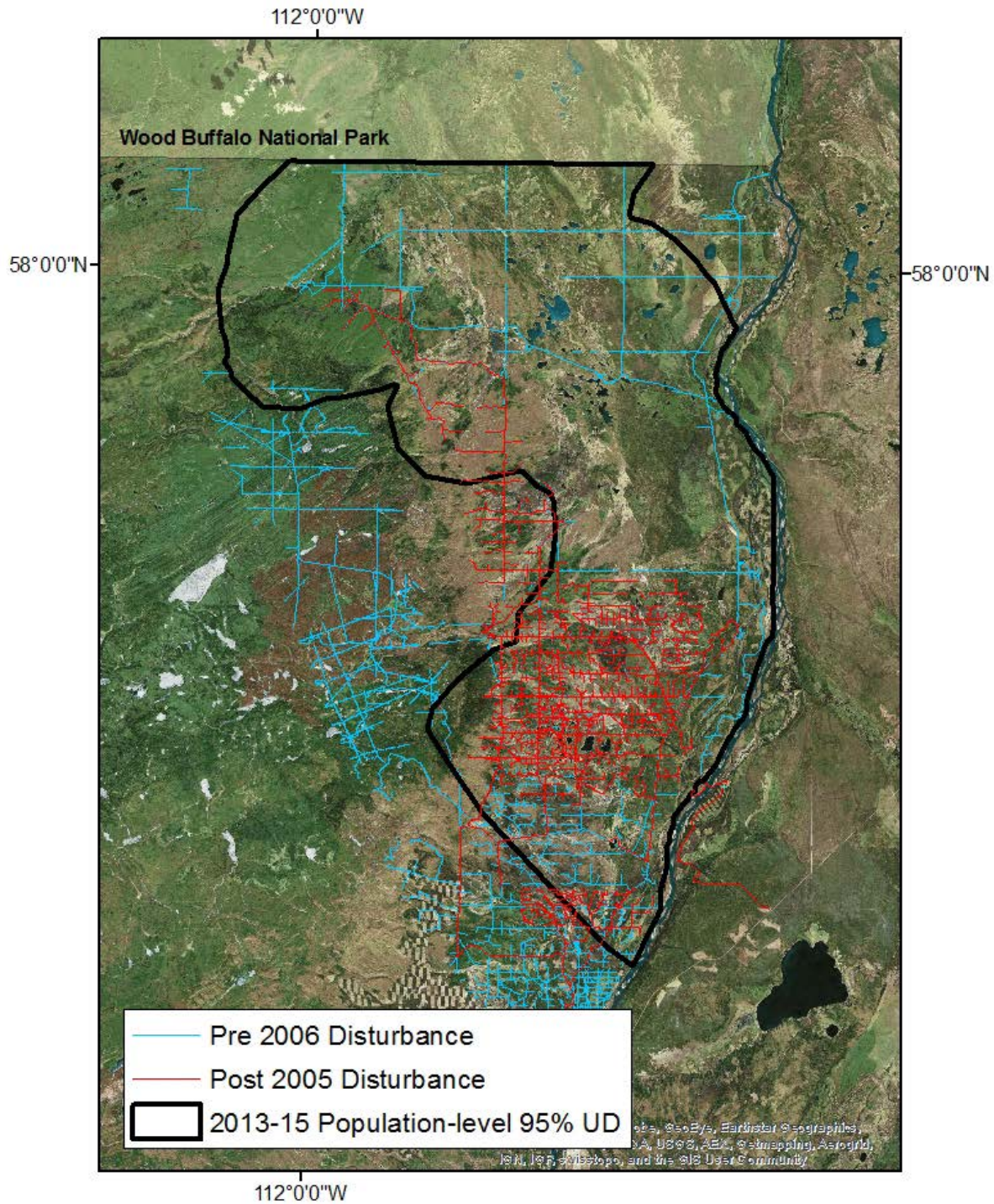


Figure 5: The extent of anthropogenic disturbance in relation to space use by Ronald Lake wood bison. Space use was modelled using a 95% utilization distribution (UD) estimated with all available bison GPS locations from 2013-2015. The resulting UD was clipped at the border of Wood Buffalo National Park and along the Athabasca River.

Resource Selection: Statistical Analyses

We estimated RSFs using generalized linear mixed effect models (GLMMs; Zuur *et al.* 2009), which account for the hierarchical structure inherent in GPS location data and unequal sample sizes among individual bison. In all GLMMs, we assigned individual bison as a random grouping effect (i.e., a random intercept). These models took the form

$$\ln \left[\frac{\pi(y_i=1)}{1-\pi(y_i=1)} \right] = \beta_0 + \beta_1 x_{1ij} + \dots + \beta_n x_{nij} + \gamma_{0j} \quad (\text{Eqn. 1; Gillies } et al. 2006)$$

where the left-hand side of the equation is the logit transformation for location y_i , β_0 is the fixed-effect intercept, β_n is the fixed-effect coefficient for each resource covariate x_n , and γ_{0j} is the random intercept for bison j . The fixed-effect coefficients yield inferences on how a typical bison selects resources and can be interpreted within the classic use-availability design of

$$\omega(x_i) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots \beta_n x_n) \quad (\text{Eqn. 2; Manly } et al. 2002)$$

where $\omega(x_i)$ is the relative selection value of a resource unit (or pixel) in category i as a function of the explanatory covariates (x_n) and their estimated coefficients (β_n). For spring, summer/fall, and winter seasonal analyses, the fixed-effects component of the model was specified as

$$\text{Land cover} * \text{fire severity} + \text{disturbance}$$

The fire severity variable was omitted from calving season analyses as no fires ≤ 10 years old occurred in the calving area. In all models, land cover was specified as a series of binary (or dummy) variables. In all cases, Upland Deciduous was used as the reference category. Thus, model results rank selection of land cover types (inferences on selection of a given land cover type) are relative to Upland Deciduous. Fire was specified as a three category variable (e.g., unburned, low severity burn, high severity burn) and we assessed fire by land cover interactions provided sample sizes were sufficient within a given land cover (see *Natural Disturbance Data* above). In final models, we excluded fire-land cover interactions when both severity parameter estimates had significance levels of $p > 0.15$ (Arnold 2010). For anthropogenic disturbance, we used Akaike's Information Criterion (AIC) to discriminate between models with a binary disturbance variable (e.g., undisturbed / disturbance) and models with a three-level disturbance variable describing age effects (e.g., undisturbed / pre-2006 disturbance / post-2005 disturbance). For the sub-analysis assessing bison response to human activity levels, the disturbance variable consisted of four categories (e.g., undisturbed / pre-2006 disturbance / post-2005 disturbance active / post-2005 disturbance non-active) and we did not assess fire interactions within these models.

We evaluated resource selection separately for males and females because, similar to other ungulate species, the two sexes are often spatially separated outside of the rutting season (Mooring *et al.* 2005). For each seasonal- and gender-specific RSF, we assessed model fit and

predictive performance by determining whether model predictions of resource selection correlated with bison space use. To do so, we used the fixed-effects output (Eqn. 2) to predict values for both bison GPS locations and available locations. We then partitioned the available locations into decile bins (i.e., 10 ordinal bins containing an equal number of random points) and assessed model prediction by comparing the proportional frequency of predicted values for bison GPS locations falling within a bin to bin rank using Spearman's correlation coefficient (r_s ; DeCesare *et al.* 2012). A significant positive correlation and higher r_s values indicate better predictive performance. We further computed the selection ratio for each bin, defined as the proportion of GPS locations falling within a bin divided by the bin's proportion of random points. Ratios > 1 indicate areas that are relatively selected (i.e., where bison use exceeds random expectation) while ratios < 1 indicate areas that are relatively avoided.

We used RSF outputs to generate seasonal- and gender-specific predictive maps of bison habitat selection. We rescaled maps to bound predicted values between 0 (perfect avoidance) and 1 (perfect selection) using a linear stretch

$$\hat{\omega}(x_i) = \frac{(\omega(x_i) - \omega_{Min})}{(\omega_{Max} - \omega_{Min})}$$

For each map, we partitioned the predictive values into the same 10 ordinal bins used to evaluate model fit and performance.

All statistical analyses were performed in R except for piece-wise linear regression which was estimated in STATA. We used the R package 'adehabitatHR' (Calenge 2006) to estimate UD's and the 'lme4' package (Bates *et al.* 2013) to estimate RSFs.

RESULTS

Bison Movement Rates

Across all individual bison and all available telemetry data, mean step length was 220.5 m (range: 157.8 – 306.1; Fig. 6). Mean step length of males ($\bar{x} = 207.8$ m) and females ($\bar{x} = 223.5$ m) were not significantly different from one another ($p = 0.60$ from a two-sided t -test). For both males and females, movement rates were highest during the month of August and lowest during winter (Fig. 7).

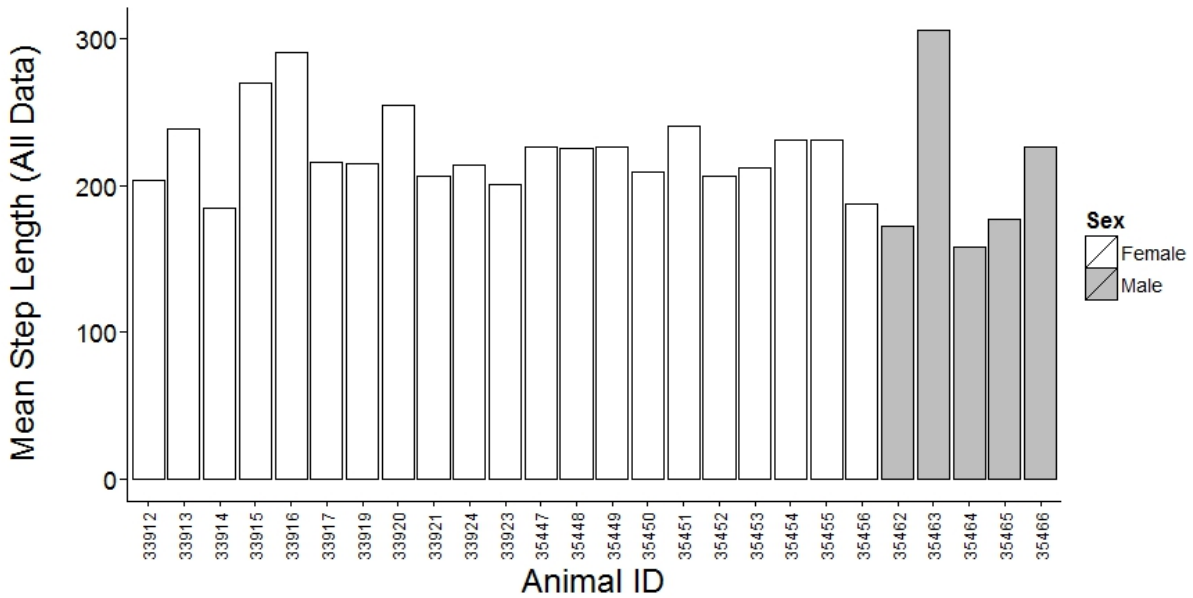


Figure 6: Mean individual bison step length (in meters) from all data collected to 21 August 2015 for the Ronald Lake herd. Step length is the straight line distance between successive GPS locations, which are recorded every 90 minutes.

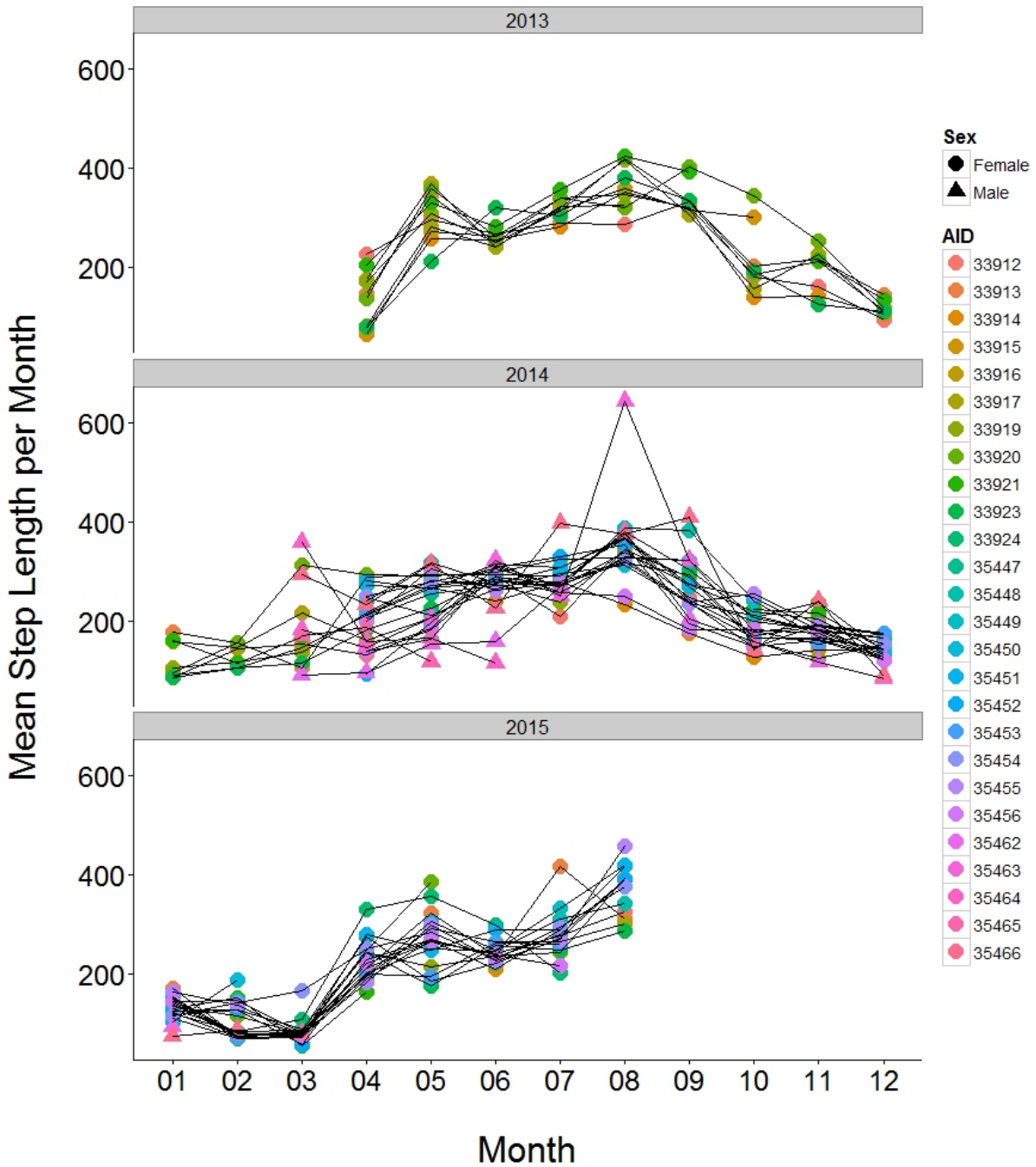


Figure 7: Mean step length (in meters) per month calculated from all data collected to 21 August 2015 from individual bison in the Ronald Lake herd. Step length is the straight line distance between successive GPS locations, which are recorded every 90 minutes.

Bison Annual and Seasonal Home Ranges and Cumulative Space Use

Across all individuals, annual MCP size for the first year of monitoring averaged 848.7 km² (range: 70.4 to 1277.7; Table 2). Seven individuals had sufficient data to calculate a second annual MCP. Overlap between successive annual MCPs was highly variable (range: 31 to 98%). Using the cumulative data for each individual, MCP size increased on average by 13% (range: 0 to 51%) compared to the Year 1 MCP. In general, UD's provided more conservative estimates of home range size than MCPs. On average, 80% and 95% UD's were 51% and 13% smaller, respectively, than cumulative MCPs, although for five bison the 95% UD exceeded the extent of the MCP.

Seasonal MCPs demonstrated strong overlap across years (Fig. 8; Appendix 5). This effect was most notable during calving illustrating fidelity to a specific calving area (Fig. 8). Pooling data across years, the estimated extent of the calving area was 88 km². Note that use of the calving area was not restricted to only the calving season as evidenced by overlap of this area by summer/fall and winter MCPs for some bison (Appendix 5).

Cumulatively, bison GPS locations followed a crescent-shaped pattern that extended north into Wood Buffalo National Park (Fig. 9). The areal extent of a 100% MCP encompassing all bison locations from 2013 – 2015 measured 1961 km². The associated 95% UD was smaller, measuring 986 km². The extent of an 80% UD, which may be indicative of core areas used by bison, measured 486 km².

Table 2: Metrics of individual home range size for female and male (in bold) bison of the Ronald Lake herd of northeastern Alberta. Minimum convex polygons (MCPs) were estimated annually and across years (All Data MCP) per individual. Utilization distributions (UDs) were estimated using all accumulated data per individual with 80% and 95% probability contour boundaries calculated.

Bison ID	Year 1 MCP	Year2 MCP	% Overlap Year 1 – 2 MCPs	All Data MCP	80% UD	95% UD
33912	594.0	693.6	94	896.7	403.5	650.3
33913	958.9	1154.9	98	1273.4	627.8	1028.2
33914	1040.6	625.1	50	1173.9	413.1	728.4
33915*	650.2	-	-	650.2	344.3	618.1
33916*	761.3	-	-	761.3	551.3	962.2
33917	712.9	603.2	61	928.4	384.2	645.8
33919	945.8	533.0	74	963.3	460.6	773.6
33920	1212.4	636.9	66	1289.8	525.1	937.1
33921	1018.6	406.8	31	1077.1	422.9	791.9
33923	931.7	621.5	56	1060.4	440.1	745.9
33924	703.8	-	-	844.9	381.0	646.0
35447	633.5	-	-	957.4	336.5	601.7
35448	1148.6	-	-	1225.0	462.8	909.5
35449	823.0	-	-	961.2	345.7	637.1
35450	621.1	-	-	621.1	336.0	553.8
35451	881.0	-	-	1093.3	440.9	802.6
35452	839.1	-	-	853.7	361.4	652.0
35453	575.4	-	-	766.5	334.8	599.1
35454	894.0	-	-	1001.2	472.9	815.3
35455	1092.3	-	-	1111.8	395.6	745.1
35456	468.1	-	-	534.5	264.1	475.3
35462	1277.7	-	-	1277.7	263.7	635.3
35463*	1269.7	-	-	1269.7	996.4	1799.3
35464*	724.4	-	-	724.4	709.6	1227.2
35465*	70.4	-	-	70.4	63.6	106.9
35466	1218.3	-	-	1218.3	698.4	1320.4
Mean	848.7	664.8	66	946.4	439.9	784.9
Minimum	70.4	406.8	31	70.4	63.6	106.9
Maximum	1277.7	1154.9	98	1289.8	996.4	1799.3

* Individual bison that were monitored < 8 months. All other bison had at least 1 year of data to estimate per year MCPs.

