Determining the influence of snow and temperature on the movement rates of wood bison (*Bison bison athabascae*)

A.H.C. Sheppard, L.J. Hecker, M.A. Edwards, and S.E. Nielsen

Abstract: Snow is understood to limit wildlife movements, often being the most important determinant of winter movement for animals in the boreal forest. However, the combined effect of snow and temperature on the movement ecology of animals at high latitudes is less understood. Here, we used GPS-collar data from a small population of wood bison (*Bison bison athabascae* Rhoads, 1898) in northeastern Alberta, Canada, to develop a series of generalized additive mixed models characterizing the effect of cumulative snow depth, daily change in snow depth, and temperature on movement rates. Our most supported model included cumulative snow depth, temperature, and day of winter. Bison movements decreased in the first 75 days of winter during snow accumulation and dramatically increased in the final 14 days of winter during snow melt. Cumulative snow depth, not daily change in snow depth, reduced wood bison movement rates, and movement rates increased more rapidly in warmer temperatures than in temperatures below −6.4 °C. By quantifying both the direction and the magnitude of snow and temperature's effects on bison movement, our study fills critical knowledge gaps relating to the winter movement ecology of wood bison and contributes to a growing body of knowledge informing their conservation in the Anthropocene.

Key words: wood bison, *Bison bison athabascae*, ungulate, winter, behaviour, seasonal, boreal forest.

Résumé : Il est établi que la neige limite les déplacements des animaux sauvages, constituant souvent le plus important déterminant des déplacements hivernaux pour les animaux de la forêt boréale. L'effet combiné de la neige et de la température sur l'écologie des déplacements des animaux à hautes latitudes est toutefois moins bien compris. Ici, nous utilisons des données de colliers GPS sur une petite population de bisons des bois (*Bison bison athabascae* Rhoads, 1898) dans le nord-est de l'Alberta (Canada) pour développer une série de modèles mixtes additifs généralisés qui caractérisent l'effet de l'épaisseur cumulative de la neige, de la variation quotidienne de l'épaisseur de la neige et de la température sur les vitesses de déplacement. Le modèle qui colle le mieux aux données intègre l'épaisseur cumulative de la neige, la température et le jour de l'hiver. Les déplacements des bisons diminuent dans les 75 premiers jours de l'hiver durant l'accumulation de la neige et augmentent de façon marquée dans les 14 derniers jours de l'hiver, durant la fonte de la neige. L'épaisseur cumulative de la neige, et non la variation quotidienne de l'épaisseur de la neige, réduit les vitesses de déplacement des bisons des bois, et ces vitesses de déplacement augmentent plus rapidement à des températures plus élevées qu'à des températures sous les −6,4 °C. En quantifiant à la fois la direction et la magnitude des effets de la neige et de la température sur les déplacements des bisons, notre étude comble d'importantes lacunes dans les connaissances sur l'écologie des déplacements hivernaux des bisons des bois et elle s'ajoute à un corpus croissant de connaissances pouvant éclairer la conservation de cette espèce à l'Anthropocène. [Traduit par la Rédaction]

Mots-clés : bison des bois, *Bison bison athabascae*, ongulé, hiver, comportement, saisonnier, forêt boréale.

Introduction

Movement ecology has gained significant attention in wildlife management and conservation over the past decade (Allen and Singh 2016). When to move, how fast, and how far has wide-ranging implications for the fitness of individual animals (Morales et al. 2010). Animal movement is determined by factors such as environmental conditions, resource availability, and intra- and inter-specific interactions (Morales et al. 2010). Implications of large-scale movements include the redistribution of fragmented populations (Tinker et al. 2008), range expansions or contractions due to climate change (Parmesan 2006), hybridization (Pongracz et al. 2017), and disease transmission (Cross et al. 2004; Flueck and Smith-Flueck 2012). Therefore, predicting animal movements in response to changes in their environment is key to managing wildlife in the presence of climate change, intra- and inter-specific competition, localized disturbance, and at-risk species management.

At higher latitudes, the onset of winter represents a dramatic shift in the relationship of animals to their environment. Density-independent processes in winter, such as precipitation and temperature, affect species survival and dispersal (Coulson et al. 2000). Snow is commonly understood as the dominant limiting factor for wildlife at higher latitudes and altitudes because it can decrease movement rates (Ratikainen et al. 2007; Singh et al. 2012; Richard et al. 2014), reduce range size (van Beest et al. 2011), alter habitat selection (Mysterud et al. 1997; Bruggeman et al. 2008), and increase predation risk (Huggard 1993; Robinson and Merrill 2012). The role of temperature in the winter ecology of wildlife has received less

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attention and there exists no strict rule on the relationship between winter temperature and animal movement rates. For example, muskoxen (*Ovibos moschatus* (Zimmermann, 1780)) vary their movements in response to temperature based on length of day (Schmidt et al. 2016), whereas white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) and elk (*Cervus canadensis* Erxleben, 1777) increase movements in warmer temperatures (van Beest et al. 2013). Both deer and elk have been shown to alter their movements within seasons, including a decrease in movement as winter progresses, and an increase in movement during the onset of spring (van Beest et al. 2013). While the effects of snow and temperature on wildlife can provide useful insights into individual- and population-level processes, the combined influence of snow and temperature on ungulate movements has received little attention.

