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Individual variation in movement ecology affect body mass in Svalbard reindeer

Even Unsgård

Management of natural resources

Preface

This master thesis is the final product of my master's degree in management of natural resources at the Norwegian University of Life Sciences (NMBU). Thank to my supervisor professor Leif Egil Loe for great supervising and the opportunity to go to Svalbard for field work. Thank to Seve Albon and Liv Monica Trondrud for all the help with analysis and writing. I would also like to thank Samantha Paige Dwinnell for organizing fieldwork at Svalbard. Lastly, I would like to thank my fellow master students Oline Eikeland and Emma Djurberg for great cooperation during field work on Svalbard.

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Abstract

Herbivore foraging is a complex interaction mainly driven by the distribution of forage in the landscape. The forage quantity and quality in the habitat influences the establishment of home ranges and diet selection from patches down to fine scale choices of plant species and plant parts. When vegetation biomass is plentiful, herbivores can feed selectively to increase the daily intake rate of digestible matter. Selective feeding that adds only small incremental gains may over time cause large gains in fitness, the so-called multiplier effect. This makes individual movement ecology a crucial aspect of foraging behaviour. Patch residence time (PRT) provides a measure of the time a herbivore stays in a patch before moving on to feed elsewhere and may serve as an estimate of how selective an individual is.

In this study I utilized GPS collar data from 10 culled female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) to document PRT as an indicator of foraging behaviour to relate individual movement ecology to October body mass. In addition, I investigated if individual variation in PRT has a carry-over effect on late winter body mass (April) by using capture and GPS-data from 156 individual years. Finally, I explored how PRT correlates with yearly plant biomass level, visually assessed foraging behaviour and home range size.

I found that individuals with lower PRT were significantly heavier in October, the individual with the lowest PRT (2.9h) was 5.5 kg lighter compared to the reindeer with the highest PRT (5.8h). There was a positive carry-over effect of lower cumulative PRT to late winter body mass and cumulative PRT increased in warmer summers when plant biomass is likely to be greater. Mean daily PRT was negatively correlated with time spent walking grazing and positively correlated with time spent standing grazing. Lastly, home range size decreased with increasing cumulative PRT.

This is the first study to relate PRT from GPS data to individual foraging behaviour and highlights how movement ecology is important for fitness. More selective grazing yields a higher energy return in a heterogenous habitat and small differences between individuals in daily foraging behaviour has a multiplier effect and results in higher body mass. Overall, this study provides evidence of individual foraging benefits through a novel approach of herbivore foraging behaviour research. By using GPS data to quantify the effects of relatively small-scaled feeding strategies body mass, a key determinant of fitness.

Sammendrag

Plantespisere sin furasjering er en kompleks interaksjon som hovedsakelig er drevet av fordelingen av fôr i landskapet. Fôr kvalitet og kvantitet i habitatet påvirker størrelsen av leveområde og små skala valg av hvilke planter og plantedeler man spiser. Når det er mye plantebiomasse, kan plantespisere være selektive for å øke inntaket av fordøyelig masse. Selektiv furasjering som medfører små fordeler på daglig basis, kan over tid få store konsekvenser for kondisjonen også kjent som «the multiplier effect». Dette gjør individuell bevegelsesøkologi et viktig aspekt i furasjeringsteori. «Patch residence time» (PRT) modellerer furasjeringsstrategi gjennom å estimere tiden en planteeter bruke i et område før den flytter seg videre og gir et estimat på hvor selektiv et individ er.

I denne studien bruker jeg GPS-data fra 10 felte simler av Svalbard reinsdyr (*Rangifer tarandus platyrhynchus*) for å dokumentere PRT som en indikator på beiteadferd for å relatere bevegelsesøkologi til kroppsvekt i oktober. I tillegg bruker jeg fangstdata fra 156 individ-år for å undersøke om individuell variasjon i PRT har en overførselseffekt til kroppsvekten etter vinteren (april). Til slutt undersøkte jeg hvordan PRT korrelerer med årlig plante biomasse, observert beiteadferd og størrelse på leveområde.

Jeg fant at individer med lavere PRT var signifikant tyngre i oktober, individet med laves PRT (2.9t) var 5.5kg tyngre sammenlignet med det som hadde høyest PRT (5.8t). Det var en positiv overførselseffekt av lavere kumulativ PRT på kroppsvekt senvinters (April). Kumulativ PRT økte i varmere somrer når nivået av plantebiomasse er forventet å være høyere. Daglig gjennomsnittlig PRT hadde en negativ korrelasjon med tid brukt på gående beiting og en positiv korrelasjon med tid brukt på stående beitende. Avslutningsvis avtok størrelsen på leveområdet med en økning i kumulativ PRT.