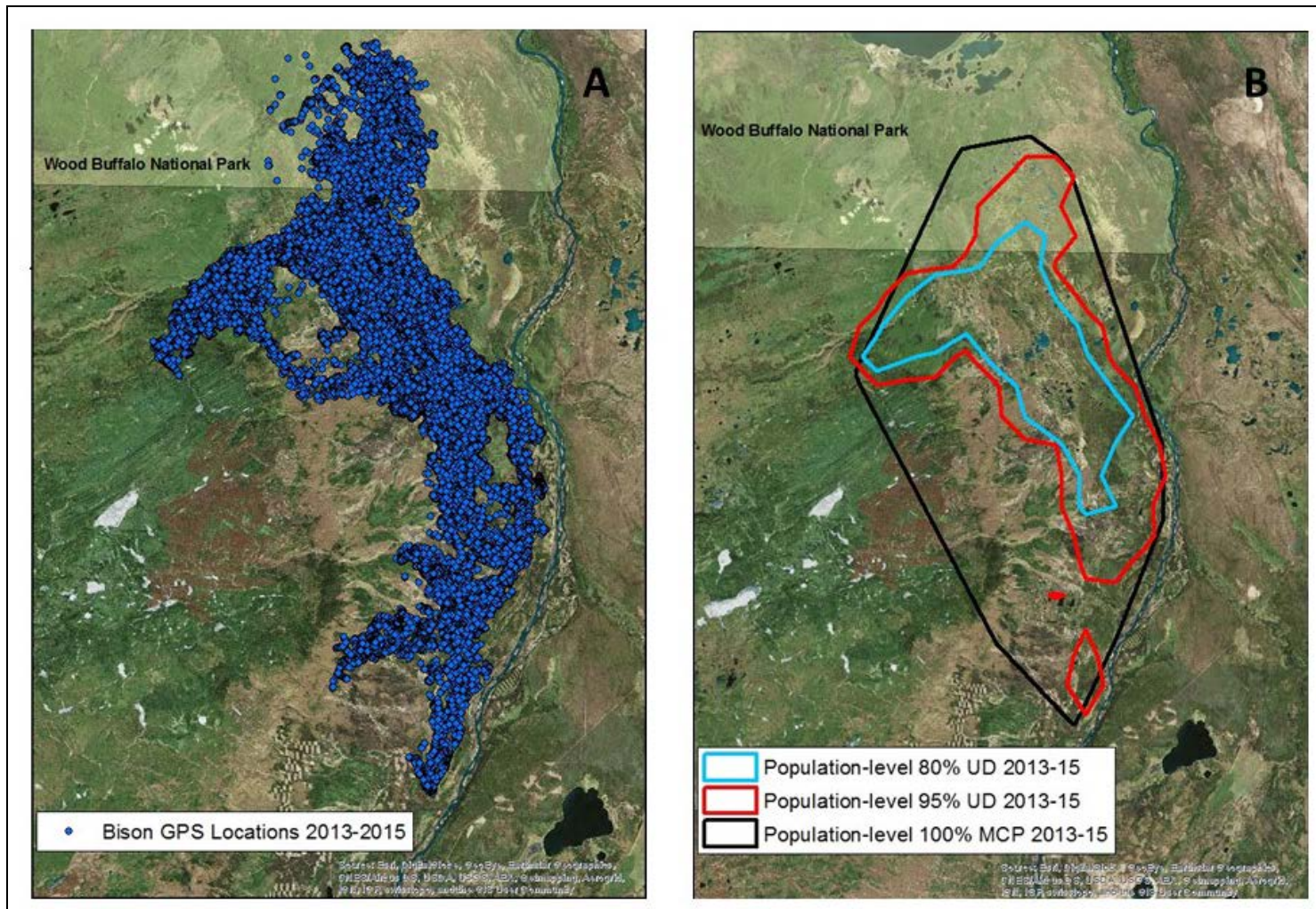


Figure 9: Cumulative space use by Ronald Lake wood bison in northeast Alberta from 2013 - 2015. GPS locations followed a crescent-shaped pattern along the west side of the Athabasca River (panel A). A minimum convex polygon (MCP) around these locations provides a more liberal estimate of space use than utilization distributions (UDs), which delineate areas of relatively high bison use (panel B).

Seasonal Habitat Selection by Bison

Spring

Habitat selection in spring qualitatively differed between females ($n = 21$) and males ($n = 3$; Table 3). This difference was exemplified in gender-specific responses to meadow marsh, emergent marsh and aquatic beds. For females, meadow and emergent marshes were the two top ranked land covers while aquatic bed was avoided relative to deciduous forests. This pattern reversed for males, with aquatic bed being the top ranked land cover and emergent and meadow marshes being avoided. Overall, males appeared to be more generalist in their response to land cover, with many cover types selected at rates similar to upland deciduous forest although this finding may be attributable to the small sample size of males.

Both genders appeared to respond favourably to fire as burnt land covers were generally selected at higher rates. One notable exception was the relative avoidance of burnt meadow marshes by females. Response to fire severity varied among land covers although in general both sexes showed weak preference for high versus low severity burns.

Bison also responded favourably to anthropogenic disturbance during spring. Female selection was generally weaker than males and the age of disturbance did not significantly affect female response. In particular, males showed strong selection for more recent disturbances (post-2005).

Table 3: Selection coefficients (β ; with standard errors [SE] and p -values) from the top resource selection functions estimated during spring for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. For fire interactions (second grouping), coefficients indicate relative selection compared to the coefficients of the given land cover. Anthropogenic disturbance coefficients (third grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.

Variable	Females ($n = 21$)			Males ($n = 3$)		
	β	SE	p	β	SE	p
Intercept	-2.13	0.08	< 0.001	-3.70	0.25	< 0.001
Open Water	-0.91	0.07	< 0.001	-1.72	0.93	0.063
Aquatic Bed	-2.02	0.28	< 0.001	-0.43	0.99	0.665
Emergent Marsh	0.38	0.06	< 0.001	-0.09	0.59	0.886
Meadow Marsh	1.83	0.03	< 0.001	-0.01	0.43	0.988
Graminoid Rich Fen	-0.55	0.12	< 0.001	0.37	0.29	0.201
Graminoid Poor Fen	-0.80	0.09	< 0.001	-1.08	0.51	0.035
Shrubby Rich Fen	0.01	0.06	0.837	-0.21	0.23	0.380
Shrubby Poor Fen	0.25	0.05	< 0.001	-0.82	0.51	0.108
Treed Rich Fen	-0.42	0.04	< 0.001	-0.38	0.15	0.010
Treed Poor Fen	-0.54	0.04	< 0.001	-1.28	0.49	0.009
Shrubby Bog	-0.57	0.11	< 0.001	-0.36	0.60	0.550
Treed Bog	0.22	0.06	0.001	-0.35	0.38	0.353
Shrub Swamp	-0.09	0.04	0.016	-1.36	0.49	0.005
Hardwood Swamp	-0.03	0.05	0.503	0.04	0.32	0.908
Mixedwood Swamp	-0.35	0.06	< 0.001	-1.54	0.51	0.002
Tamarack Swamp	-2.12	0.17	< 0.001	-2.69	0.92	0.004
Conifer Swamp	0.05	0.03	0.094	0.60	0.13	< 0.001
Upland Conifer	-0.66	0.06	< 0.001	-1.82	0.65	0.005
Upland Mixedwood	-2.20	0.17	< 0.001	-0.14	0.14	0.289
Cutblock	0.24	0.13	0.052	-13.69	3.30	< 0.001
Anthropogenic	-2.11	0.25	< 0.001	0.25	0.12	0.034
Fire: Low Severity	-0.62	0.04	< 0.001	1.05	0.11	< 0.001
Fire: High Severity	-0.21	0.03	< 0.001	1.72	0.09	< 0.001
Open Water: Fire Low	1.35	0.20	< 0.001	-	-	-
Open Water: Fire High	2.25	0.14	< 0.001	-	-	-
Emergent Marsh: Fire Low	0.34	0.22	0.121	-	-	-
Emergent Marsh: Fire High	1.04	0.13	< 0.001	-	-	-
Meadow Marsh: Fire Low	-1.48	0.23	< 0.001	-	-	-
Meadow Marsh: Fire High	-1.12	0.11	< 0.001	-	-	-
Graminoid Rich Fen: Fire Low	-7.34	0.85	< 0.001	-	-	-

Variable	Females (<i>n</i> = 21)			Males (<i>n</i> = 3)		
	β	SE	<i>p</i>	β	SE	<i>p</i>
Graminoid Rich Fen: Fire High	2.02	0.13	< 0.001	-	-	-
Graminoid Poor Fen: Fire Low	1.00	0.26	< 0.001	-	-	-
Graminoid Poor Fen: Fire High	0.50	0.13	< 0.001	-	-	-
Shrubby Rich Fen: Fire Low	1.11	0.23	< 0.001	-	-	-
Shrubby Rich Fen: Fire High	0.30	0.08	< 0.001	-	-	-
Shrubby Poor Fen: Fire Low	2.56	0.24	< 0.001	-	-	-
Shrubby Poor Fen: Fire High	-0.21	0.09	0.024	-	-	-
Treed Rich Fen: Fire Low	0.41	0.14	0.003	-	-	-
Treed Rich Fen: Fire High	0.69	0.06	< 0.001	-	-	-
Treed Poor Fen: Fire Low	0.44	0.18	0.016	-0.43	1.06	0.688
Treed Poor Fen: Fire High	0.49	0.07	< 0.001	2.25	0.49	< 0.001
Treed Bog: Fire Low	1.12	0.20	< 0.001	-	-	-
Treed Bog: Fire High	-0.75	0.18	< 0.001	-	-	-
Shrub Swamp: Fire Low	0.92	0.17	< 0.001	1.90	0.59	0.001
Shrub Swamp: Fire High	0.04	0.09	0.680	1.13	0.51	0.028
Hardwood Swamp: Fire Low	-	-	-	0.93	0.56	0.098
Hardwood Swamp: Fire High	-	-	-	-1.18	0.67	0.078
Conifer Swamp: Fire Low	-0.65	0.19	< 0.001	-	-	-
Conifer Swamp: Fire High	0.24	0.07	< 0.001	-	-	-
Upland Conifer: Fire Low	0.30	0.09	0.001	2.06	0.67	0.002
Upland Conifer: Fire High	1.35	0.07	< 0.001	2.89	0.66	< 0.001
Disturbance (no age effect) ¹	0.43	0.05	< 0.001	-	-	-
Disturbance: ≤ 2005 ²	-	-	-	0.81	0.15	< 0.001
Disturbance: ≥ 2006	-	-	-	2.09	0.10	< 0.001

¹ AIC of disturbance models for females: age effects = 152652; no age effects = 152576

² AIC of disturbance models for males: age effects = 9400, no age effects = 9456

Calving

During calving, females showed high selection for meadow marsh and, to a lesser extent hardwood swamp, relative to upland deciduous forests (Table 4). All other land cover types were avoided relative to deciduous forests. Bogs, tamarack swamp, upland mixedwoods and cutblocks were the lowest ranked land covers. For males, upland deciduous forest was the highest ranked land cover during this time although two of the three males had a few locations within anthropogenic areas. Similar to females, males also strongly avoided bogs, shorelines (e.g., open water and aquatic beds) and shrubby poor fens. Interactions with fire were not considered during calving.

Bison selection for anthropogenic disturbance in the spring extended into calving. Because no recent disturbances (post-2005) are present in the calving area, the most supported model for females did not include age effects for disturbance. As in spring, males continued to show strong selection for new disturbance features.

Table 4: Selection coefficients (β ; with standard errors [SE] and p -values) from the top resource selection functions estimated during calving for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. Anthropogenic disturbance coefficients (second grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.

Variable	Females ($n = 21$)			Males ($n = 3$)		
	β	SE	p	β	SE	p
Intercept	-2.37	0.03	< 0.001	-2.83	0.13	< 0.001
Open Water	-2.80	0.20	< 0.001	<i>perfect avoidance</i>		
Aquatic Bed	<i>perfect avoidance</i>			<i>perfect avoidance</i>		
Emergent Marsh	-3.17	0.38	< 0.001	-0.78	0.72	0.278
Meadow Marsh	1.57	0.04	< 0.001	-0.27	0.41	0.511
Graminoid Rich Fen	-2.31	0.23	< 0.001	<i>perfect avoidance</i>		
Graminoid Poor Fen	-2.20	0.17	< 0.001	-1.02	0.52	0.048
Shrubby Rich Fen	-4.32	0.38	< 0.001	-2.40	0.72	0.001
Shrubby Poor Fen	-2.81	0.21	< 0.001	<i>perfect avoidance</i>		
Treed Rich Fen	-1.66	0.06	< 0.001	-2.40	0.36	< 0.001
Treed Poor Fen	-1.32	0.06	< 0.001	-3.04	0.51	< 0.001
Shrubby Bog	-4.63	1.00	< 0.001	-1.48	1.01	0.143
Treed Bog	<i>perfect avoidance</i>			-2.07	0.73	0.004
Shrub Swamp	-1.58	0.07	< 0.001	-1.59	0.25	< 0.001
Hardwood Swamp	0.55	0.04	< 0.001	-1.00	0.29	0.001
Mixedwood Swamp	-0.13	0.06	0.039	-3.40	1.01	0.001
Tamarack Swamp	-4.49	0.71	< 0.001	-1.83	0.60	0.002
Conifer Swamp	-0.88	0.05	< 0.001	-3.98	1.00	< 0.001
Upland Conifer	-3.44	0.11	< 0.001	-1.97	0.21	< 0.001
Upland Mixedwood	<i>perfect avoidance</i>			-0.65	0.19	0.001
Cutblock	<i>perfect avoidance</i>			<i>perfect avoidance</i>		
Anthropogenic	<i>perfect avoidance</i>			0.14	0.11	0.183
Disturbance (no age effects)	0.86	0.05	< 0.001	-	-	-
Disturbance (≤ 2005) ¹	-	-	-	1.03	0.25	< 0.001
Disturbance (≥ 2006)	-	-	-	2.95	0.09	< 0.001

¹ AIC of disturbance models for males: age effects = 4815, no age effects = 4895. Note effects of disturbance were not considered for females as the calving area did not contain post-2005 disturbances.

Summer / Fall

Females continued to show relatively high selection for meadow marshes after calving and extending into the fall (Table 5). In contrast to calving, females appeared to make more use of upland conifer forests and conifer swamps. Emergent marsh and upland mixedwood forests were selected at rates similar to upland deciduous forest while other land covers were relatively avoided. The lowest ranked land covers for females were mixedwood swamp and treed bog. For males, the highest ranked land covers for summer and fall were graminoid rich fen, upland conifer forest, meadow marsh and conifer swamp. All other land covers were avoided relative to deciduous forests with males showing particularly strong avoidance of shrubby bogs and fens as well as mixedwood swamps. Note that during this season, both male and female bison showed the highest variation in land cover use as no one land cover type was completely avoided.

Fire continued to modify bison selection of land cover types during the summer and fall. In general, fire increased selection for most land cover types and this trend appeared to be stronger for males. There were, however, notable exceptions to this trend. For females, fire did not increase selection of meadow marshes, the top ranked land cover, and lowered selection of upland conifer forests and conifer swamps, ranked second and third, respectively. For males, fire also lowered selection of the two top ranked land covers, graminoid rich fens and upland conifer. For both genders, response to fire severity was variable and depended on land cover type.

Consistent with the previous two seasons, bison appeared to respond favourably to anthropogenic disturbance. Again, this effect was stronger in males, particularly in the positive response by males to newer disturbances. Females also demonstrated selection for post-2005 disturbance features but were generally ambivalent to older disturbances.

Table 5: Selection coefficients (β ; with standard errors [SE] and p -values) from resource selection functions estimated during summer and fall for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. For fire interactions (second grouping), coefficients indicate relative selection compared to the coefficients of the given land cover. Anthropogenic disturbance coefficients (third grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.