American bison (*Bison bison* (Linnaeus, 1758)) are the largest extant land animals in North America (Soper 1964). There are two subspecies; the plains bison (*Bison bison bison* (Linnaeus, 1758)) currently exist in isolated populations across the great plains of the western United States and southern Canada (Aune et al. 2017), whereas the wood bison (*Bison bison athabascae* Rhoads, 1898) are located in the boreal forests of Alaska (USA) and northern Canada (Sanderson et al. 2008). Wood bison are listed as a species of "Special Concern" by the Committee on the Status of Endangered Wildlife in Canada because of threats that include poaching, diseases, and severe weather events (COSEWIC 2013). Several studies have identified snow as a limiting factor for bison movement (Bjornlie and Garrott 2001; Bruggeman et al. 2007), habitat selection (Larter and Gates 1991; Steenweg et al. 2016), and body condition (DelGiudice et al. 1994). Still, there lacks a specific understanding of the relationship between snow depth and bison movement rates. Similarly, the extent to which temperature is limiting or facilitative for bison movement has not yet been fully explored. Finally, between-season trends in bison movement rates have been examined, although not while considering the effects of weather (McMillan et al. 2021).

Here, we examined wood bison movements as influenced by winter conditions. Within-season variation in winter precipitation and temperature, as well as long-term alteration as a result of climate change, have the capacity to influence bottom-up (forage availability) and top-down (predation) processes affecting bison movement (Bruggeman et al. 2008; Jung 2015; Boelman et al. 2019). Despite these wide-ranging implications, there lacks an explicit understanding of both the direction and the magnitude of the response of bison movements to within-season changes in snow and temperature. To address this knowledge gap, we used GPS-collar data from eight adult females in the Ronald Lake wood bison herd (RLBH) during the winter of 2018–2019 (2 November 2018 – 26 March 2019) to compare a series of generalized additive mixed models (GAMMs) characterizing the influence of cumulative snow depth, daily change in snow depth, temperature, and day of winter on daily wood bison movement rates. Because snow is understood to influence bison behaviour and bison are a cold-adapted species known for enduring temperatures as low as −30 °C (Christopherson et al. 1979; Meagher 1986), we hypothesized that movement rates would be inversely related to snow depth and that bison would be limited by snow more than cold temperatures. The objective of this study was to examine within-season trends in winter bison movements and to identify both the direction and the magnitude of the effects of snow and temperature on daily bison movement rates to improve our understanding of the winter movement ecology of wood bison.

Materials and methods

Study area

The RLBH occupy an area centred around Ronald Lake in northeastern Alberta, Canada, that extends from the southeastern corner of Wood Buffalo National Park and south out of the park to approximately 25 km north of the hamlet of Fort McKay (Fig. 1). Our study-area extent (4531 km^2) was determined by the 100% minimum convex polygon of GPS-collared bison with a 15 km buffer (Alberta Government 2013; DeMars et al. 2020). The study area's eastern boundary ends at the Athabasca River because no bison locations have been recorded east of the river since collaring was initiated in 2013. Local climate consists of short, warm summers with a mean daily temperature above 15 °C and long, cold winters with a mean daily temperature below −10 °C (Downing and Pettapiece 2006). The landscape is characterized by undulating terrain (240 to 300 m above sea level) with a mixture of deciduous, coniferous, and mixedwood forests in the uplands and a network of marshes, bogs, and other peatlands in the lowlands (Downing and Pettapiece 2006).

The RLBH is distinguished from the nearby Wood Buffalo National Park meta-population by its status as disease-free (Ball et al. 2016) and its unique genetic structure that includes less introgression with plains bison (Shury et al. 2015). The RLBH is located on Treaty 8 Territory in the traditional lands of the Athabasca Chipewyan and Mikisew Cree First Nations. The herd holds important cultural value and is a traditional food source for local Indigenous peoples (Candler et al. 2013). The RLBH is considered a population of "Subject Animals" under Alberta's *Wildlife Act*, and as of 2013, the population size of the RLBH is estimated to be 186 individuals (Alberta Government 2017). Calving for the RLBH typically occurs between 3 May and 28 June, and the rut occurs in late summer as is typical of wood bison (Komers et al. 1994; Hecker et al. 2020). Major winter diet components of the RLBH include bur-reed (*Sparganium angustifolium* Michx.), slough sedge (*Carex atherodes* Spreng.), low bush cranberry (*Viburnum edule* (Michx.) Raf.), and redosier dogwood (*Cornus sericea* L.) (Dewart et al. 2020). While there are several wolf (*Canis lupus* Linnaeus, 1758) packs overlapping the RLBH's range, preliminary scat analyses show that bison are a relatively small portion of their diet (Dewart et al. 2020).