Dette er den første studien som bruker PRT fra GPS data for å dokumentere individuelle forskjeller i beiteadferd og viser hvordan bevegelsesøkologi er viktig for kondisjon. Økende selektiv beiting medfører høyere energiretur i et heterogent habitat og små forskjeller i individuell beiting på daglig basis har over tid en «multiplier effect» som medfører høyere kroppsmasse. Denne studien viser individuelle fordeler av beitestrategi gjennom en ny framgangsmåte for å studere plantespisere sin furasjering. Ved bruk av GPS data kvantifiseres effekten av små skala beitestrategier på kroppsvekt, en viktig faktor for kondisjon.

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1 Introduction

Herbivore foraging behaviour is mainly driven by the distribution of forage in the landscape and the trade-off between quantity and quality (Bergman et al., 2001, Fortin et al., 2003) with the goal to achieve as high net energy return as possible (Westoby, 1974, Owen-Smith and Novellie, 1982, Belovsky, 1986). The forage quality in the habitat influences diet selection from establishment of home ranges down to fine scale choices of plant species and plant parts (Johnson et al., 2001, Vivås et al., 1991). The nutritional values of plants vary between species, but also between flower, leaves, stems, and roots. Foraging strategy involves everyday choices of where and what to eat. Differences among individuals might not be great on daily scale, but over time small improvements in vegetation biomass and quality tend to increase intake rate of digestible matter (White, 1983). Higher intake rates allow herbivores to select forage species which balance the intake of nutrients versus the intake of antagonistic plant secondary compounds (Kuropat and Bryant, 1980, White and Trudell, 1980). Combined, small differences in grazing patterns and forage selection can result in a multiplier effect on body mass gain and, ultimately, fitness (White, 1983).

In a seasonal and spatially heterogeneous habitat, the multiplier effect is achieved by feeding at the right place at the right time to target the present seasons best habitat and forage. This makes individual movement ecology a crucial aspect of foraging behaviour among herbivores to explain how they try to achieve diets which maximize digestible matter and optimize net energy return through spatial use of the habitat. When choosing where to forage an individual ideally would select a patch with abundant high-quality forage (Hansen et al., 2009). However, often this is not the case, and there is usually a trade-off between patches of high quality and patches of high biomass, which influences habitat selection and foraging behaviour (Wittmer et al., 2006). Low quality forage may limit the herbivore through increased digestion time (Mertens, 1987, Wilmshurst et al., 1999, Spalinger et al., 1986) restricting total forage intake. An optimal foraging strategy will change over the season as the relative nutritive value of species vary and requires tracking of resources in real time to access the current best forage.

In addition to seeking out the best forage, optimizing time spent in every patch is an important aspect of foraging behaviour. A herbivore has to trade off how selective it should be when foraging in a patch, and if it should move on to a new patch or reduce selectivity to

forage on more abundant low-quality forage (Yoccoz et al., 1993, Parker and Stuart, 1976). The time an individual stays in the same patch can be quantified as their patch residence time. Patch residence time (PRT) provides a measure of foraging behaviour through estimating how long an herbivore stays in a patch before moving on. This indicates how selective an individual is, and on how much it roves through the landscape in search of forage. This is similar to the marginal value theorem (Charnov, 1976) which explains that an individual should move on at the threshold where it is more beneficial to seek out a new patch of higher quality (Owen-Smith et al., 2010). This requires familiarity with the habitat and knowledge of where to find adequate forage in a landscape and awareness of fluctuations in forage quality and abundance to match the energy use of movement and search behaviour (Anderson et al., 2005, Tufto et al., 1996). The tracking of forage quality on a spatial scale is expected to yield a fitness benefit from accessing better foraging patches (Pyke et al., 1977). More movement often results in a larger home range (Predavec and Krebs, 2000), areas that an individual have increased familiarity with (Van Moorter et al., 2009), and are often a function of quality and quantity of forage (Van Beest et al., 2010, Dussault et al., 2005). Large home ranges are often linked to search effort and high quality of grazing conditions where it is beneficial to move around targeting high quality forage (Kohlmann and Risenhoover, 1994, Sæther and Andersen, 1990). Individual knowledge of the distribution of seasonal forage is incomplete, and large individual variation in foraging behaviour can be expected.

Herbivores would ideally search for food solely based on the habitat nutrient quality, with foraging limited by only digestion time (Belovsky, 1978, Owen-Smith and Novellie, 1982) and intake rate (Bergman et al., 2001), but herbivores are usually exposed to constraints influencing foraging strategies (Schoener, 1971, Hixon, 1982). Foraging behaviour is a complex interaction affected by top-down factors (Pyke, 1984, Illius and Gordon, 1990). Predation (Frair et al., 2005), human disturbance (Hebblewhite and Merrill, 2008) and insect harassment (Colman et al., 2003) all influence herbivore foraging behaviour (Bailey et al., 1996, Parker et al., 2009) alongside intra- and interspecific competition (Skogland, 1985). This makes differentiating between top-down and bottom-up influenced decision-making for foraging behaviour difficult.