Variable	Females ($n = 21$)			Males ($n = 3$)		
	β	SE	p	β	SE	p
Intercept	-1.67	0.06	<0.001	-1.11	0.15	<0.001
Open Water	-0.93	0.06	<0.001	-2.29	0.42	<0.001
Aquatic Bed	-0.25	0.14	0.064	-1.09	0.56	0.054
Emergent Marsh	-0.01	0.06	0.916	-1.25	0.43	0.004
Meadow Marsh	0.85	0.04	<0.001	0.58	0.19	0.002
Graminoid Rich Fen	-0.13	0.05	0.009	1.58	0.30	<0.001
Graminoid Poor Fen	-0.52	0.06	<0.001	-1.40	0.31	<0.001
Shrubby Rich Fen	-0.95	0.07	<0.001	-2.44	0.46	<0.001
Shrubby Poor Fen	-0.71	0.06	<0.001	-2.53	0.58	<0.001
Treed Rich Fen	-0.15	0.03	<0.001	-0.27	0.10	0.007
Treed Poor Fen	-0.34	0.03	<0.001	-0.70	0.12	<0.001
Shrubby Bog	-0.35	0.10	<0.001	-1.95	0.55	<0.001
Treed Bog	-1.02	0.08	<0.001	-1.43	0.25	<0.001
Shrub Swamp	-0.89	0.04	<0.001	-1.63	0.18	<0.001
Hardwood Swamp	-0.68	0.05	<0.001	-0.45	0.12	<0.001
Mixedwood Swamp	-1.21	0.07	<0.001	-2.61	0.34	<0.001
Tamarack Swamp	-0.17	0.07	0.014	-1.26	0.26	<0.001
Conifer Swamp	0.64	0.02	<0.001	0.36	0.10	<0.001
Upland Conifer	0.75	0.03	<0.001	1.14	0.08	<0.001
Upland Mixedwood	-0.04	0.11	0.719	-0.79	0.33	0.015
Cutblock	-1.27	0.13	<0.001	-0.68	0.33	0.040
Anthropogenic	-1.48	0.16	<0.001	-0.64	0.08	<0.001
Fire: Low Severity	1.39	0.02	<0.001	-0.15	0.07	0.024
Fire: High Severity	0.61	0.02	<0.001	-0.37	0.07	<0.001
Open Water: Fire Low	1.24	0.12	<0.001	2.67	0.79	<0.001
Open Water: Fire High	2.33	0.10	<0.001	3.58	0.57	<0.001
Emergent Marsh: Fire Low	0.56	0.13	<0.001	1.88	0.78	0.016
Emergent Marsh: Fire High	0.43	0.12	<0.001	1.32	0.72	0.066
Meadow Marsh: Fire Low	-0.55	0.12	<0.001	1.56	0.51	0.002
Meadow Marsh: Fire High	0.00	0.08	0.956	0.15	0.39	0.694
Graminoid Rich Fen: Fire Low	-	-	-	-12.69	4.05	0.002

Variable	Females (<i>n</i> = 21)			Males (<i>n</i> = 3)		
	β	SE	<i>p</i>	β	SE	<i>p</i>
Graminoid Rich Fen: Fire High	-	-	-	-3.42	0.61	<0.001
Graminoid Poor Fen: Fire Low	0.14	0.16	0.369	-	-	-
Graminoid Poor Fen: Fire High	-0.40	0.09	<0.001	-	-	-
Shrubby Rich Fen: Fire Low	1.52	0.15	<0.001	2.50	0.82	0.002
Shrubby Rich Fen: Fire High	0.79	0.08	<0.001	2.13	0.50	<0.001
Shrubby Poor Fen: Fire Low	1.96	0.17	<0.001	5.56	1.18	<0.001
Shrubby Poor Fen: Fire High	0.05	0.09	0.543	0.73	0.79	0.354
Treed Rich Fen: Fire Low	-0.18	0.07	0.009	0.84	0.22	<0.001
Treed Rich Fen: Fire High	0.00	0.04	0.931	0.32	0.16	0.050
Treed Poor Fen: Fire Low	-0.15	0.09	0.087	0.57	0.32	0.077
Treed Poor Fen: Fire High	-0.15	0.05	0.004	0.55	0.18	0.002
Shrubby Bog: Fire Low	-0.46	0.33	0.167	-	-	-
Shrubby Bog: Fire High	-0.36	0.16	0.026	-	-	-
Treed Bog: Fire Low	0.62	0.20	0.001	-	-	-
Treed Bog: Fire High	0.84	0.13	<0.001	-	-	-
Shrub Swamp: Fire Low	0.20	0.14	0.162	0.48	0.40	0.224
Shrub Swamp: Fire High	1.13	0.06	<0.001	0.57	0.26	0.030
Hardwood Swamp: Fire Low	0.70	0.12	<0.001	-	-	-
Hardwood Swamp: Fire High	1.17	0.09	<0.001	-	-	-
Mixedwood Swamp: Fire Low	-0.99	0.18	<0.001	-	-	-
Mixedwood Swamp: Fire High	0.20	0.14	0.164	-	-	-
Tamarack Swamp: Fire Low	-1.65	0.20	<0.001	-0.69	0.91	0.447
Tamarack Swamp: Fire High	-0.43	0.13	<0.001	0.96	0.44	0.030
Conifer Swamp: Fire Low	-0.69	0.06	<0.001	0.56	0.22	0.011
Conifer Swamp: Fire High	-0.83	0.05	<0.001	0.09	0.17	0.596
Upland Conifer: Fire Low	-0.27	0.04	<0.001	-0.06	0.12	0.639
Upland Conifer: Fire High	-0.58	0.04	<0.001	-0.49	0.11	<0.001
Upland Mixedwood: Fire Low	0.00	0.11	0.995	0.91	0.35	0.009
Upland Mixedwood: Fire High	0.39	0.12	0.001	0.20	0.36	0.579
Disturbance: \leq 2005 ^{1, 2}	-0.06	0.05	0.234	0.49	0.12	<0.001
Disturbance: \geq 2006	0.11	0.05	0.055	1.97	0.07	<0.001

¹ AIC of disturbance models for females: age effects = 258557, no age effects = 258560

² AIC of disturbance models for males: age effects = 20752, no age effects = 20879

Winter

During winter, both genders had relatively high selection for marshes and treeless fens (Table 6). Both marsh types were the top ranked land cover types for females, while aquatic bed and graminoid rich fens were ranked highest for males. Interestingly, aquatic bed was the lowest ranked land cover for females. Compared to other seasonal periods, upland deciduous forests had their lowest ranking for both genders. For females, the top seven land cover types were treeless, while among treed cover types, rich fens and swamps had the highest selective values. For males, the highest ranked treed cover was tamarack swamp.

The genders differed in their responses to burnt land covers during winter. In general, males demonstrated increased selection for burnt areas, particularly fens. For females, recent fires decreased the selective value of marshes and, for the most part, fens. Responses to fire severity were variable for both genders with the relative selective value of fire severity varying by land cover type.

The genders also differed in their response to anthropogenic disturbance during winter. Females avoided disturbed areas, particularly new disturbances, while males showed mild selection for these areas with no apparent effect of age of disturbance. Using 2013 data for females, we also assessed bison response to human activity levels on disturbance features (Table 7). Here, the response to disturbance was more nuanced. Females were generally ambivalent to newer, non-active disturbances but highly avoided newer active disturbances.

Table 6: Selection coefficients (β ; with standard errors [SE] and p -values) from resource selection functions estimated during winter for female and male wood bison of the Ronald Lake herd of northeast Alberta. For land cover (first grouping), positive coefficients (> 0) indicate relative selection compared to Upland Deciduous forests while negative coefficients indicate relative avoidance. For fire interactions (second grouping), coefficients indicate relative selection compared to the coefficients of the given land cover. Anthropogenic disturbance coefficients (third grouping) are in reference to selection of undisturbed areas. Dashes indicate variables not included in each gender-specific top model.

Variable	Females ($n = 19$)			Males ($n = 2$)		
	β	SE	p	β	SE	p
Intercept	-1.41	0.05	< 0.001	-2.25	0.19	< 0.001
Open Water	0.87	0.03	< 0.001	0.46	0.27	0.088
Aquatic Bed	-2.18	0.41	< 0.001	2.35	0.30	< 0.001
Emergent Marsh	2.46	0.04	< 0.001	0.58	0.39	0.137
Meadow Marsh	3.36	0.03	< 0.001	-0.33	0.46	0.471
Graminoid Rich Fen	1.96	0.07	< 0.001	2.12	0.18	< 0.001
Graminoid Poor Fen	1.22	0.04	< 0.001	0.87	0.34	0.001
Shrubby Rich Fen	1.88	0.03	< 0.001	0.36	0.35	0.314
Shrubby Poor Fen	1.60	0.03	< 0.001	1.25	0.31	< 0.001
Treed Rich Fen	0.72	0.02	< 0.001	-0.14	0.20	0.49
Treed Poor Fen	0.06	0.03	0.04	-0.05	0.20	0.803
Shrubby Bog	-0.74	0.14	< 0.001	0.00	0.43	0.999
Treed Bog	-0.55	0.08	< 0.001	-1.09	0.45	0.0154
Shrub Swamp	1.98	0.02	< 0.001	0.04	0.20	0.841
Hardwood Swamp	0.68	0.03	< 0.001	-0.23	0.21	0.263
Mixedwood Swamp	0.09	0.05	0.059	-1.50	0.42	< 0.001
Tamarack Swamp	-1.58	0.15	< 0.001	1.00	0.17	< 0.001
Conifer Swamp	-0.38	0.03	< 0.001	-1.75	0.54	0.001
Upland Conifer	-0.53	0.06	< 0.001	-1.49	0.44	< 0.001
Upland Mixedwood	-0.67	0.11	< 0.001	0.52	0.40	0.186
Cutblock	-1.07	0.31	< 0.001	-12.84	4.28	0.003
Anthropogenic	-0.78	0.29	0.007	1.05	0.09	< 0.001
Fire: Low Severity	-1.22	0.05	< 0.001	-0.22	0.12	0.057
Fire: High Severity	-0.78	0.04	< 0.001	0.40	0.09	< 0.001
Open Water: Fire Low	-1.97	0.72	0.006	-	-	-
Open Water: Fire High	0.67	0.15	< 0.001	-	-	-
Emergent Marsh: Fire Low	-1.42	0.29	< 0.001	-	-	-
Emergent Marsh: Fire High	-1.45	0.20	< 0.001	-	-	-
Meadow Marsh: Fire Low	-2.51	0.26	< 0.001	-	-	-
Meadow Marsh: Fire High	-1.57	0.10	< 0.001	-	-	-
Graminoid Rich Fen: Fire Low	-10.01	98.41	0.919	-	-	-

Variable	Females (n = 19)			Males (n = 2)		
	β	SE	p	β	SE	p
Graminoid Rich Fen: Fire High	0.71	0.08	< 0.001	-	-	-
Graminoid Poor Fen: Fire Low	-0.40	0.42	0.342	-12.98	11.57	0.2617
Graminoid Poor Fen: Fire High	-1.04	0.11	< 0.001	0.90	0.43	0.0347
Shrubby Rich Fen: Fire Low	-2.21	0.73	0.002	2.11	0.70	0.0024
Shrubby Rich Fen: Fire High	-0.99	0.07	< 0.001	0.84	0.39	0.0328
Shrubby Poor Fen: Fire Low	1.23	0.44	0.0050	-13.09	7.75	0.0914
Shrubby Poor Fen: Fire High	-0.77	0.08	< 0.001	0.94	0.40	0.0201
Treed Rich Fen: Fire Low	0.25	0.13	0.048	1.91	0.31	< 0.001
Treed Rich Fen: Fire High	-0.28	0.06	< 0.001	1.24	0.24	< 0.001
Treed Poor Fen: Fire Low	0.61	0.17	< 0.001	0.22	0.55	0.6967
Treed Poor Fen: Fire High	0.17	0.07	0.017	1.06	0.23	< 0.001
Shrubby Bog: Fire Low	-7.16	65.27	0.913	-	-	-
Shrubby Bog: Fire High	1.29	0.22	< 0.001	-	-	-
Treed Bog: Fire Low	2.85	0.34	< 0.001	-	-	-
Treed Bog: Fire High	1.75	0.17	< 0.001	-	-	-
Shrub Swamp: Fire Low	-1.07	0.23	< 0.001	1.37	0.33	< 0.001
Shrub Swamp: Fire High	0.08	0.06	0.194	-0.27	0.27	0.328
Hardwood Swamp: Fire Low	-0.59	0.35	0.094	-	-	-
Hardwood Swamp: Fire High	0.46	0.14	< 0.001	-	-	-
Mixedwood Swamp: Fire Low	-	-	-	-	-	-
Mixedwood Swamp: Fire High	-	-	-	-	-	-
Tamarack Swamp: Fire Low	-	-	-	-	-	-
Tamarack Swamp: Fire High	-	-	-	-	-	-
Conifer Swamp: Fire Low	-0.32	0.26	0.22	0.83	0.87	0.34
Conifer Swamp: Fire High	-0.79	0.15	< 0.001	2.27	0.57	< 0.001
Upland Conifer: Fire Low	0.14	0.10	0.196	1.21	0.49	0.0139
Upland Conifer: Fire High	-0.18	0.08	0.02	2.19	0.45	< 0.001
Upland Mixedwood: Fire Low	-	-	-	-0.94	0.50	0.058
Upland Mixedwood: Fire High	-	-	-	-1.32	0.45	0.004
Disturbance (no age effects) ¹	-	-	-	0.38	0.10	< 0.001
Disturbance: \leq 2005 ²	-0.48	0.07	< 0.001	-	-	-
Disturbance: \geq 2006	-1.04	0.10	< 0.001	-	-	-

¹ AIC of disturbance models for males: age effects = 9758, no age effects = 9757

² AIC of disturbance models for females: age effects = 185694, no age effects = 185714

Table 7: Selection coefficients (β ; with standard errors [SE] and p-values) from a resource selection function assessing the response of female wood bison of the Ronald Lake herd to human activity levels on anthropogenic disturbance features (e.g., roads, seismic lines and well sites) during winter 2013. Coefficients for disturbance effects (in bold) are relative to undisturbed areas.

Variable	Females ($n = 8$)		
	β	SE	p
Intercept	-1.31	0.15	< 0.001
Open Water	0.52	0.07	< 0.001
Aquatic Bed	-1.37	0.38	< 0.001
Emergent Marsh	1.87	0.07	< 0.001
Meadow Marsh	3.09	0.05	< 0.001
Graminoid Rich Fen	2.54	0.06	< 0.001
Graminoid Poor Fen	0.22	0.08	0.009
Shrubby Rich Fen	0.87	0.05	< 0.001
Shrubby Poor Fen	1.30	0.05	< 0.001
Treed Rich Fen	0.51	0.04	< 0.001
Treed Poor Fen	0.05	0.05	0.279
Shrubby Bog	-0.23	0.16	0.156
Treed Bog	0.07	0.09	0.431
Shrub Swamp	1.37	0.04	< 0.001
Hardwood Swamp	0.23	0.07	< 0.001
Mixedwood Swamp	-0.58	0.10	< 0.001
Tamarack Swamp	-1.58	0.19	< 0.001
Conifer Swamp	0.04	0.04	0.392
Upland Conifer	-0.69	0.04	< 0.001
Upland Mixedwood	-1.61	0.14	< 0.001
Cutblock	-1.28	0.29	< 0.001
Anthropogenic	-2.52	0.40	< 0.001
Disturbance (≤ 2005)	-0.67	0.14	< 0.001
Disturbance (≥ 2006, active)	-3.31	0.42	< 0.001
Disturbance (≥ 2006, non-active)	-0.06	0.13	0.637

RSF Model Validation

Predictive performance was strong across all seasonal and gender-specific models with ordinal RSF bin values positively correlating with bison selection ratios (all $r_s \geq 0.93$, all $p \leq 0.003$; Table 8). Because models were developed using only categorical variables, which leads to a finite number of predicted values, validation procedures resulted in the reduction of the total number of RSF bins from 10 across all models due to a lack of bison GPS or available locations in one or more bins. In general, bison showed disproportionate use (i.e., selection ratios > 1) of the top 2-3 RSF bins although females in summer, and males in winter, had a wider range of selected areas (the top 4 bins), while females during calving were more restricted (i.e., selection of the top bin only).

Table 8: Model validation of seasonal resource selection functions estimated for female and male wood bison of the Ronald Lake herd in northeastern Alberta. Listed seasonal values by gender are selection ratios, defined as the proportion of GPS locations falling within an ordinal RSF bin divided by the bin's proportional area. Values > 1 indicate selection while values < 1 indicate avoidance. Predictive performance was evaluated by the strength of correlation (Spearman's correlation coefficient, r_s) between selection ratios and RSF bin rank. Note that validation procedures resulted in the total number of RSF bins varying by season.

RSF Bin	Spring		Calving		Summer / Fall		Winter	
	Females	Males	Females	Males	Females	Males	Females	Males
1	0.32	0.04	0.01	0.03	0.25	0.17	0.10	0.13
2	0.52	0.03	0.07	0.04	0.40	0.26	0.13	0.39
3	0.65	0.17	0.29	0.14	0.57	0.39	0.24	0.60
4	0.81	0.13	0.37	0.23	<u>0.65</u>	0.76	0.37	0.40
5	0.93	0.27	<u>0.90</u>	<u>0.81</u>	1.05	0.76	0.42	<u>0.40</u>
6	<u>0.99</u>	<u>0.79</u>	1.98	1.05	1.22	0.94	0.56	1.06
7	1.24	1.22	-	5.00	1.40	<u>0.86</u>	<u>0.61</u>	2.36
8	2.16	2.42	-	-	2.81	1.36	1.25	1.64
9		3.69	-	-	-	3.42	5.18	2.55
<i>Statistical rank correlation:</i>								
r_s	1	0.97	1	1	1	0.97	1	0.93
p	< 0.001	< 0.001	0.003	< 0.001	< 0.001	< 0.001	< 0.001	0.001

DISCUSSION

During two and a half years of monitoring, Ronald Lake wood bison demonstrated seasonal and gender-specific variation in their space use and habitat selection. However, the herd showed relatively high fidelity to seasonal ranges across years, particularly by females to the calving area previously identified by Tan *et al.* (2015). Developed models of seasonal habitat selection had good predictive performance for both genders and should provide useful tools for landscape-level planning within the herd's range. Our analyses further highlight the influence of fire and anthropogenic disturbance on bison selection of habitat.

Response to Land Cover

Male and female bison demonstrated divergent seasonal patterns of selection for land cover types. For females, meadow marsh was the top ranked land cover across all seasons with the strongest selection occurring in the winter, a finding consistent with results reported by Larter & Gates (1991) for wood bison in the Northwest Territories. Meadow marshes primarily consist of bluejoint grass (*Calamagrostis canadensis*) and broadleaf sedges (*Carex* spp.; DU 2011), the latter being a dominant component of wood bison diet (Larter & Gates 1991; Jung 2015). In boreal forests, wetland meadows such as marshes and fens also contain the highest amounts of herbaceous biomass (Strong & Gates 2009). Bison are considered a bulk feeder (i.e., can subsist on a low-quality but high volume diet; Hawley *et al.* 1981) and a capital breeder (i.e., depend on accumulated body reserves for reproduction; Hamel *et al.* 2012); consequently, females may be consistently using areas with high forage biomass throughout the year to meet annual reproductive requirements.