Animal location data and daily movement rates

Bison were fitted with Vectronic Vertex Plus GPS radio collars programmed at a 90 min fix interval. Adult female bison were selected for collaring due to their importance in ungulate population dynamics (Gaillard et al. 2000), grouping behaviour, and selection of higher quality habitats or forages in winter due to greater energetic demands when carrying a fetus (Post et al. 2001). Bison were handled in accordance with approved protocols and procedures of the Alberta Wildlife Animal Care Committee (permit nos. 51244, 53893, 54723, and 55748). After location data were acquired, we subset bison location data for the winter of 2018–2019 when daily snow depths in the study area were monitored. Out of 19 collared bison, we used location data from 8 individuals (∼4% of RLBH population). We excluded data from the remaining 11 individuals due to collar malfunction and data gaps. Next, we removed records with no coordinate information or low fix accuracy with a dilution of precision (DOP) value greater than 10 m (Bjørneraas et al. 2010). For each individual, we calculated movement rate (v_i) as

$$v_i = l_i/t_i$$

where l_i is the step length between location i and location $i + 1$ and t_i is the time between location i and location $i + 1$ (Johnson et al. 2002; Gurarie and Palm 2018). Because our predictor variables are presented as daily means, we calculated movement rates for each bison as kilometres per day (km/day).

Snow depth, temperature, and day of winter

We established four camera stations with snow gauges adjacent to an accessible trail network (majority of study area is

Fig. 1. Map of the Ronald Lake wood bison (*Bison bison athabascae*) herd study area in northeast Alberta, Canada, defined as the 100% minimum convex polygon (MCP) of GPS-collared female bison locations with a 15 km buffer. Map created in ArcMap version 10.7.1 (ESRI 2019). Base map of provincial and continental boundaries from ESRI Canada © 2003.
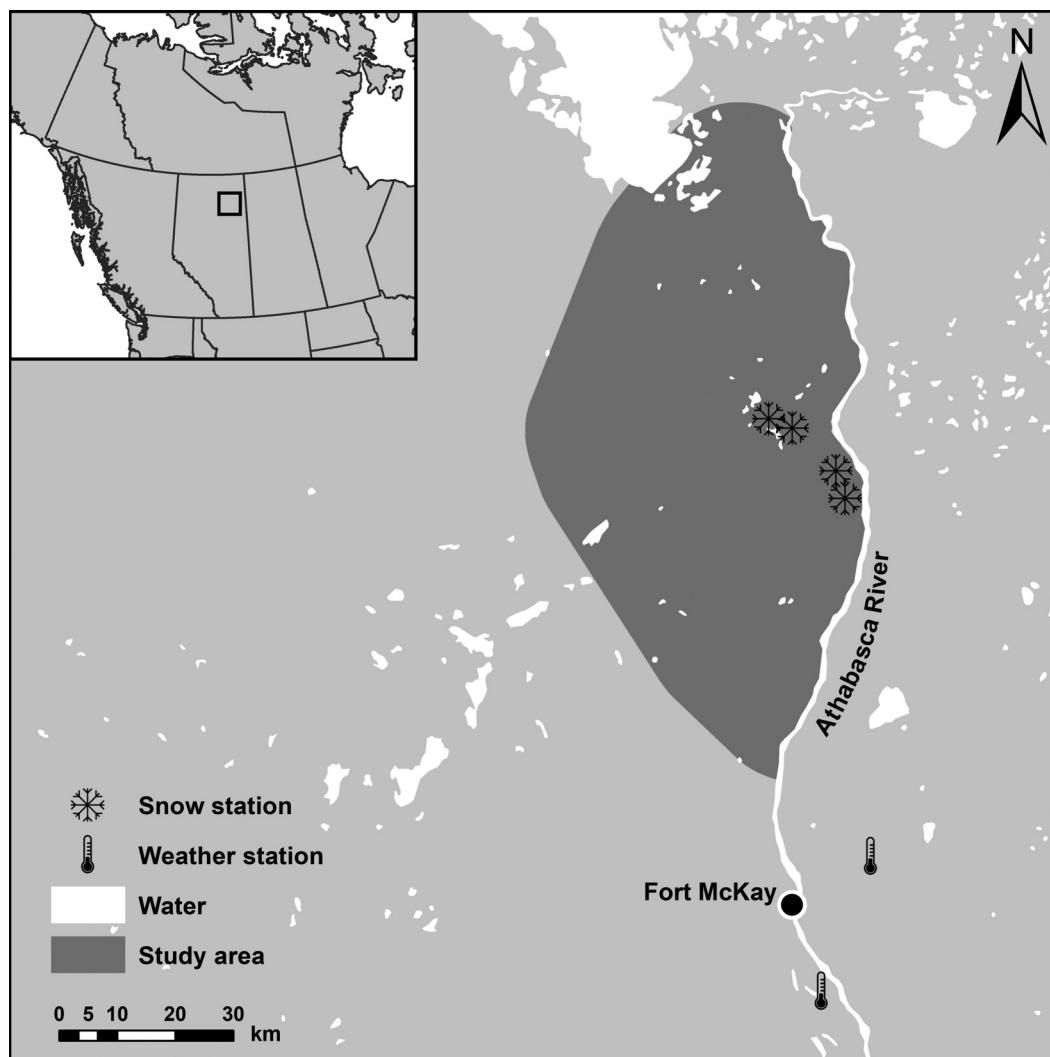

highly inaccessible especially in the winter) to monitor snow depths in the study area (Fig. 2*b*). We collected daily snow depth measurements in pine, deciduous, cut block, and marsh landcover types as defined by the Ducks Unlimited Enhanced Wetland Classification (Ducks Unlimited Canada 2011) near the middle parts of the study area to capture possible variation between landcover types (Watson et al. 2006). An analysis of variance (ANOVA) on snow depths between sites did not reveal significant differences between landcover types ($F_{[3,848]} = 2.25$, $P = 0.08$). Therefore, we aggregated snow depths across all landcover types and calculated a mean daily cumulative snow depth (cm) for the study area. We defined winter as occurring from the first day of continuous snow cover (snow depth measured >1 cm for entire day) to the last day of continuous snow cover as measured by our snow stations (2 November 2018 – 26 March 2019). We also calculated daily change in snow depth (cm) to test the influence of recently fallen and melted or windblown snow on bison movement (Fig. 2*c*). We gathered temperature data from the nearest available weather stations at Aurora and Mildred Lake (Alberta Agriculture and Forestry 2020) and calculated the mean daily temperature (°C) across both stations (Fig. 2*d*). Finally, we used day of winter to assess within-season variation in bison movement rates (day 1 corresponding to the first day of our study period).

Statistical analyses

To test the influence of cumulative snow depth, daily change in snow depth, day of winter, and temperature on wood bison movement rates, we used generalized additive mixed models (GAMMs) using the "GAMM" function from the package "mgcv" (Wood 2017) in the R programming environment (R Core Team 2017). GAMMs allowed us to examine both linear and non-linear associations between our response and predictor variables. Thus, we fit cumulative snow depth and recently fallen snow as linear terms and temperature and day of winter as splines with low basis dimensions to avoid overfitting these data (Sebastian-Azcona et al. 2019), with bison ID included as a random effect to account for variation among individuals. Considering the right-skewed distribution of daily movement rate observations (high frequency of slow movements), we log-transformed (natural logarithm) movement rates and performed a Shapiro–Wilk's normality test (Shapiro and Wilk 1965) to confirm the efficacy of the log transformation. We specified a Gaussian family identity link function in our models and confirmed model fit by examining diagnostic plots for a normality of residuals and homogeneity of variances. After fitting our candidate models (Table 1), we ranked their support using Akaike's information criterion corrected for small sample sizes (AIC$_c$) and associated Akaike weights (Burnham and Anderson 2002). We