The relative strength of female selection for marshes was lowest during summer and fall. The following factors may have influenced this seasonal change. First, insect harassment is known to influence bison behaviour (Melton *et al.* 1989) and insect abundance peaks during the summer in the boreal forest with wet areas having particularly high concentrations. Thus, decreased selection of marshes and increased selection of drier upland forests during summer may stem from increased use of areas that are relative insect refugia. Second, bison diets vary seasonally and late summer and fall is a period where body fat deposition becomes important to overwinter survival and reproduction (Larter & Gates 1991; Delgiudice *et al.* 2001; Parker *et al.* 2009). Because digestibility of grasses and sedges decreases during the fall, bison may increase use of upland conifer forests to access more highly digestible, carbohydrate-rich lichens to aid in body fat deposition (Larter & Gates 1991). Finally, the soft footing within marshes during the snow-free season may elevate predation risk due to lowered mobility (L. Carbyn, personal communication).

Male bison were more variable in their selection of land cover types, which may be in part due to our small sample size. Meadow marsh, however, was still a highly ranked land cover type for males, particularly during calving and summer / fall. Surprisingly, aquatic bed was the highest ranked land cover in two seasons, spring and winter. In spring, this response may indicate that

males are foraging along the interface between marshes and aquatic beds or perhaps feeding on newly emergent vegetation along shorelines. In winter, the selection of aquatic beds may result from basking in open areas (i.e., frozen lakes and ponds) to ruminate, a behaviour known to occur in northern ungulates to aid in thermoregulation (Signer *et al.* 2011). Males also had relatively higher selection for graminoid rich fens than did females, a result that may be explained by potential dietary drivers of sexual segregation in bison. Under the “sexual-dimorphism body size hypothesis”, the larger-bodied males are predicted to select areas with higher per-capita abundance of lower quality forage as their larger rumen can more efficiently process high fibre forage (Main *et al.* 1996; Mooring *et al.* 2005). By selecting fens that are potentially lower in forage quality than marshes (Gordon 1989), males may be avoiding spatial overlap – and thus competition – with females to maximize per capita forage abundance.

Response to Fire

In this update, we evaluated whether burn severity of historical forest fires influenced bison selection of various land covers. In their initial report, Tan *et al.* (2015) modelled fire as a binary variable (burnt / unburnt) and tested fire interactions during fall and winter with two land cover types: meadow marsh and upland pine. Their findings indicated that while fire increased female selection of meadow marshes during fall, it generally diminished selection of upland pine in both seasons and meadow marsh during winter. In our analyses, we found similar contrasting results with only weak trends evident in specific seasons. This variability may be due in part to the time since the 2011 Richardson Fire. Bison selection of burnt areas is likely to be strongest in the first 1-2 years post-fire when fire-released nutrients result in a flush of herbaceous vegetation with high nutritional quality (Larter 1988; Allred *et al.* 2011; Raynor *et al.* 2015). Beyond this time frame, bison response is likely to attenuate.

Across land cover types, bison selection for burnt areas was generally strongest in the spring and stronger in males. Female response was somewhat surprising as they avoided burnt meadow marsh, their top ranked land cover, yet selected for burnt areas in most other land cover types. For both genders, the increased selection of burnt areas in spring relative to other seasons may be indicative of bison maximizing short-term energy intake when forage is at its highest nutritional value to regain body mass after winter (Raynor *et al.* 2015). Relative to unburnt areas, forage within burnt areas may still have higher peak nutritional values due to residual effects of fire-released nutrients. Maximizing short-term energy intake may also explain why bison demonstrated higher selection for high severity burns as these areas may have relatively higher forage biomass (Lord 2008), although this relationship has not been fully investigated for wood bison in the boreal forest.

In summer and winter, bison selection of burnt areas was more variable; however, as with spring, fire continued to decrease the selective value of the top ranked land cover types for females, namely marshes, graminoid rich fens and upland conifer. Similarly for males, fire decreased selection of graminoid rich fens and upland conifer in summer. It is uncertain as to why bison might avoid these burnt areas 2-4 years post-fire, but it may be due to changes in

forage quality and abundance associated with seral stage (Raynor *et al.* 2015) or, in the case of upland conifer forests, post-fire downed woody debris may impart movement costs that outweigh any small nutritional advantages. The land cover-specific response of bison to fire severity was generally uninformative in elucidating clear trends in bison behavioural response to burnt areas during these seasons.

Response to Anthropogenic Disturbance

In general, both genders responded positively to anthropogenic disturbance across all seasons except females during winter. This result differs from the findings of Tan *et al.* (2015) who reported female avoidance occurring in spring and fall, as well as winter. These differences may indicate annual variation in bison response but may also be influenced by our different analytical approaches as we modelled the proportion of bison locations occurring within the disturbance footprint, whereas Tan *et al.* (2015) modelled the relative proximity of bison locations to the footprint.

In our analysis, the response of males was stronger than females and seasonally both genders demonstrated higher selection during spring and calving. The selection of disturbance features likely reflects basic foraging and movement behaviour by wood bison. For example, linear features such as seismic lines and low-traffic roads may function as travel corridors between feeding patches (Bruggeman *et al.* 2007). Moreover, as an obligate grazer, bison may select linear features themselves as feeding patches because these disturbances create forest gaps where the abundance of grasses and forbs is higher than within the surrounding forest (Kuijper *et al.* 2009). This response is likely amplified during the early growing season when increased light in forest gaps results in earlier spring green-up within these patches (Lieffers *et al.* 1999). During the winter, selection may diminish for these features as bison switch to larger open habitats, as evidenced by increased selection of treeless land covers, to maximize forage quantity within their immediate surroundings given the constraints on movement imposed by snow (Fortin *et al.* 2003).

Bison selection of disturbances, such as seismic lines, may be somewhat surprising given the reported avoidance of these features by other boreal ungulates (e.g., caribou [*Rangifer tarandus caribou*], Dyer *et al.* 2001). This avoidance behaviour is thought to be driven by predation risk as wolves are known to select lines as travel corridors (Latham *et al.* 2011; Dickie 2015). For bison, however, the elevated predation risk represented by lines may be minimal as mature bison are difficult for wolves to kill and thus may not constitute primary prey for wolves (Smith *et al.* 2000). Nevertheless, the predation risk associated with linear features may partially explain gender differences in the strength of selection as female groups with calves are much more likely to be attacked by wolves (Carbyn & Trottier 1988).

Human activity negatively impacted bison selection of disturbance features. During the winter of 2013, the odds of female bison selecting an active disturbance feature were 29 times lower than the odds of selecting a non-active feature of the same age class. Avoidance of human

activity by free-ranging bison –and other ungulates – has been reported previously, although it is unclear as to whether this behaviour adversely affects bison population dynamics (Fortin & Andruskiw 2003; Borkowski *et al.* 2006; Leblond *et al.* 2013). Note that our analysis of bison response to human activity is restricted to females and it is unknown whether human activity affects males in a similar manner.

FUTURE CONSIDERATIONS

Effective wildlife management requires monitoring changes in a species' spatial distribution, population size and population trend (Williams *et al.* 2002, Sinclair *et al.* 2006). These population characteristics are necessary for assessing current population status and provide a basis for evaluating management decisions in an adaptive management framework (Holling 1978). In this report, we focused on the spatial distribution of Ronald Lake bison within and across biologically relevant seasons and specifically assessed biotic (e.g., land cover type) and abiotic (e.g., linear features) attributes influencing bison use of space. These analyses yielded season-specific predictive maps of habitat selection for both male and female bison (Appendix 6). Such maps should inform landscape-level planning within the range of the Ronald Lake herd and provide a foundation for monitoring potential changes in bison distribution. Monitoring distributional changes will require maintaining a sample of radio-collared individuals through time. We suggest that information from radio-collared individuals can also form the basis of a comprehensive monitoring program as such data can be used to assess other drivers of bison space use, facilitate estimation of herd size and trend, and provide information on factors limiting population abundance (i.e., cause-specific mortality). Below, we discuss further avenues of investigation to better understand the population dynamics and behaviour of Ronald Lake bison.

Spatial Distribution

A key outcome of our analyses is the consistent use of a discrete area by female bison at a time that coincides with likely calving (Fuller 1962). Calving areas are important habitats in ungulate population dynamics because calf survival through the neonate period (< 6 weeks of age) has high influence on subsequent calf recruitment (survival to 1 year of age; Gaillard *et al.* 2000; Keech *et al.* 2011). We suggest that a better understanding of the calving area would be beneficial, in particular confirmation of calving events and the identification of specific calving sites. Such information is currently lacking for the Ronald Lake herd and may require more intensive monitoring. More frequent GPS location acquisition may further assist in identifying the relative importance of finer-scale features (e.g., specific meadows) within the calving area. Also, because the post-partum lactation period has high energy requirements for female ungulates (Parker *et al.* 2009), an analysis of bison diet may be informative for identifying important forage species within the calving area.

Outside of calving, determining why specific seasonal areas are highly used by bison may require a better understanding of seasonal diets to adequately assess changes in forage quality

and abundance both within and across years. Additional seasonal drivers of space use by bison should also be investigated. In this report, we modelled bison use of space as a function of land cover classes and disturbance but other biotic and abiotic factors, such as spatial and temporal variation in insect abundance and access to thermal refugia, may influence bison spatial behaviour, potentially forcing temporal trade-offs with forage quantity and/or quality.

Bison response to anthropogenic features also warrants further investigation. Our results suggest that bison selected linear features in most seasons, which differs from the findings of Tan *et al.* (2015). This discrepancy suggests the need for further analyses, perhaps at a finer scale (e.g., step selection functions; Fortin *et al.* 2005), to better understand how bison are using linear features. Our results also highlighted that human activity on lines fundamentally alters bison response to these features. If human activity is expected to increase within bison range, then further analyses evaluating the potential zone of influence surrounding human activity may be warranted.

Our analyses of bison response to cutblocks were limited by data quality. Exploration of these data, however, suggests that the extent of cutblocks with the Ronald Lake bison range is more extensive than what is modelled by the Enhanced Wetland Classification. The extent of cutblock disturbance warrants a better understanding of how these features affect bison space use. Of interest is whether cutblocks function similar to recent forest fires as both types of disturbance fundamentally alter vegetation structure, potentially increasing the amount of early seral habitat favourable to a grazing species like bison. Further effort should therefore be made to enhance the quality of cutblock data.

Population Size

Reliable estimates of population size represent a key metric for evaluating a population's ability to withstand natural and human-mediated disturbances (Wittmer *et al.* 2010). In 2013, a minimum population count was conducted for the Ronald Lake herd (Government of Alberta 2013). While this count can give an indication of current herd size, the lack of uncertainty surrounding minimum population counts impairs assessing changes in population size when comparing survey results. Future assessments of population size should employ a probabilistic sampling design that accounts for imperfect detection of all individuals and produces estimates of parameter uncertainty. A transect-based design using distance sampling has been successfully used to estimate population size of wood bison in a relatively cost-effective manner (Boulanger 2014). Mark-resight methods have also been used to estimate population size of wood bison (Hegel *et al.* 2012), an approach that may be advantageous for future size estimates of the Ronald Lake herd if a sample of radio-collared individuals is maintained. Note that annual estimates of population size are not necessary to adequately inform assessments of bison demography; rather, bi- or tri-annual estimates may be sufficient when combined with other sources of demographic data (Boulanger *et al.* 2015).

Population Trend

Evaluating population trend (i.e., the magnitude and directional of population size through time) is a fundamental objective of wildlife management and can be estimated by direct and/or indirect methods. Estimating trend directly entails comparing population size estimates from sequential surveys while indirect methods rely on age ratios and vital rates to infer trend. In ungulates, trend is often indirectly estimated using calf:cow ratios and adult female survival (Hatter & Bergerud 1991). Radio-collar data to date from the Ronald Lake herd may provide initial estimates of annual adult female survival. However, evaluating changes in population trend in response to increasing anthropogenic disturbance will require longer-term monitoring, which may necessitate the deployment of additional collars with longer expected lifespans. For this purpose, recently developed radio-collars that provide two locations per day yet last up to 5 years may be appropriate. These collars also communicate remotely via satellite, allowing for the rapid investigation of mortalities to determine potential causes.

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APPENDIX 1: SUMMARY STATISTICS OF GPS RADIO-COLLAR FIX RATES

Prior to data analyses, we assessed the performance of bison GPS radio-collars in terms of their consistency in acquiring GPS locations (fix rate) and the length of data collection (Table A1.1). This assessment was done after the first two weeks of data were removed and the remaining raw GPS data had been screened for potential errors (see *Bison Spatial Data* in main text).

Table A1. 1: Summary statistics of GPS location data by individual bison after data screening procedures. The number of time steps refers to the maximum number of GPS fixes that would have been recorded given the length of time the collar collected data.

Animal ID	Sex	No. of Time Steps	No. of Missed Fixes	Begin Date	End Date	Fix Rate
33912	F	13842	756	4/8/2013	8/21/2015	0.95
33913	F	13842	359	4/8/2013	8/21/2015	0.97
33914	F	13173	640	4/8/2013	7/10/2015	0.95
33915	F	3236	249	4/6/2013	10/25/2013	0.92
33916	F	2255	254	4/8/2013	8/27/2013	0.89
33917	F	13883	414	4/6/2013	8/21/2015	0.97
33919	F	13884	593	4/6/2013	8/21/2015	0.96
33920	F	12528	1085	4/6/2013	5/29/2015	0.91
33921	F	11929	5509	4/6/2013	4/21/2015	0.54
33923	F	13883	620	4/6/2013	8/21/2015	0.96
33924	F	6868	1983	4/30/2014	7/3/2015	0.71
35447	F	8064	387	4/4/2014	8/21/2015	0.95
35448	F	8033	564	4/6/2014	8/21/2015	0.93
35449	F	8033	379	4/6/2014	8/21/2015	0.95
35450	F	5088	190	4/6/2014	2/18/2015	0.96
35451	F	8032	324	4/6/2014	8/21/2015	0.96
35452	F	8033	483	4/6/2014	8/21/2015	0.94
35453	F	7436	203	4/6/2014	7/15/2015	0.97
35454	F	8033	559	4/6/2014	8/21/2015	0.93
35455	F	8001	297	4/8/2014	8/21/2015	0.96
35456	F	7432	286	4/6/2014	7/15/2015	0.96
35462	M	4827	37	3/28/2014	1/23/2015	0.99
35463	M	2855	295	3/28/2014	9/22/2014	0.90
35464	M	1407	43	3/28/2014	6/24/2014	0.97
35465	M	615	2	3/28/2014	5/5/2014	1.00
35466	M	5857	409	3/28/2014	3/29/2015	0.93
Mean						0.92
Minimum						0.54
Maximum						1.00

APPENDIX 2: MOVEMENT BEHAVIOUR OF FEMALE WOOD BISON DURING MAY AND JUNE, 2013 - 2015

We assessed female movement during May and June to identify the calving season for Ronald Lake wood bison. The Preliminary Summary Report (Tan *et al.* 2015) demonstrated that female bison migrate in late May to the northwest portion of the study area and congregate in a discrete area during June to calve. To identify this area, we created a minimum convex polygon (MCP) around bison GPS locations starting when the last female had completed her migration and all females were therefore highly aggregated (see Fig. 8 in main text). This MCP included all GPS locations across all years (2013 – 2015). We defined the start of calving as the date when the last female migrated to and settled in the calving area (Figs. A2.1 – A2.3) and the end of calving when the last female departed the calving area (Figs. A2.4 – A2.6).

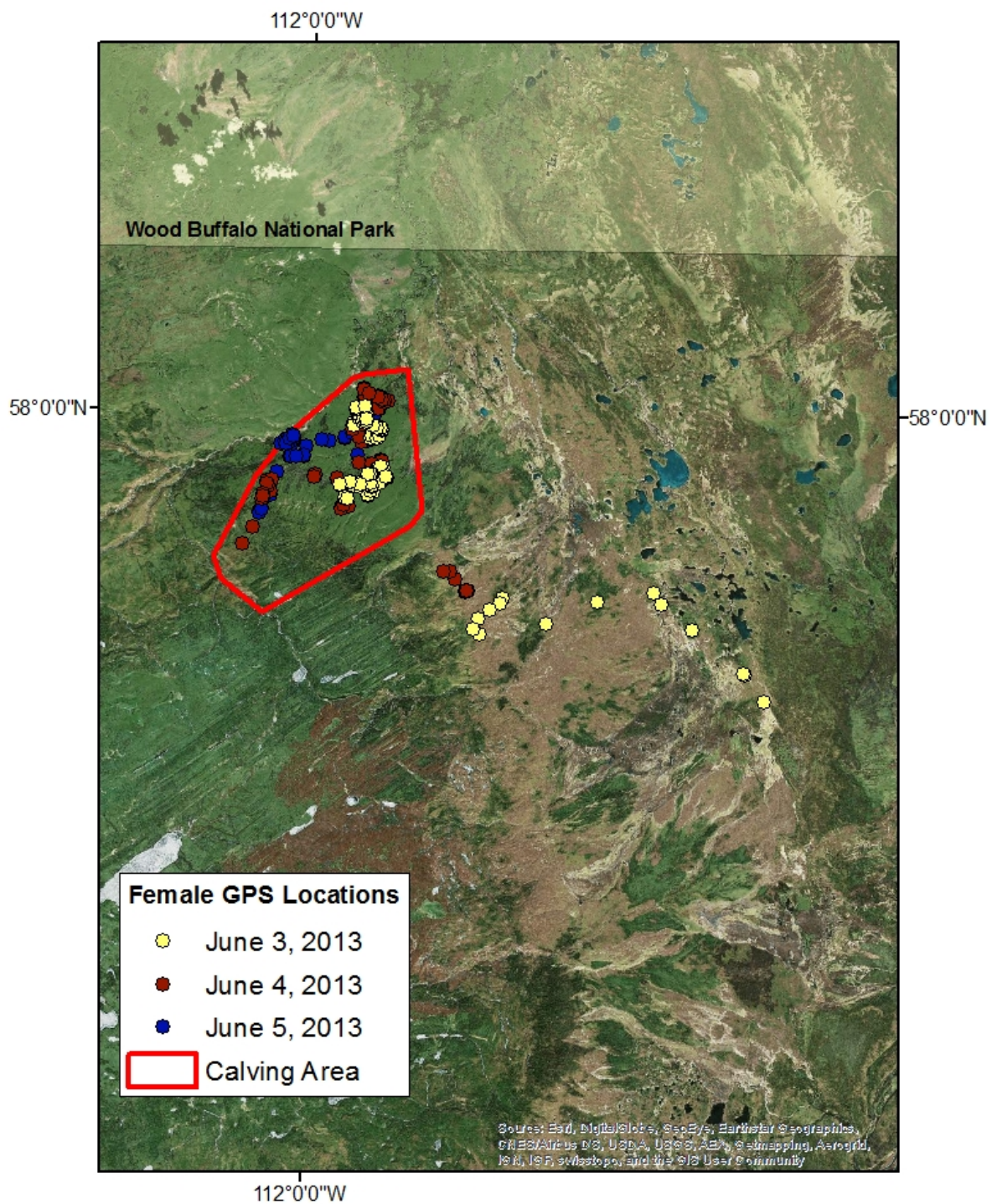


Figure A2. 1: Movements of Ronald Lake female bison during June 2013. The last female settled in the calving areas by June 5.

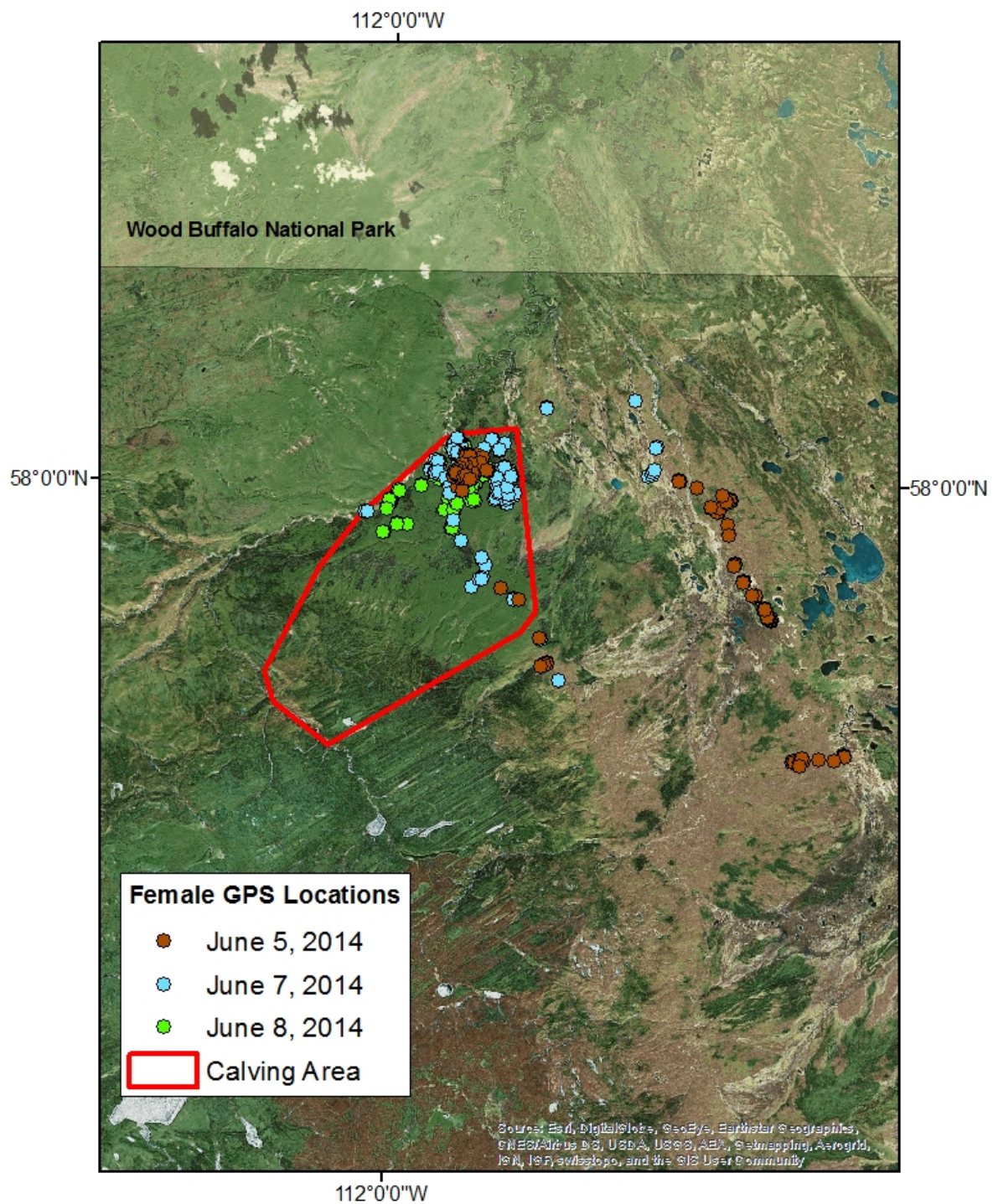


Figure A2. 2: Movements of Ronald Lake female bison during June 2014. The last female settled in the calving area by June 8.

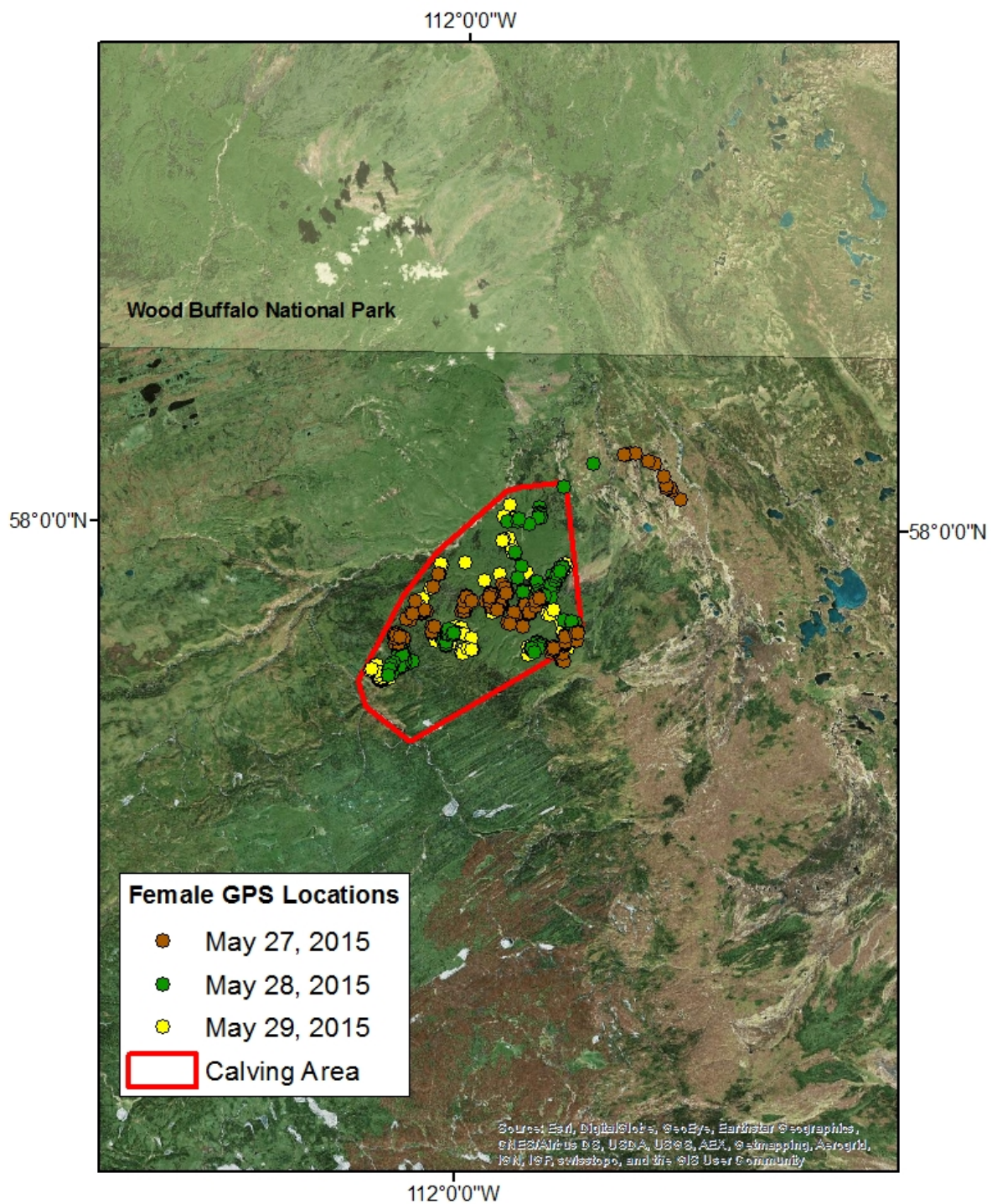


Figure A2. 3: Movements of Ronald Lake female bison during May 2015. The last female settled in the calving area by May 29.

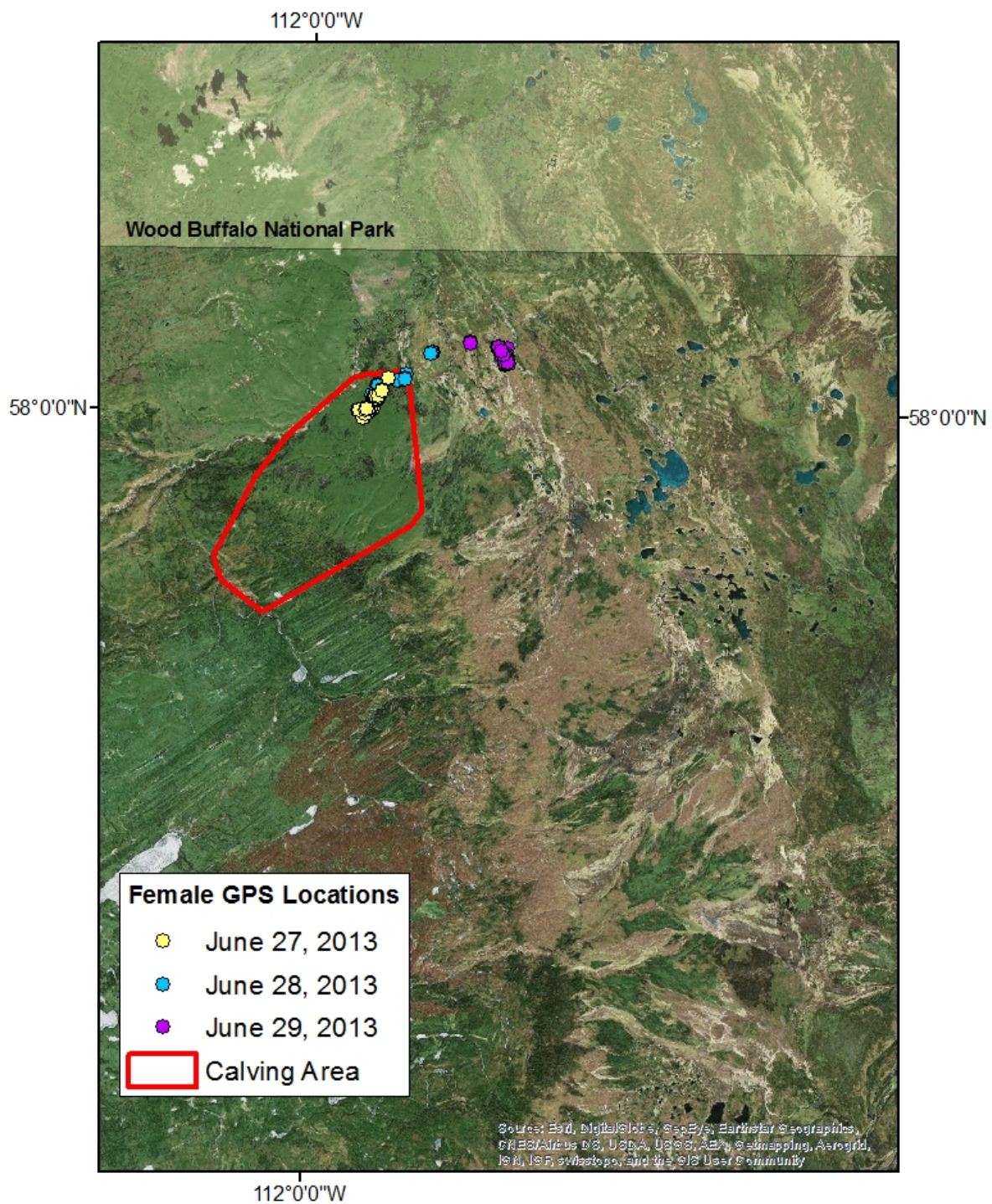


Figure A2. 4: Movements of Ronald Lake female bison during June 2013. The last female departed the calving area on June 29.

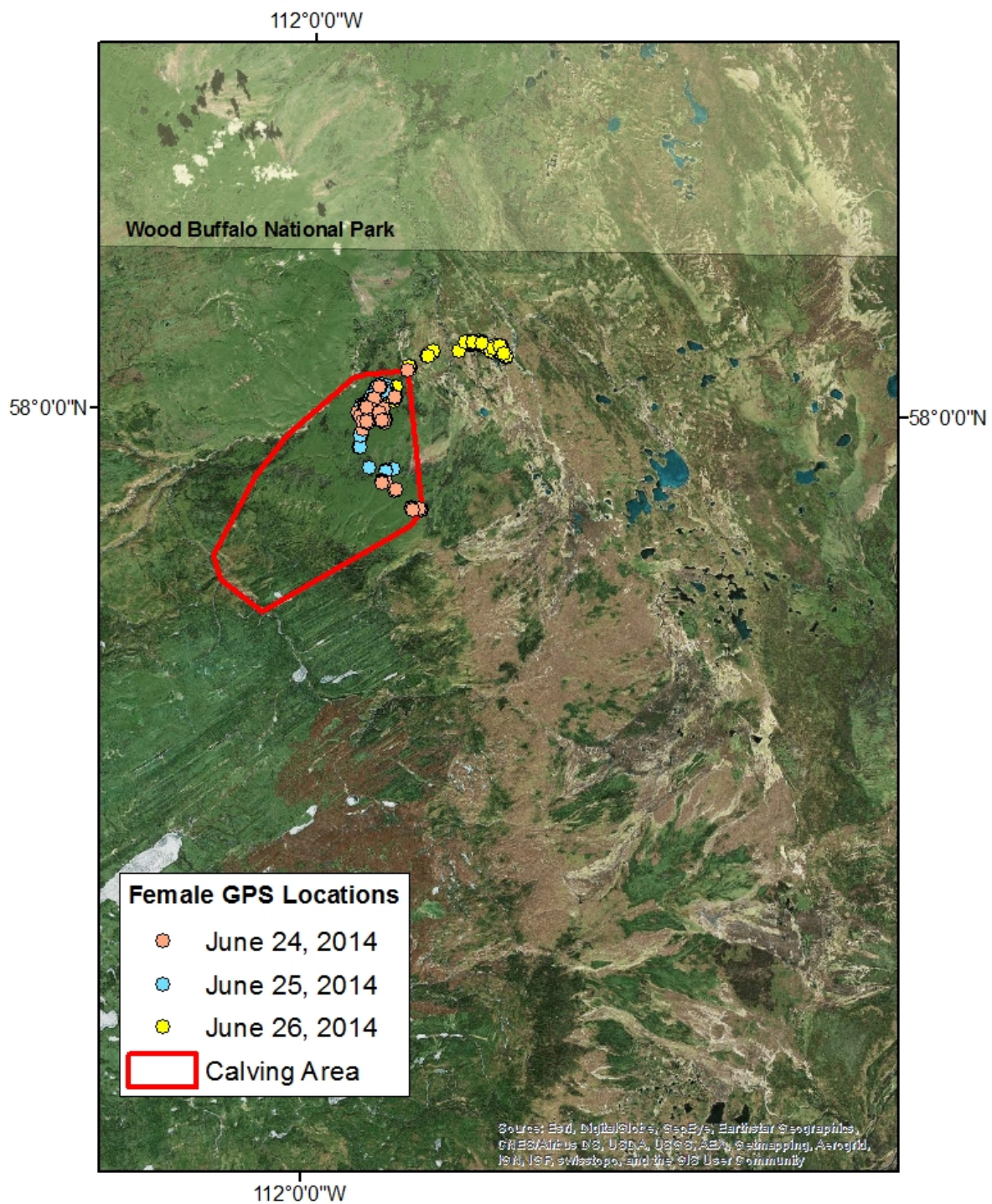


Figure A2. 5: Movements of Ronald Lake female bison during June 2014. The last female departed the calving area on June 26.