Fig. 2. Summary plots depicting (*a*) mean daily movement rates (km/day) for eight female wood bison (*Bison bison athabascae*) from the Ronald Lake herd during the winter of 2018–2019, (*b*) mean daily cumulative snow depth (cm), (*c*) mean daily change in snow depth (cm), and (*d*) mean daily temperature (°C). Shaded regions represent standard errors and broken horizontal lines show the mean value for each variable.
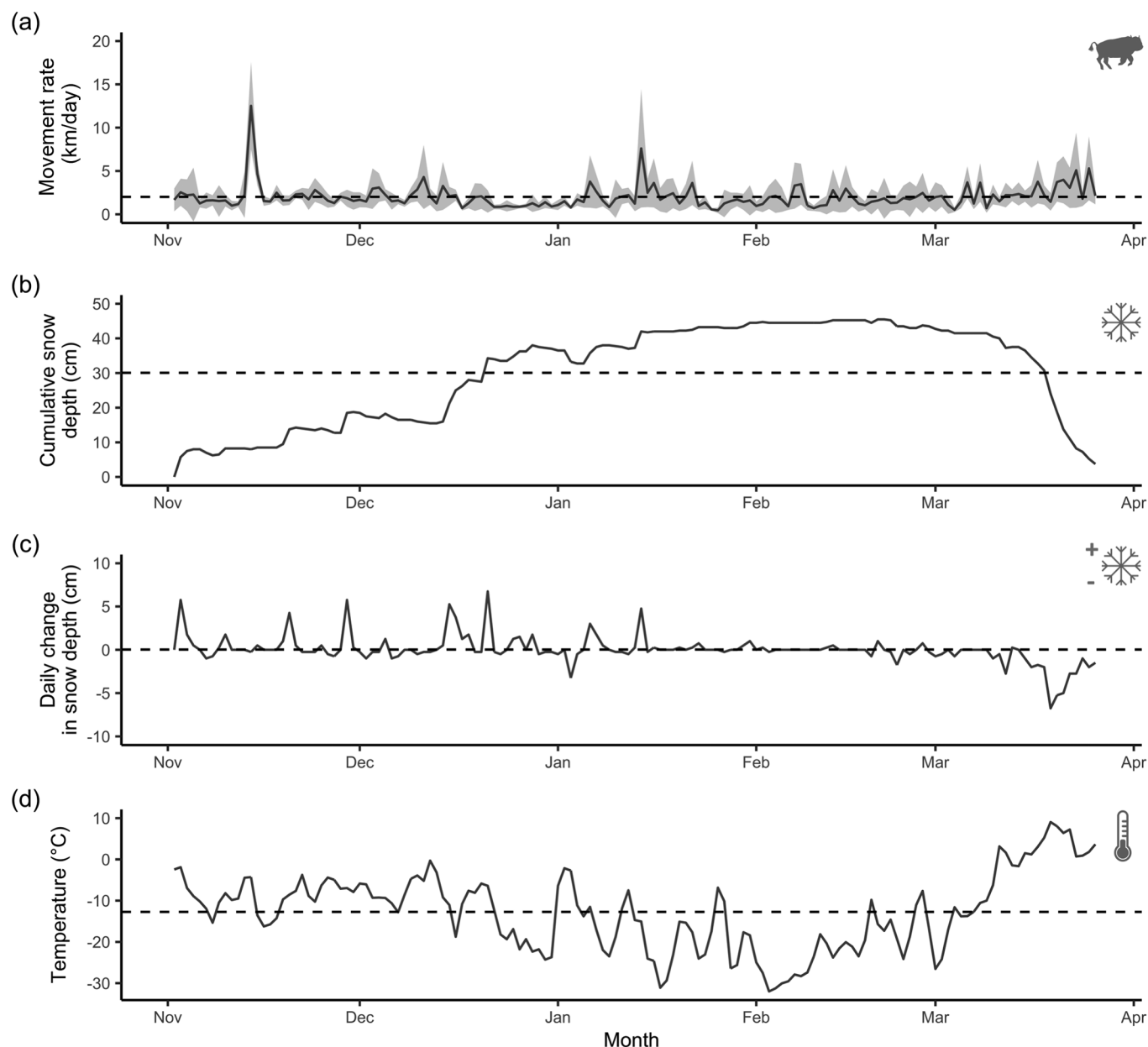
chose the model with the lowest AIC_c as the most supported (Burnham and Anderson 2002). Although GAMMs are useful predictive tools, we wanted to make statistical inferences about model results (specifically for non-linear terms). Thus, we used breakpoint regression using the package "segmented" (Muggeo 2008) to approximate breakpoints and coefficients of individual splines predicted from GAMMs. We report back-transformed effect sizes for both linear and non-linear terms as the percent change in mean daily movement rates (km/day) for each 10-unit increase in model variables.

Results

After applying selection criteria of GPS-collared bison recording locations across the winter period, eight female wood bison individuals provided 10 421 locations (mean = 1303.0 locations,

SD = 459.4 locations). Daily movement rates ranged from 0.09 to 18.40 km/day (mean = 2.01 km/day, SD = 1.99 km/day; Fig. 2*a*). Daily snow depth ranged from 0.0 to 45.5 cm (mean = 30.1 cm, SD = 14.2 cm; Fig. 2*b*), daily change in snow depth ranged from −6.8 to 6.8 cm (mean = 0.03 cm, SD = 1.66 cm; Fig. 2*c*), and mean daily temperature ranged from −32.0 to 9.1 °C (mean = −12.7 °C, SD = 9.3 °C; Fig. 2*d*). Log-transforming movement rates produced a normal distribution and diagnostic plots for all models satisfied the assumptions for normality of residuals and homogeneity of variances. The top two GAMMs accounted for 94% of the AIC_c weight and had AIC_c values within a difference of 2 (Table 1). Both models predicted the similar effects of cumulative snow depth and day of winter on movement rates, but the model with the lowest AIC_c also included the effect of temperature, which is of biological interest (Burnham and Anderson 2002). Therefore, we discuss effect sizes as predicted by the most supported model,

Table 1. Candidate set of generalized additive mixed models (GAMMs) explaining mean daily movement rates (log km/day) of adult female wood bison (*Bison bison athabascae*) in the Ronald Lake study area, Alberta, Canada, during the winter of 2018–2019.