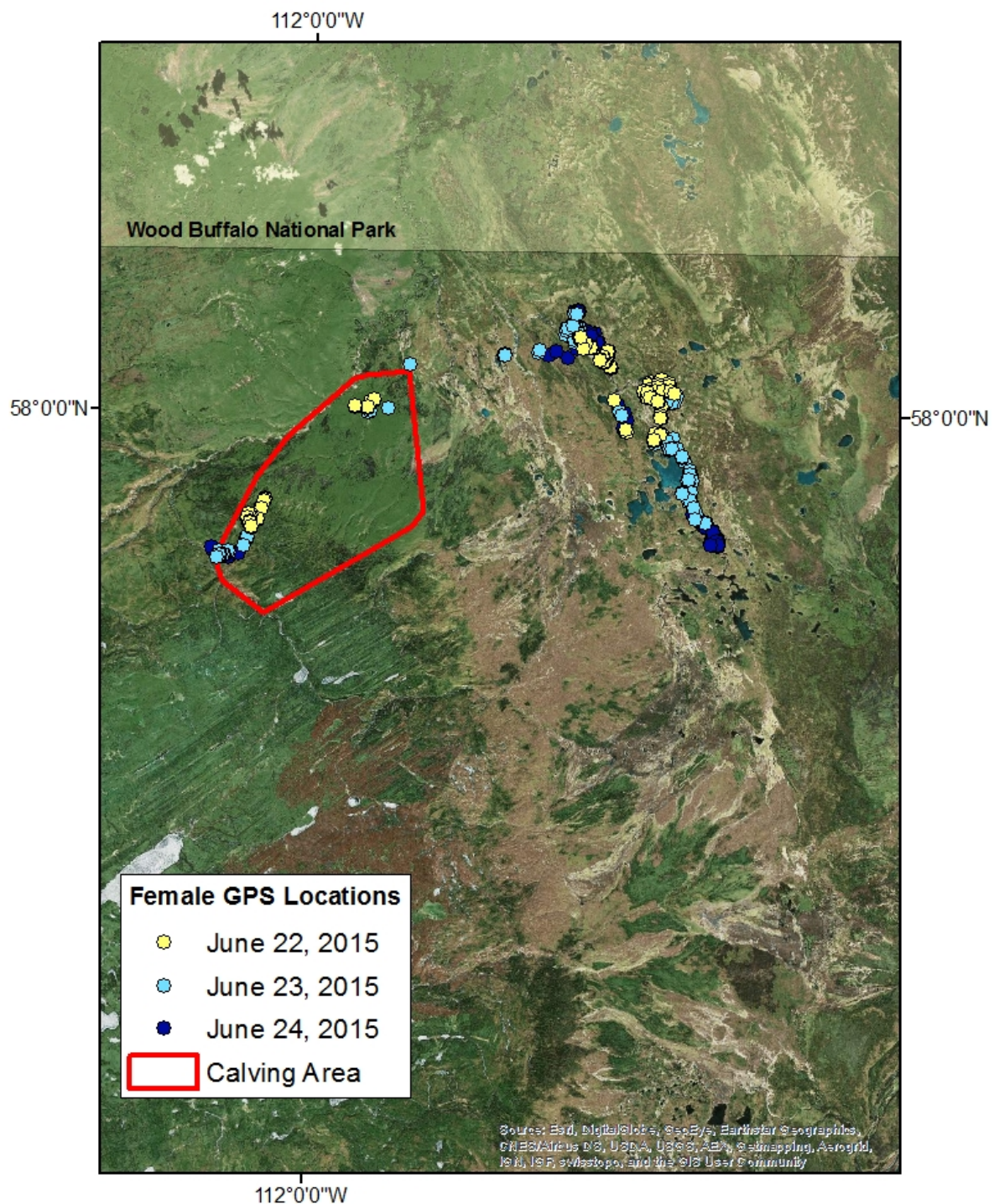


Figure A2. 6: Movements of Ronald Lake female bison during June 2015. The last female departed the calving area on June 24.

APPENDIX 3: SENSITIVITY OF HOME RANGE ESTIMATOR TO MONITORING TIME

We conducted a sensitivity analysis to determine the amount of time (in months) required for estimates of annual home range size for bison to stabilize. Because of our data screening procedures (see *Bison Spatial Data* in main text) and the timing of radio-collar deployment (late March), the starting month for all individual bison was April. For habitat selection analyses, annual home ranges were characterized by 95% utilization distributions (UDs). We used piecewise linear regression to determine the monitoring time required for UD size to reach an asymptote (Fig. A3.1).

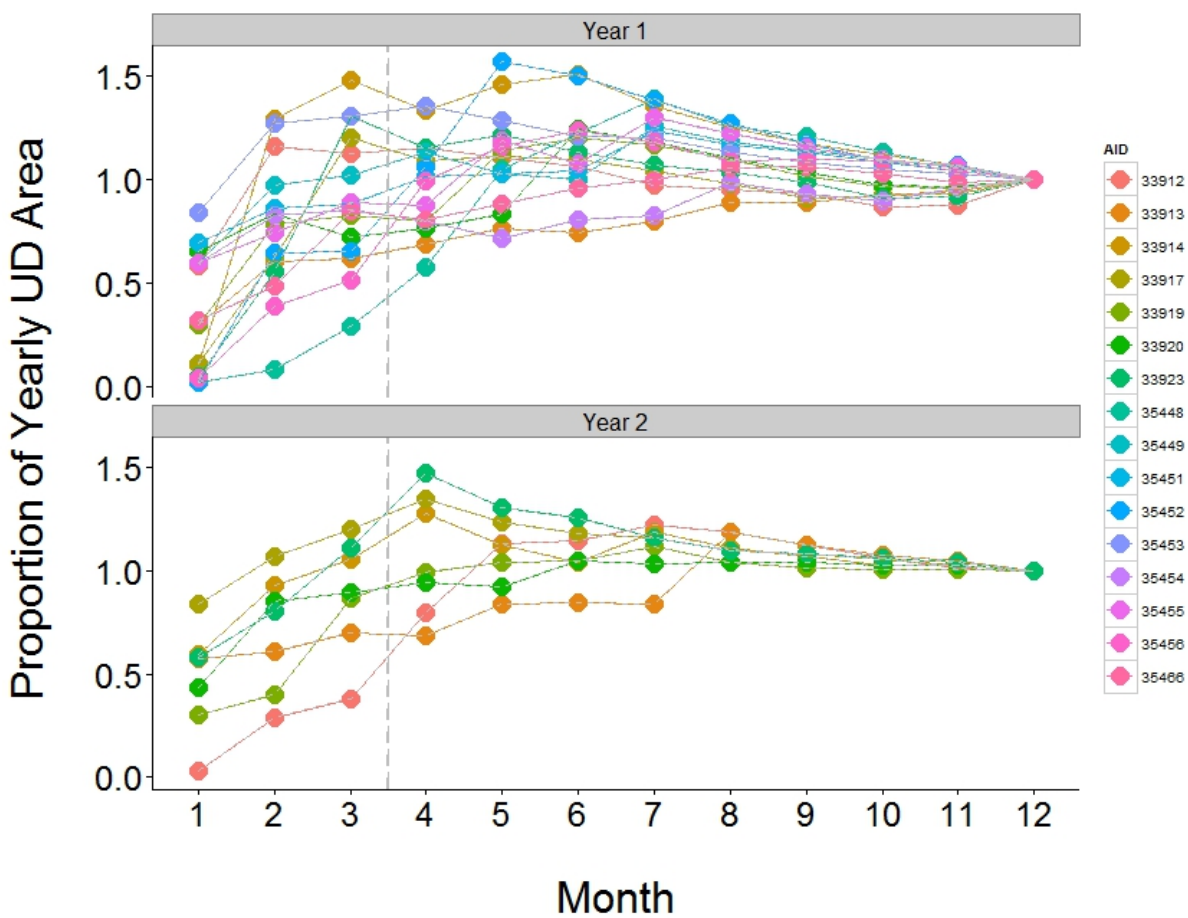


Figure A3. 1: Sensitivity analysis to determine the minimum number of months required for estimating annual home range size of wood bison in the Ronald Lake herd of northeastern Alberta. From break point regression analysis, the grey dotted line indicates the point where home range size reaches an asymptote (break point = 3.5 months, SE = 0.2, $p < 0.001$).

APPENDIX 4: RANDOM POINT SENSITIVITY ANALYSIS

We conducted sensitivity analyses to determine the number of random points to adequately characterize availability within bison home ranges. We used the 95% probability contour of utilization distributions to delineate bison home ranges. To identify the number of random points where parameter estimates for land cover stabilized, we conducted repeated RSFs using the summer / fall data, varying the number of random points used each time (range: 200 – 20,000). This analysis suggested that parameter estimates stabilized at c.a. 5000 random points (Fig. A4.1).

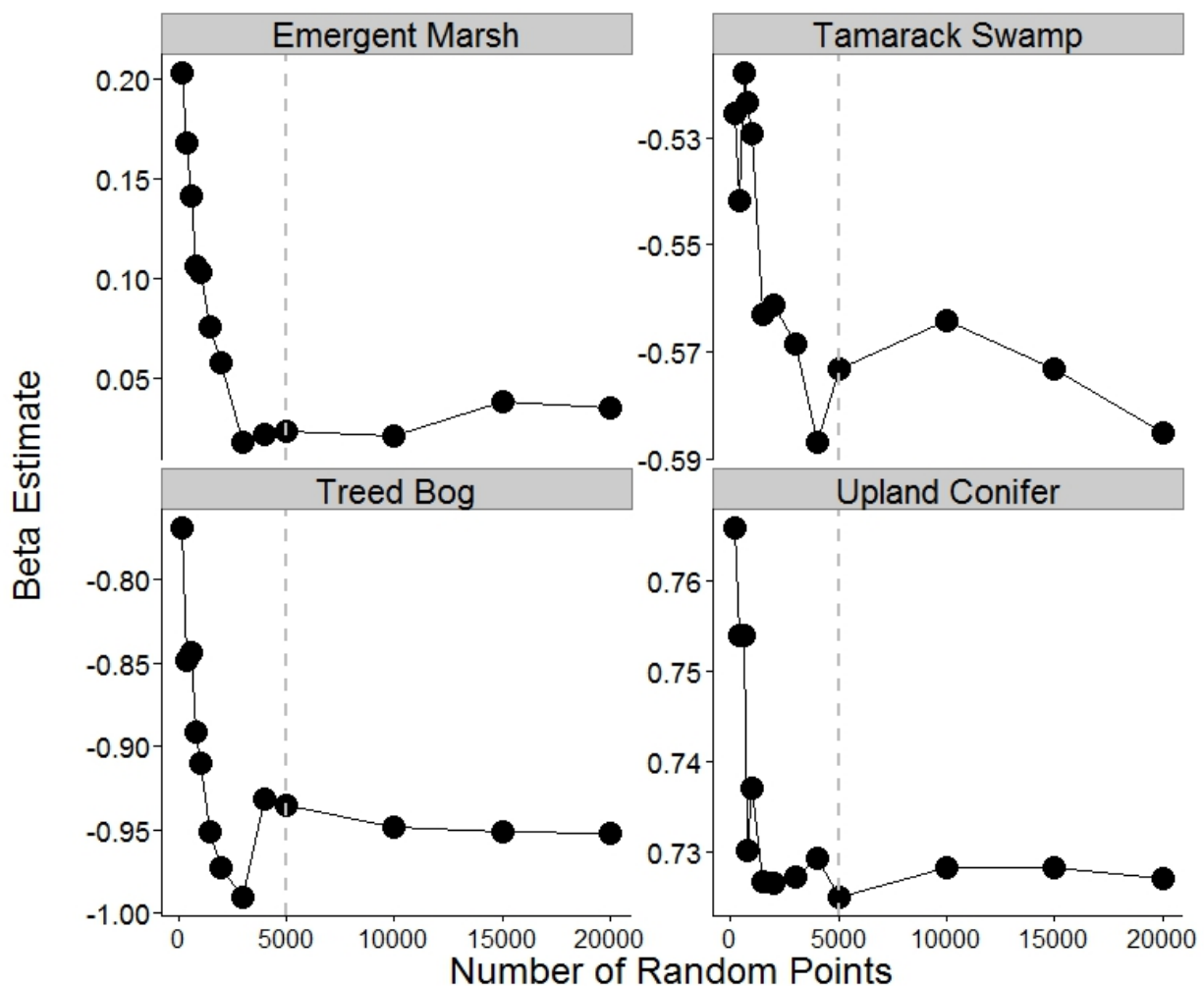


Figure A4. 1: Sensitivity analysis to determine the number of random points required to adequately characterize availability within bison home ranges. Parameter (Beta) estimates for land cover types stabilized at c.a. 5000 points (grey dashed line).

APPENDIX 5: SEASONAL RANGES OF RONALD LAKE WOOD BISON

We estimated seasonal range use of Ronald Lake wood bison by constructing minimum convex polygons (MCPs) around all GPS locations falling within the seasonal periods defined in the main text. Here, we show population-level MCPs by year for spring, summer/fall and winter and further include the cumulative MCP of the calving area as a reference (Figs. A5.1 – A5.3).

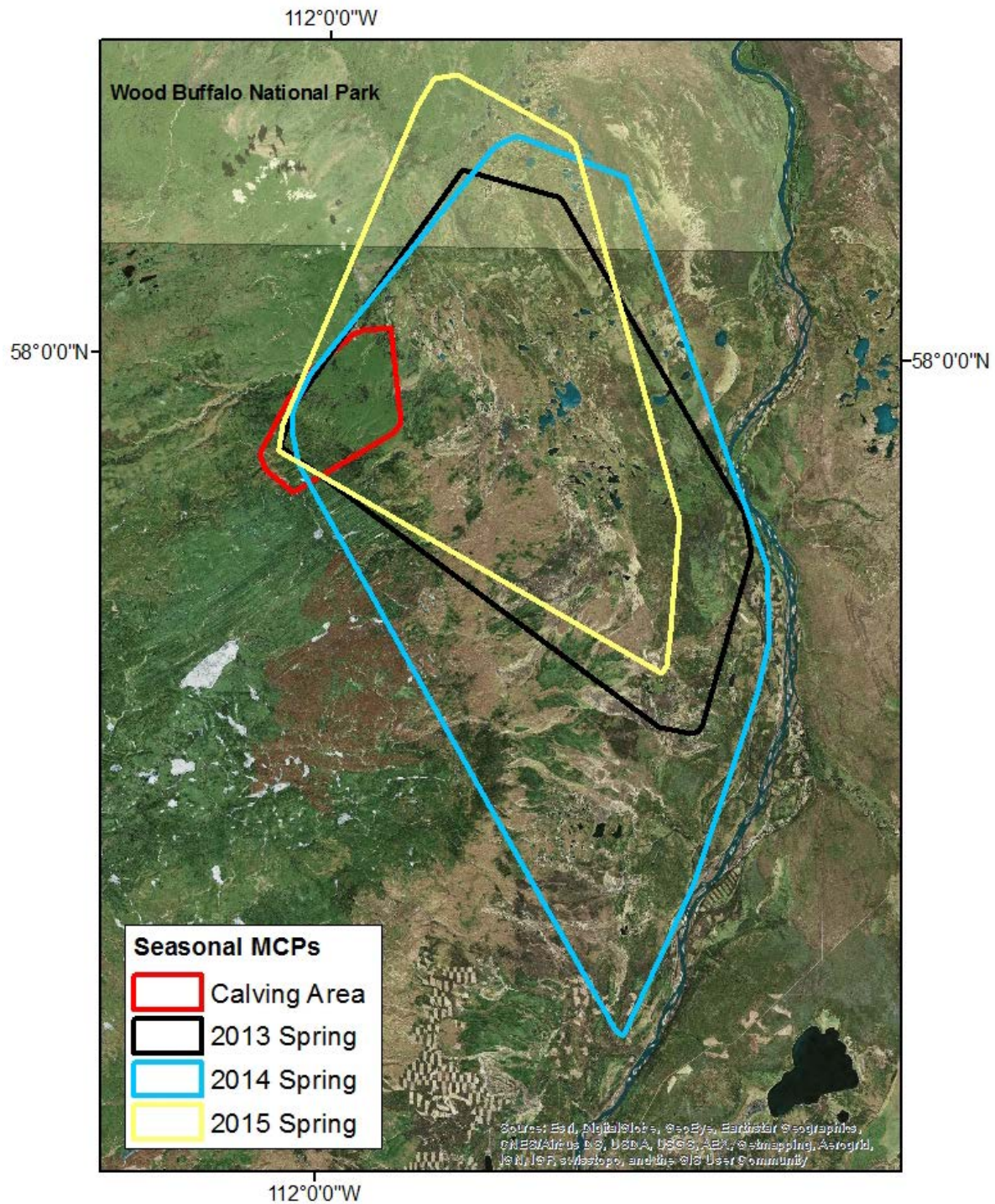


Figure A5. 1: Space use by Ronald Lake wood bison during spring (c.a. mid-April to end-May). Minimum convex polygons (MCPs) were constructed yearly using all bison GPS locations falling within the spring period. The calving area MCP is shown for reference.

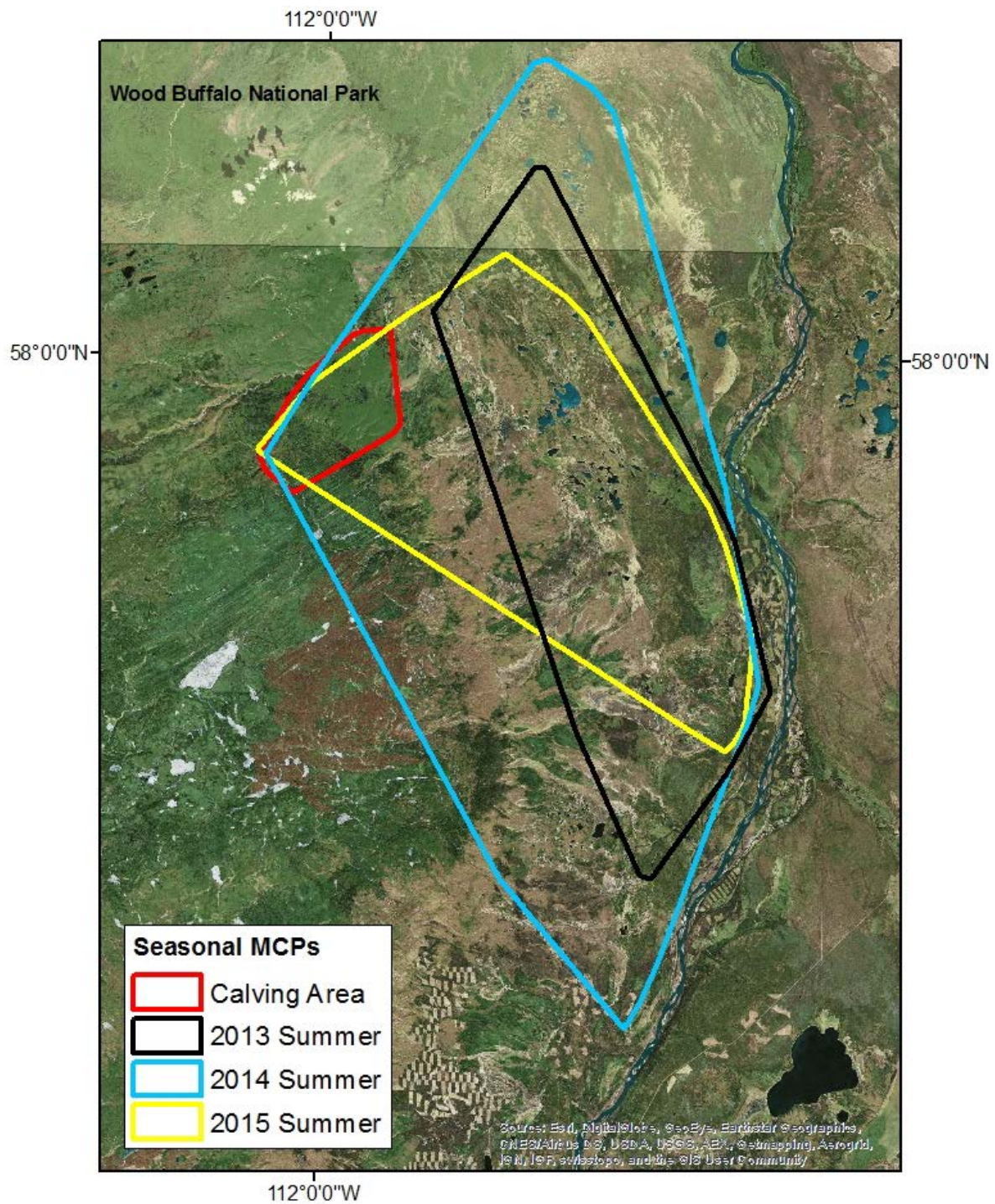


Figure A5. 2: Space use by Ronald Lake wood bison during summer and fall (c.a. end-June to early- November). Minimum convex polygons (MCPs) were constructed yearly using all bison GPS locations falling within the summer / fall period. The calving area MCP is shown for reference.

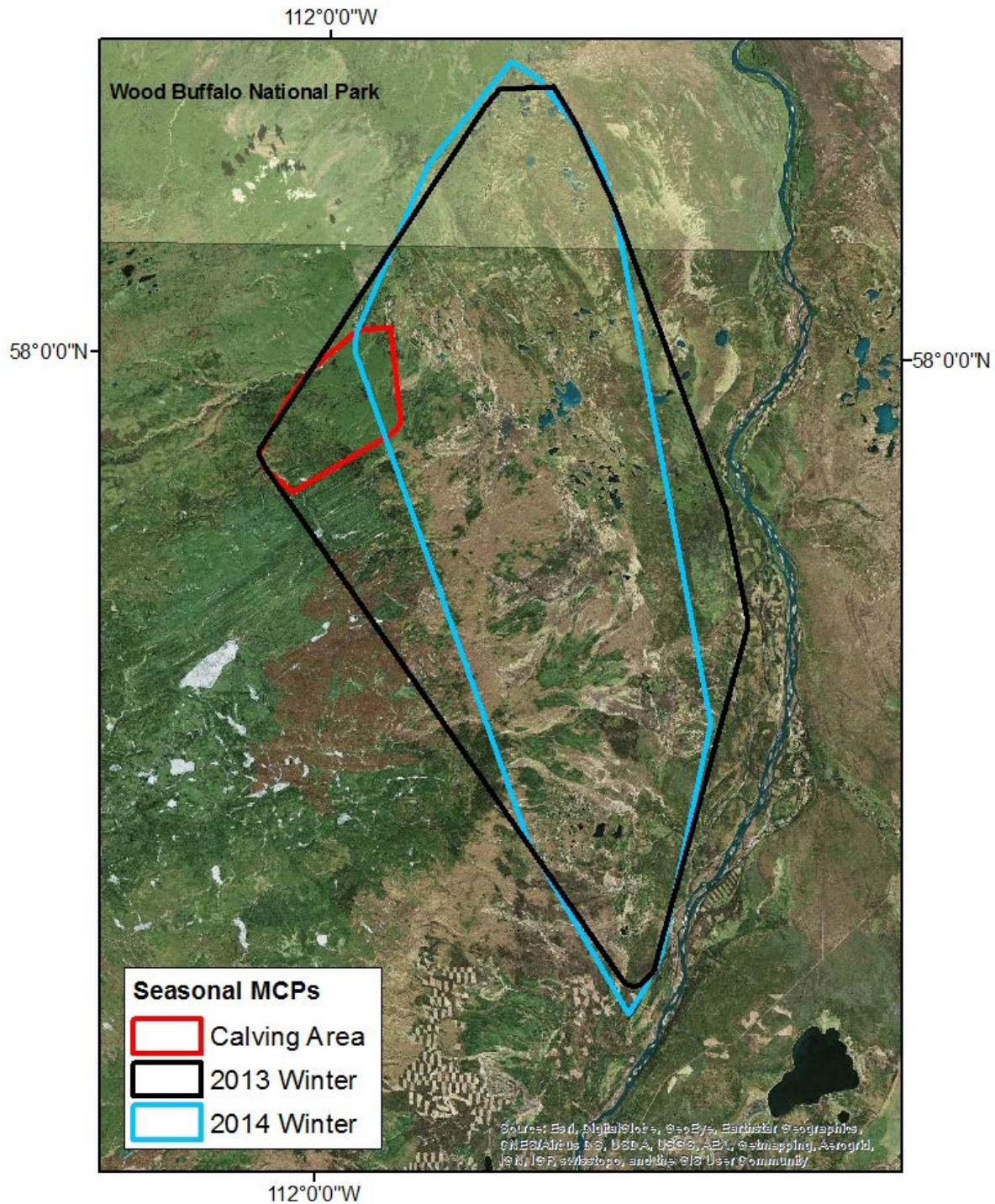


Figure A5. 3: Space use by Ronald Lake wood bison during winter (c.a. early-November to mid-April). Minimum convex polygons (MCPs) were constructed yearly using all bison GPS locations falling within the winter period. The calving area MCP is shown for reference.

APPENDIX 6: PREDICTIVE MAPS OF SEASONAL HABITAT SELECTION BY MALE AND FEMALE WOOD BISON

We used the output from seasonal resource selection functions (RSFs) to generate spatial predictions (i.e., maps) of habitat selection by male and female wood bison of the Ronald Lake herd (Figs. A6.1 – A6.8). Predictions are constrained to the maximal extent of bison range use from April 2013 – August 2015, as defined by a 100% minimum convex polygon surrounding all bison GPS locations recorded during that time period. Note that predictions may only be applicable to each gender's season-specific extent of use. We further highlight the following caveats:

1. Each predictive map represents a continuum of relative habitat suitability. It does not represent the absolute probability that a bison will occur at a given location.
2. Even in areas with apparently high suitability, the actual probability of bison occurrence may be relatively low because bison groups likely occur at low densities throughout their range.
3. Bison can – and probably do – occur in areas with relatively low suitability.

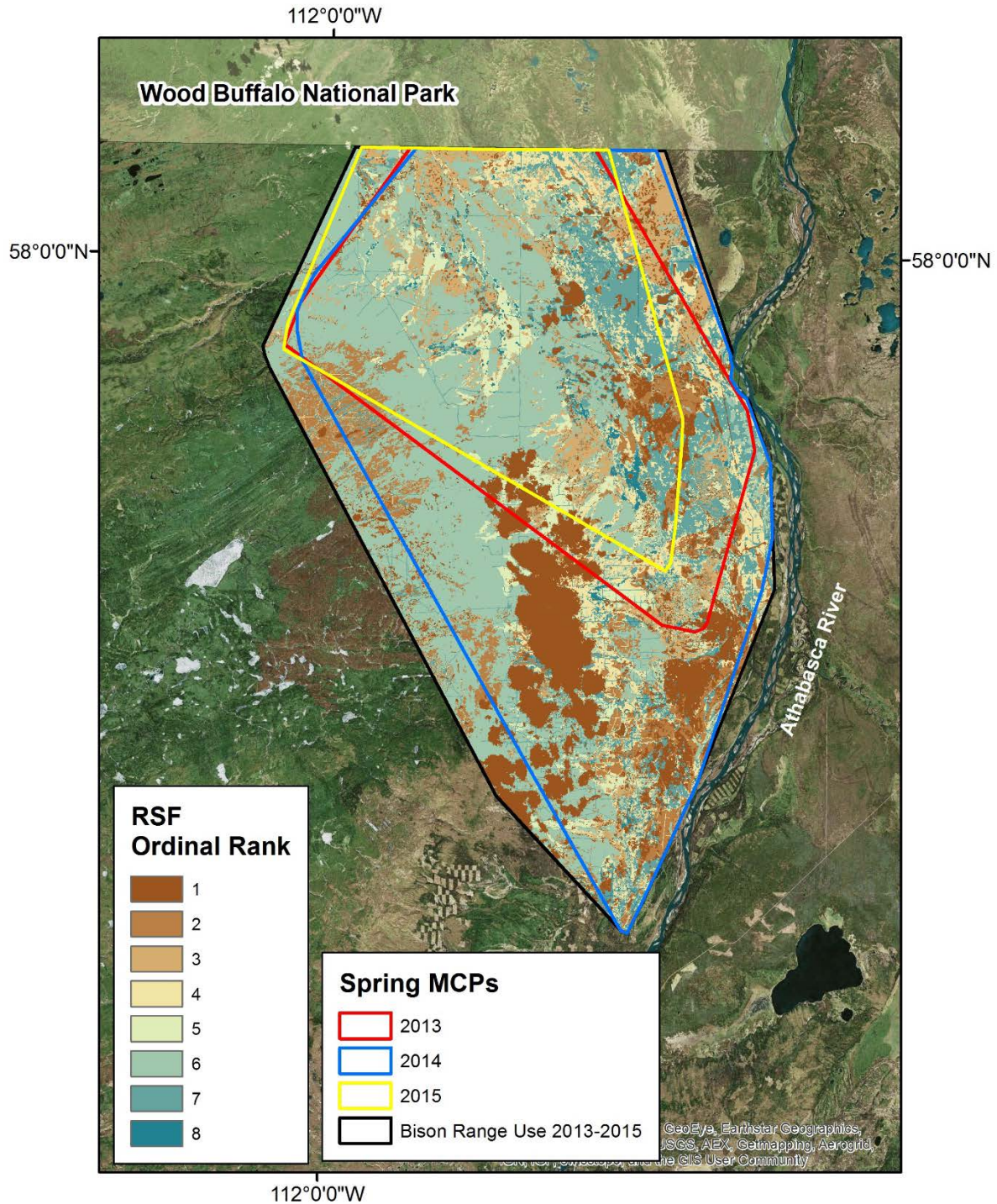


Figure A6.1: Spatially explicit predictions of habitat selection by female wood bison of the Ronald Lake herd during the spring (c.a. mid-April to early-June). Annual 100% minimum convex polygons (MCPs) surrounding bison GPS locations (males and females) recorded during the spring are shown for reference. Females showed disproportionate use of areas with RSF ordinal rank values ≥ 7 .

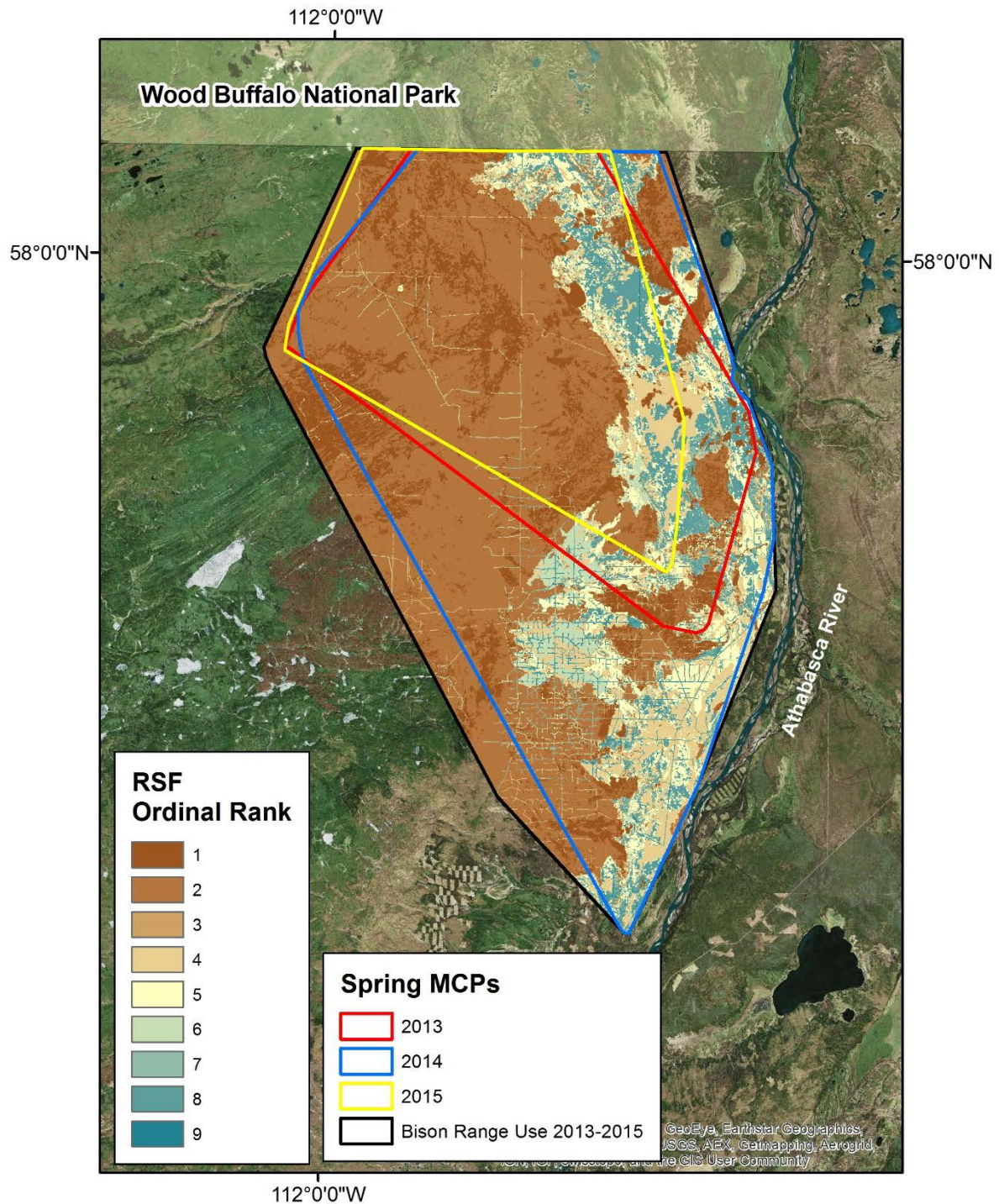


Figure A6.2: Spatially explicit predictions of habitat selection by male wood bison of the Ronald Lake herd during the spring (c.a. mid-April to early-June). Annual 100% minimum convex polygons (MCPs) surrounding bison GPS locations (males and females) recorded during the spring are shown for reference. Males showed disproportionate use of areas with RSF ordinal rank values ≥ 7 .

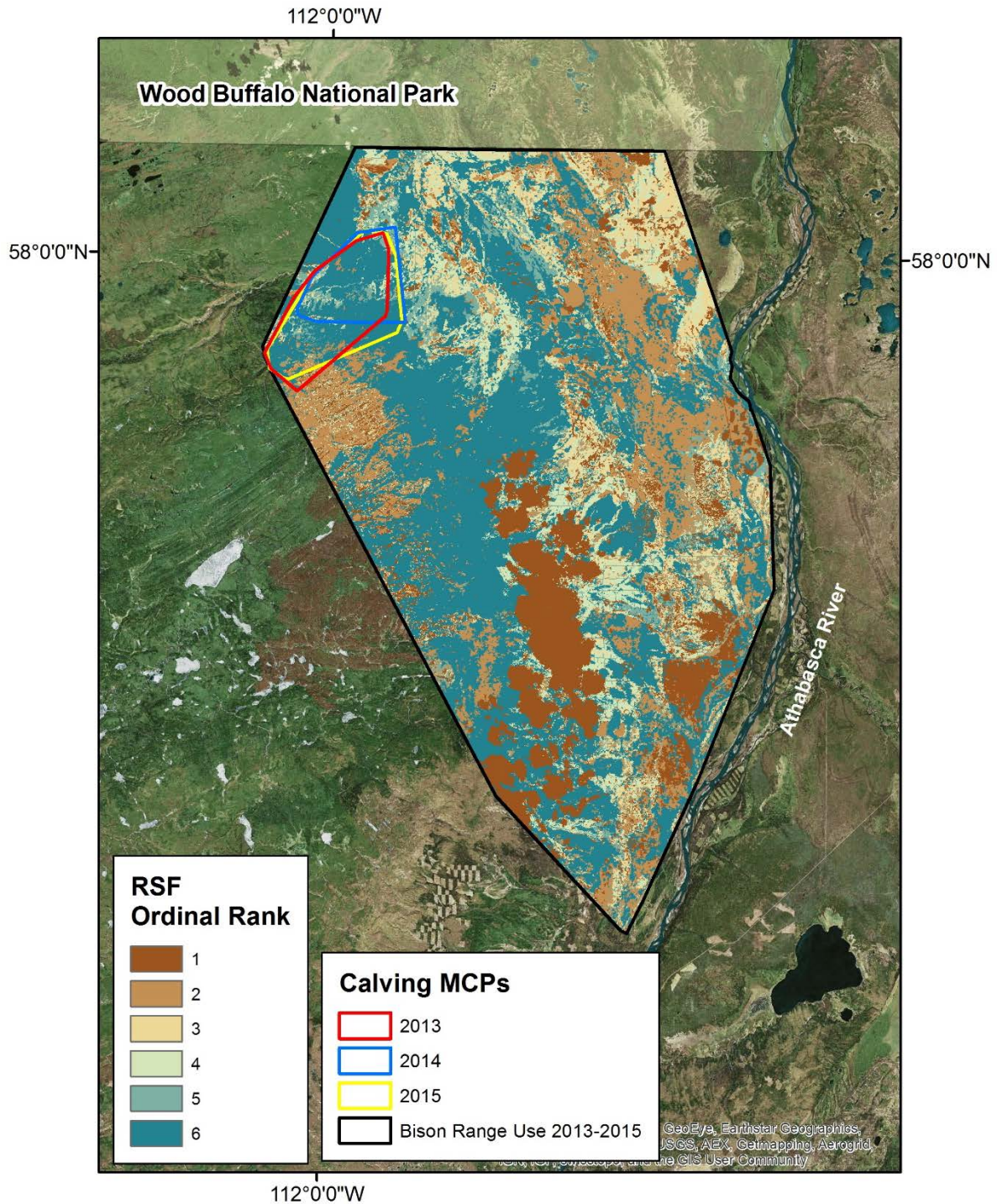


Figure A6.3: Spatially explicit predictions of habitat selection by female wood bison of the Ronald Lake herd during calving (c.a. early-June to end-June). Annual 100% minimum convex polygons (MCPs) surrounding female bison GPS locations recorded during calving are shown for reference. Females showed disproportionate use of areas with RSF ordinal rank values ≥ 6 .