Model	ΔAIC_c	AIC_c weight	Adjusted R^2
Cumulative snow depth + day of winter + temperature	0.00	0.51	0.10
Cumulative snow depth + day of winter	0.36	0.43	0.10
Cumulative snow depth + temperature	4.37	0.06	0.10
Day of winter	17.16	0.00	0.09
Cumulative snow depth	27.22	0.00	0.08
Temperature	28.79	0.00	0.08
Daily change in snow depth	84.78	0.00	0.03
Null	113.18	0.00	0.00

Note: All models include bison ID as a random effect to account for variation among bison individuals. GAMMs were ranked for support using Akaike's information criterion corrected for small sample sizes (AIC_c). We report AIC_c differences, AIC_c weight, and adjusted R^2.

Table 2. Summary of fixed effects from the most supported generalized additive mixed model (GAMM) predicting mean daily movement rates (log km/day) of adult female wood bison (*Bison bison athabascae*) in the Ronald Lake study area, Alberta, Canada, during the winter of 2018–2019.

Model	Variable	β	Back-transformed (%)	95% CI
Snow depth + day of winter + temperature	Cumulative snow depth	−0.017	−15.6	−0.023, −0.011
	Day of winter			
	2 Nov to 15 Jan	−0.009	−8.6	−0.010, −0.008
	16 Jan to 12 Mar	0.003	3.1	0.002, 0.005
	13 to 26 Mar	0.126	252.5	0.115, 0.137
	Temperature (°C)			
	−32.0 to −6.4	0.015	16.2	0.008, 0.021
	−6.5 to 9.1	0.074	109.6	0.055, 0.092

Note: Cumulative snow depth is a linear term and day of winter and temperature are non-linear terms fitted as splines with low basis dimensions. Effect size coefficients for non-linear terms are derived from a breakpoint regression analysis of GAMM model predictions and are approximations meant to facilitate statistical inference. Back transformed coefficients are the percent change in movement rates (km/day) for a 10-unit change in each model variable. We report 95% confidence intervals (95% CI) for the linear coefficient of cumulative snow depth and for the approximate linear coefficients of smooth terms derived from breakpoint regression.

which accounted for 51% of model weights with an adjusted R^2 value of 0.10 (Table 1).

Our most supported model confirmed the expected, negative effect of cumulative snow depth on wood bison movement rates. The linear coefficient for cumulative snow depth revealed that a 10 cm increase in mean daily cumulative snow depth decreased mean daily movement rates by 15.6% ($\beta = -0.017$ and 95% confidence interval (95% CI) = −0.023, −0.011; Table 2 and Fig. 3*a*). Day of winter revealed a gradual decrease in movement rates as winter progressed and snow accumulated, with an increase in movement rates in the final weeks of winter during snowmelt. Specifically, movement rates decreased by approximately 8.6% every 10 days from 2 November 2018 to 15 January 2019 ($\beta = -0.009$ and 95% CI = −0.010, −0.008), increased by 3.1% every 10 days from 16 January 2019 to 12 March 2019 ($\beta = 0.003$ and 95% CI = 0.002, 0.005), and then increased rapidly by 252.5% during snowmelt between 13 March 2019 and 26 March 2019 ($\beta = 0.126$ and 95% CI = 0.115, 0.137; Table 2 and Fig. 3*b*). Mean daily temperature confirmed our prediction of warmer temperatures increasing movement and also revealed slower increases in movements below a threshold temperature. Specifically, a 10 °C increase in mean daily temperature increased movement rates by approximately 16.2% between −32.0 and −6.4 °C ($\beta = 0.015$ and 95% CI = 0.008, 0.021) and by 109.6% between −6.4 and 9.1 °C ($\beta = 0.074$ and 95% CI = 0.055, 0.092; Table 2 and Fig. 3*c*).

Discussion

We used GAMMs to examine how cumulative snow depth, daily change in snow depth, day of winter, and temperature affected bison movement rates. Trends in winter habitat selection and space use are both major themes in the northern ungulate literature (Larter and Gates 1991; Bruggeman et al. 2007; Laurent et al. 2021), but our study is unique in quantifying the effect of cumulative and daily changes in snow depth, day of winter, and temperature on bison movements. Our main findings provide support for the limiting effect of snow on wood bison movements, but we make the distinction that cumulative snow depth is a much stronger predictor of bison movement than daily changes in snow depth. Furthermore, we demonstrate within-season trends in winter wood bison movements, with movements gradually decreasing in the first 75 days of winter, gradually increasing for the next 56 days, and dramatically increasing in the last 14 days during snowmelt. We also demonstrate a non-linear association between bison movement rates and daily temperature, in which movements gradually increase up to −6.4 °C and then dramatically increase thereafter as temperatures increase up to 9.1 °C.

The negative effect of cumulative snow depth on wood bison movement rates in our study is expected and in agreement with other studies showing a reduction of movement in deep snow as a strategy used by many ungulates to conserve energy, including moose (*Alces alces* (Linnaeus, 1758); van Beest et al. 2011; Singh et al. 2012), deer (genus *Odocoileus* Rafinesque, 1832), and elk (Poole and Mowat 2005). Bison travel less in the winter because of the additional energetic cost associated with travelling through snow (Telfer and Kelsall 1979). Not only are the energetic costs higher for bison travelling through snow in the winter, but as grazers, their forage supply is limited to standing dead graminoids (i.e., sedges and grasses) of a lower quality than their summer forages (Larter and Gates 1991; Hecker et al. 2021). Therefore, forage supply becomes a limiting factor for bison during the winter and they spend more time digging craters and foraging in

Fig. 3. Predicted mean daily movement rates (km/day) for eight female wood bison (*Bison bison athabascae*) from the Ronald Lake herd during the winter of 2018–2019 as a function of (*a*) snow depth (cm), (*b*) day of winter, and (*c*) temperature (°C). Points show mean estimates of daily movement rates (km/day). Lines represent predictions from the most supported generalized additive mixed model. Shaded regions represent 95% confidence intervals of predictions.
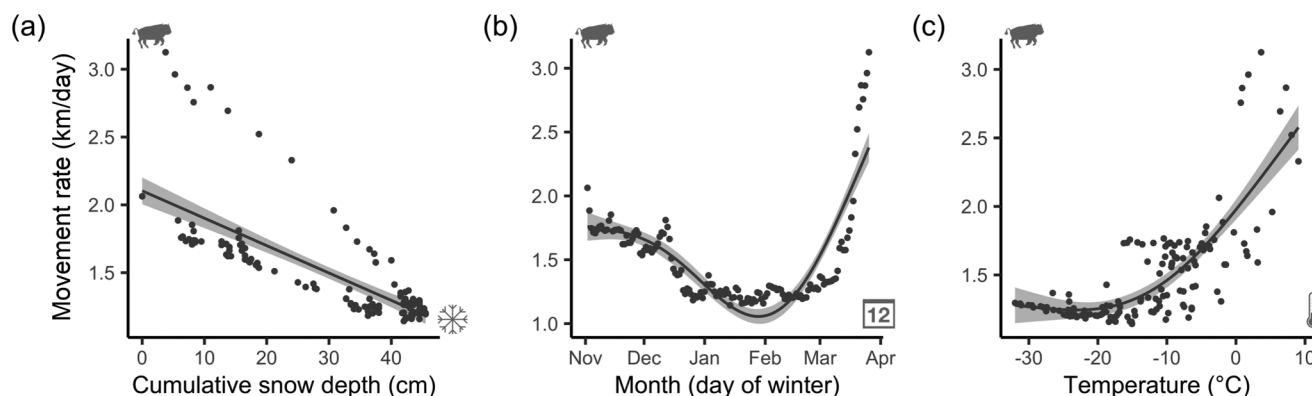
winter than travelling (Fortin 2002; Steenweg et al. 2016). In one case, up to 70% of winter behavioural observations of bison were foraging activities (Bruggeman et al. 2006). To put this in context of our work, the mean daily movement rate for bison in our study was 2 km/day (Fig. 2*a*); thus, reduced movement rates associated with increased cumulative snow depth is likely attributed to the greater energetic cost of travel between forage patches and time spent cratering in deeper snow to reach forage. The limiting effect of cumulative snow depth on bison foraging efficiency contrasts the poor performance of daily change in snow depth in our models. Other ungulates, such as mountain goats (*Oreamnos americanus* (Blainville, 1816)), respond more strongly to daily changes in snow depth because they reside in arctic or alpine environments where winds increase snowpack density, allowing animals to travel on top of snow (Déry and Yau 2001; Richard et al. 2014). Bison, on the other hand, would be less influenced by a recent snow fall than the accumulation of snow over time, which would limit access to forage (Larter and Gates 1991) and make travelling very difficult considering their low chest height and high foot load (Telfer and Kelsall 1979). Importantly, snow depths reported in our study are characteristic of a "typical" year in the region, but we acknowledge that results from our study may not be generalizable for years with particularly deep snow where the magnitude of the effect of snow on movement could be much larger.