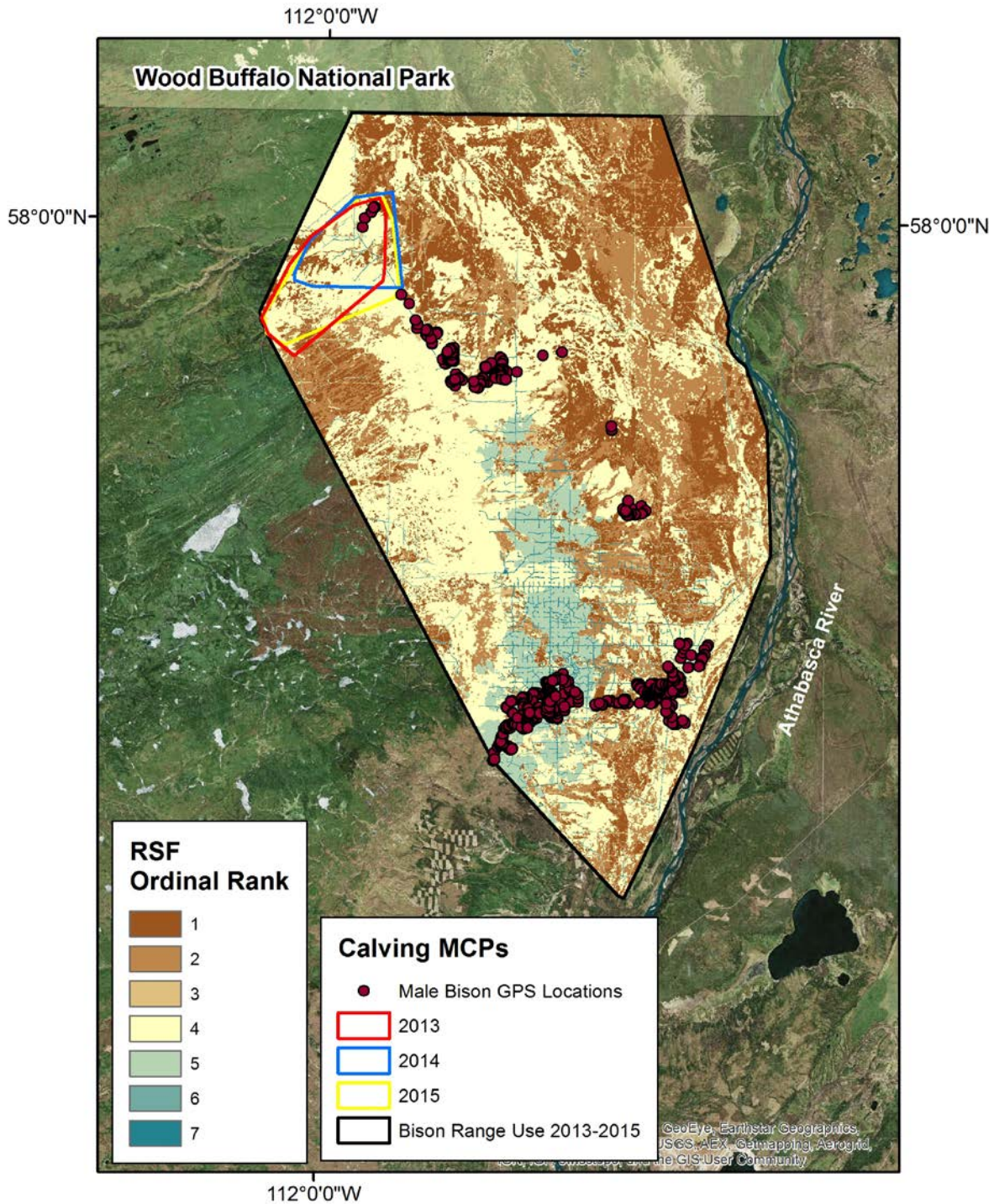


Figure A6.4: Spatially explicit predictions of habitat selection by male wood bison of the Ronald Lake herd during calving (c.a. early-June to end-June). Annual 100% minimum convex polygons (MCPs) surrounding female bison GPS locations recorded during calving are shown for reference. Because males are predominantly segregated from females at calving, GPS locations for male bison area also shown. Males disproportionately used of areas with RSF ordinal rank values ≥ 6 .

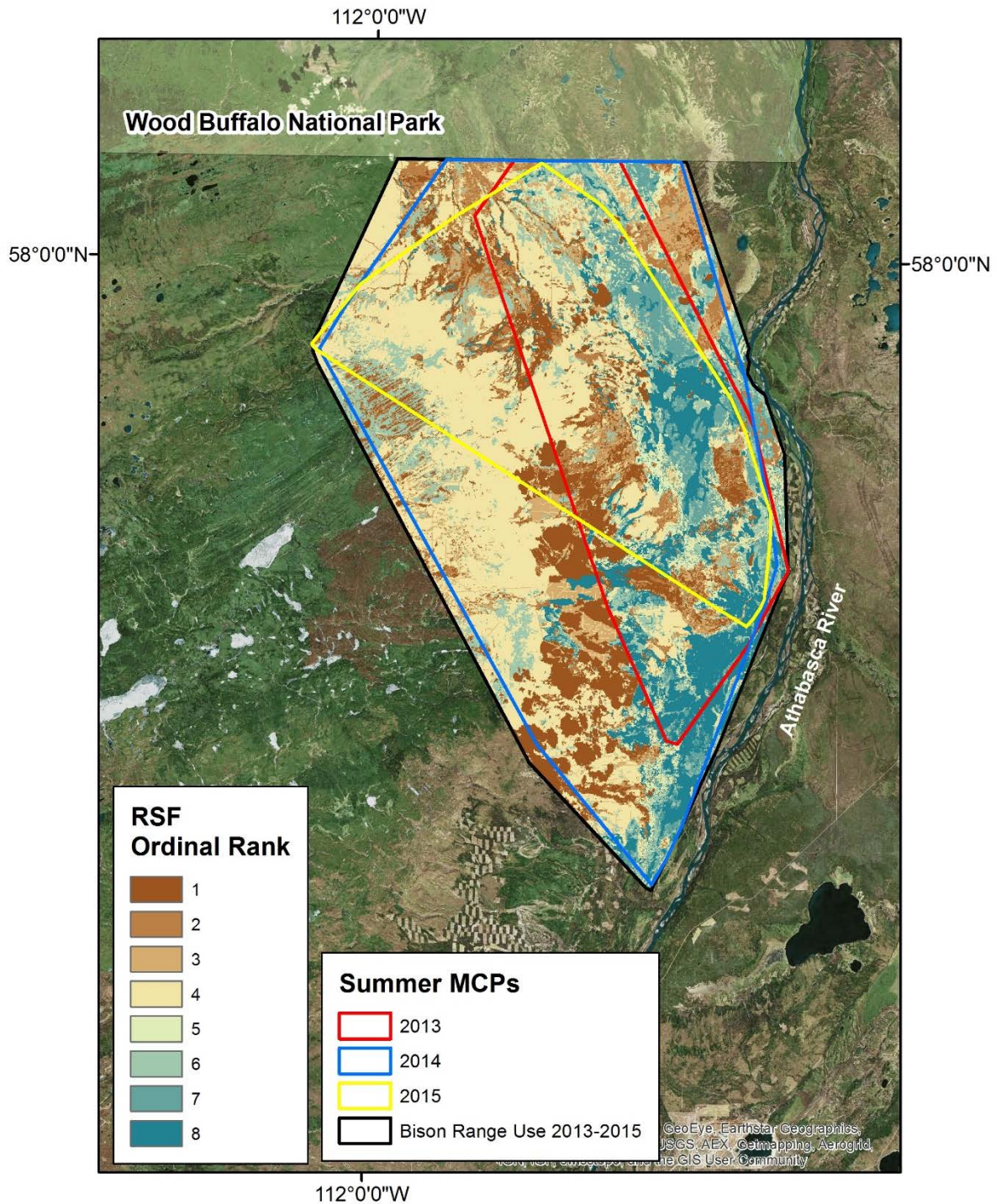


Figure A6.5: Spatially explicit predictions of habitat selection by female wood bison of the Ronald Lake herd during the summer and fall (c.a. early-November to end-October). Annual 100% minimum convex polygons (MCPs) surrounding all bison GPS locations (female and male) recorded during summer and fall are shown for reference. Females showed disproportionate use of areas with RSF ordinal rank values ≥ 5 .

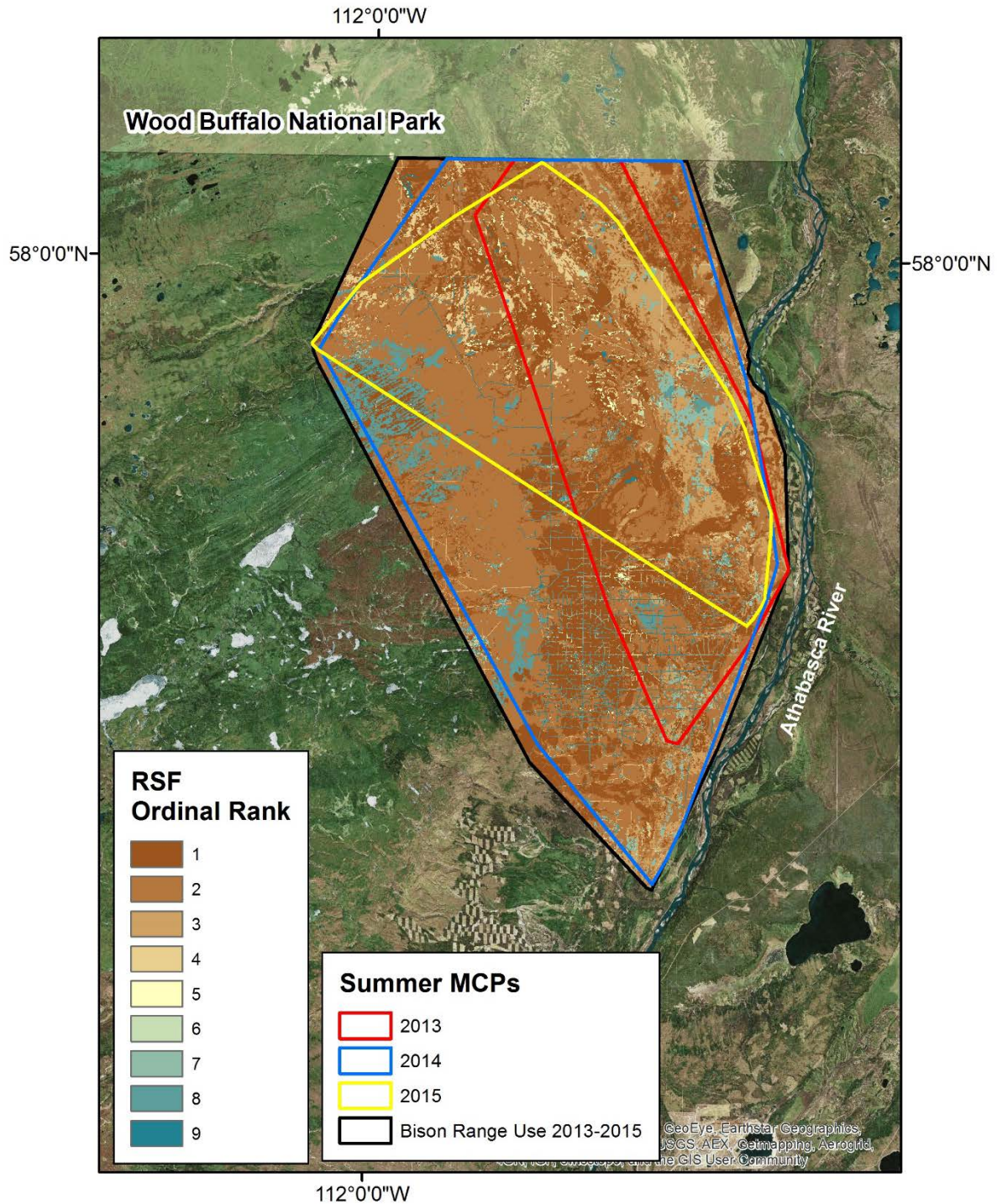


Figure A6.6: Spatially explicit predictions of habitat selection by male wood bison of the Ronald Lake herd during the summer and fall (c.a. early-November to end-October). Annual 100% minimum convex polygons (MCPs) surrounding all bison GPS locations (female and male) recorded during summer and fall are shown for reference. Males showed disproportionate use of areas with RSF ordinal rank values ≥ 8 .

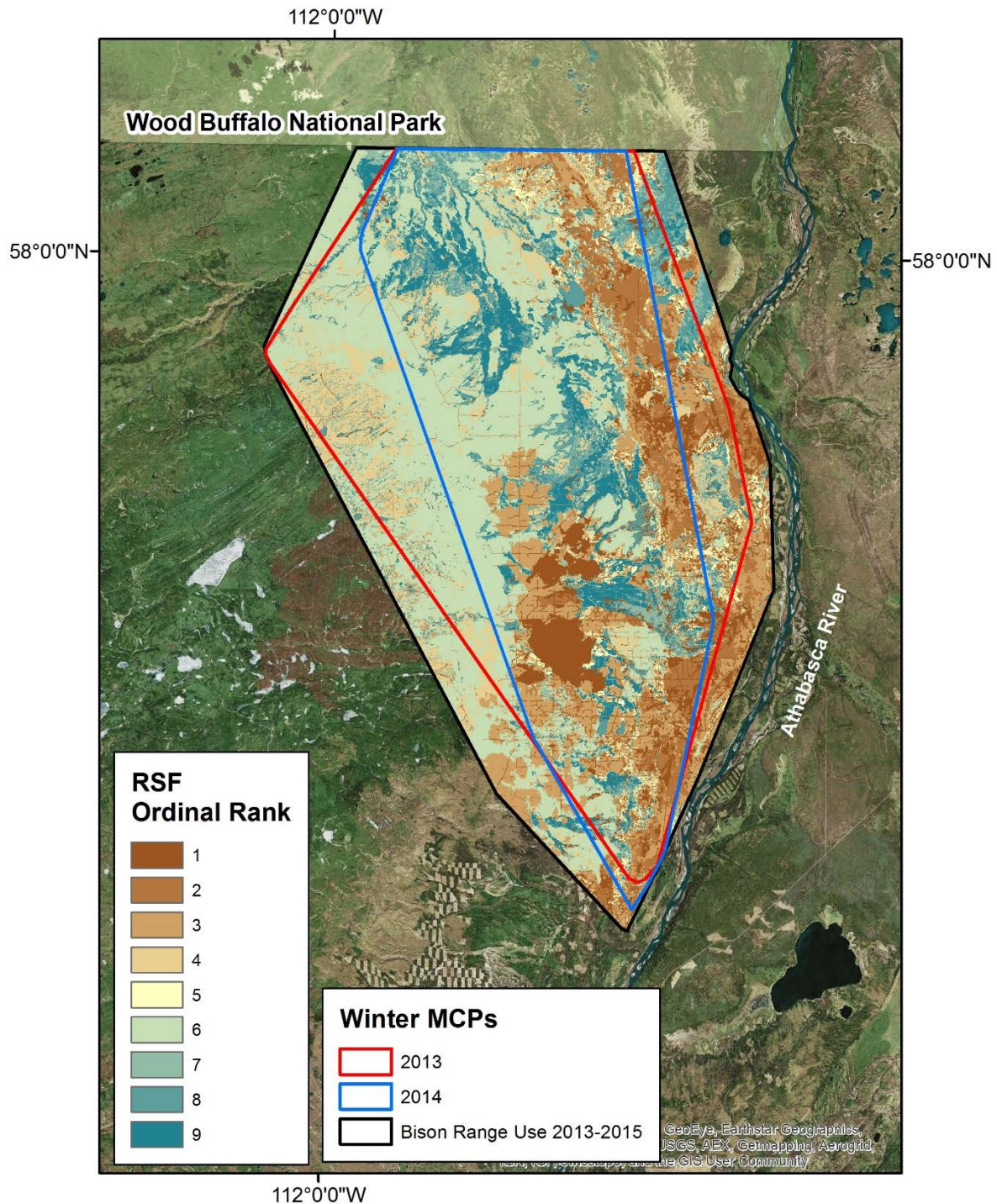


Figure A6.7: Spatially explicit predictions of habitat selection by female wood bison of the Ronald Lake herd during the winter (c.a. early-November to mid-April). Annual 100% minimum convex polygons (MCPs) surrounding all bison GPS locations (female and male) recorded during winter are shown for reference. Females showed disproportionate use of areas with RSF ordinal rank values ≥ 8 .