Although snow can be the most limiting factor for ungulate movement and space use, we show that day of winter is also an important predictor of winter bison movement. Northern ungulates have been shown to respond strongly to within-season changes in ambient temperature (Rivrud et al. 2010; van Beest et al. 2011), which van Beest et al. (2013) showed to be highly correlated with movement rates of elk and white-tailed deer. Surprisingly, bison movement rates were not as strongly correlated with temperature. Instead, day of winter accounted for much of the variation in movement rates explained by temperature. This suggests that other within-season factors not accounted for may affect bison movements, as opposed to temperature alone, which most investigations use to describe such behaviour (Rivrud et al. 2010; van Beest et al. 2011, 2013). Faecal samples collected from the Aishihik wood bison herd in the southwest Yukon (Canada) revealed a higher proportion of lower quality forages (such as shrubs) in bison diets when snow was deepest (Jung 2015), suggesting that poor availability of higher quality forage could also decrease movement rates. As snow melts in late winter, bison may increase their movements in an attempt to find newly available forage when their body mass is most depleted (Parker et al. 2009), especially pregnant females. Our work supports McMillan

et al. (2021) who showed that bison reduce movement rates in winter and increase movement the most in the spring. McMillan et al. (2021) provide an excellent examination of between-season bison movement rates, but we report a within-season analysis of winter movement that incorporates snow and temperature. Results from our study and McMillan et al. (2021) paint a more complete picture of winter bison movement, but further necessitate a more comprehensive investigation into bison winter ecology that incorporates a multitude of factors suggested to impact their movement.

Mean daily temperature revealed an interesting association with movement rates. Bison moved much slower when temperatures were less than approximately −6.4 °C and increased by close to 100% for each 10 °C increase in temperature thereafter. Bison are cold-adapted animals possessing thick, woolly undercoats and large guard hairs suited for temperatures reaching far below 0 °C (Meagher 1986). Bison calves have been shown to maintain or reduce their metabolic rate at −30 °C, increasing it only above 10 °C (Christopherson et al. 1979). Other ungulates, such as white-tailed deer and elk, have been shown to increase their movements in response to increasing mean daily temperature during the winter (van Beest et al. 2013). Muskoxen increase movement in colder temperatures to maintain their metabolic rate, decreasing movement in warmer temperatures on shorter days with less daylight (Schmidt et al. 2016). Similarly, cattle have been shown to increase feeding activity and reduce resting time in colder temperatures (Graunke 2011). Further research is needed to understand the non-linear effect of temperature on bison movement rates in our study, but our results suggest a limiting threshold effect of winter temperatures on bison movement.

Although our models revealed important associations between bison movement rates and winter conditions, much of the variance remained unexplained. Because we report data from female wood bison, it is worth noting that the movement rates here may be different for males, as bison exhibit sex-specific differences in response to snow depth (Telfer and Kelsall 1984). Females take more steps per minute than males (Komers et al. 1993), in part due to their shorter legs (Telfer and Kelsall 1979), and because they are more selective foragers than males (Komers et al. 1993). We did not test group-size effects on bison movement; however, bison are known to create trails in the snow enabling faster movement and this could be affected by snow hardness (Bruggeman et al. 2006; Dancose et al. 2011). Females in the RLBH tend to stay together during the winter, thus it is likely that bison in our study used the same trails. We also recognize that our study is limited to one winter and therefore does not

account for interannual differences in winter conditions. This is especially important for using day of winter to predict within-season movement rates because different winters could have different dates of initial snowfall and date of snowmelt. We recommend further investigations into the relationship between temperature, snow hardness, group size, and foraging efficiency of wood bison for a more comprehensive understanding wood bison winter movement ecology.

Understanding the behavioural response of an animal to changes in their environment is an important aspect of wildlife management (Allen and Singh 2016). Movement is of particular interest in the context of wood bison where limiting range expansion and connectivity between populations is essential for preventing the spread of disease and maintaining genetic integrity (Hedrick 2009; Shury et al. 2015). A comprehensive examination of the winter ecology of wood bison that accounts for the multitude of factors driving their behaviour and space use will improve our understanding and contribute towards effective management of this species at risk. We suggest that future studies not only collect in situ snow depth information, but also consider other properties of winter snowpack such as snow hardness (Mahoney et al. 2018). Winter resource selection studies that focus on the interaction between landscape characteristics, snow depth, snow hardness, and forage availability will improve our understanding of wood bison winter ecology. We echo the recommendations of McMillan et al. (2021) and call for studies on bison movement and habitat selection in the late-winter and spring when bison movements appear to increase most dramatically. We suggest that future studies investigate forage availability, body condition, predation risk, and the impacts of climate change (Craine 2015) on bison movements. Long-term monitoring of these animals and their environments is needed to collect the data necessary to make inferences about environmental change, as well as predict impacts to populations over a wide variety of landscapes and scales. By quantifying both the direction and the magnitude of the response of bison movements to within-season changes in snow and temperature, our study fills critical knowledge gaps relating to the winter movement ecology of wood bison. Our study contributes to a growing body of knowledge informing the conservation of wood bison in the Anthropocene, hopefully inspiring further research on this culturally significant yet understudied northern ungulate.

Conflict of interest statement

The authors declare that they have no conflict of interest.

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