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) are in a unique situation in terms of foraging behaviour because of little to no predation (Derocher et al., 2000), no insect harassment (Williamsen et al., 2019), and no competition from other herbivores (Reimers, 1977). Svalbard reindeer experience low rates of intra-specific competition during summer

and autumn (Albon et al., 2017), even though the population has increased (Le Moullec et al., 2019). Living in an environment with two highly contrasting seasons Svalbard reindeer should adapt foraging in summer and autumn to maximize weight gain on the basis of few restraints and high seasonality of forage, with food of high quality only available for a short period (Ernakovich et al., 2014). In addition to high seasonality, there is substantial difference between years and warmer summers are associated with higher plant productivity (Van Der Wal and Stien, 2014). Plant productivity has consequences for autumn body mass which is important for survival and reproduction (Albon et al., 2017). For Svalbard reindeer search behaviour is likely driven at individual level (Loe et al., 2016), but there is lack of knowledge about how these individual differences relates to fitness. Before winter season Svalbard reindeer need to accumulate as much fat as possible and regain weight lost during the previous winter. Living in an environment with few constraints, they are an ideal species to investigate how movement ecology and small foraging decisions have a multiplier effect on fitness.

In this study I utilize GPS collar data to estimate patch residence time (Barraquand and Benhamou, 2009) and home range size (Worton, 1989) as indicators of foraging behaviour to relate individual movement ecology with fitness. In particular, I investigate 1) how patch use affects body condition in autumn, 2) the potential carry-over effects of PRT to late winter body mass over a period of 12 years and 3) individual-level drivers of PRT. Specifically, I predict that 1) individuals with a lower PRT will be heavier in autumn. 2) and that this relationship is weaker, but still present in late winter body mass. 3) Finally, I predict that a) lower PRT will occur in warmer summers when plant-productivity is higher, and b) increased PRT will correlate positively with more standing grazing (SG) and negatively with more walking grazing (WG). Lastly, 4) I predict larger home range for reindeers with low PRT. PRT derived from GPS collars to model unconstrained foraging behaviour has to my knowledge not been used in studies on herbivores. My study investigates individual foraging benefits through a novel approach of herbivore foraging behaviour research to quantify the effects on fitness and shows how movement ecology is important at the individual level.

2 Materials and methods

Study area

The main study area is in Nordenskiöld land and consists of the valleys Colesdalen, Reindalen, and Semmeldalen with side valleys (78° N 16° E). The Archipelago of Svalbard has a rugged topography, numerous fjords, and the study area is characterized by wide valleys surrounded by steep moderately glaciated mountains with peaks up to 1000 m (Major and Nagy, 1972). The climate on Svalbard is polar (Major and Nagy, 1972) with a mean summer temperature around 5°C and annual precipitation less than 200 mm (Førland et al., 2011). Temperature and precipitation have been increasing on Svalbard and the expectation is a continuous increase due to climate change (Førland et al., 2011). Being located high in the Arctic, Svalbard experiences two contrasting faces with the sun continuously above the horizon in summer from 19 April to 24 August while the polar night lasts from around 25 October until the mid-February.

The vegetation in the study area reaches a height of 250 meters above sea level and plant cover is continuous in the valleys up to about 100 m (Van Der Wal and Stien, 2014). Above 100m vegetation becomes increasingly sporadic, and above 200m only scattered patches of plant cover prevails (Brattbakk 1986). The vegetation is diverse, mainly dominated by herbs, graminoids and acidic mires (Van der Wal et al., 2000). There are no trees and bushes, and the resident vegetation rises no more than 5- 15 cm from the ground (Hansen 2008). Because of the polar environment plant growth is limited to the period between the beginning of June and around first of August (Albon et al., 2017). The variation in snow cover and plant growth is large between years (Karlsen et al., 2014, Albon et al., 2017), and there is permafrost in the ground throughout the whole year with only 2-3 meters thaw during summer. The study area has no roads and human presence in summer is rare, but in winter a snowmobile track running through parts of the study area is frequently used.

Study species

The Svalbard reindeer is the only large resident herbivore on the Svalbard archipelago (Banfield, 1961). They have several adaptations to living in the arctic like dense fur, small body size, short legs, and small ears. In autumn female Svalbard reindeer weigh around 70 kg, about 20 kg heavier than the average late winter weight of 50 kg (Albon et al., 2017). They are non-migratory, and live in small family groups of two to five individuals (Loe et al., 2006) and mother-calf pairs seem to be the only strong social bond, based on repeated observations

of marked individuals (L.E.Loe, unpublished data). Behavioural decisions can therefore be expected to occur on the level of individuals, unlike many other herd-living Rangifer populations. Their summer diet consists of different grass and sedges (Brattbakk and Øritsland, 1986). Hunting of Svalbard reindeer is restricted to 150–200 reindeer in the period 20 August–10 September (Svalbard, 2023).

There has been research conducted on Svalbard reindeer in the main study area since 1994 and most of the data is from a long-term individual-based study system (Albon et al. 2017) in which female reindeer are marked as calves and followed throughout their life. A subset of this study population have been instrumented with GPS-collars since April 2009. In October 2022, ten of these instrumented animals (hereafter focal animals) were culled as part of a larger scientific collaboration and are the main study individual in this thesis.

October data of culled individuals

The ten focal individuals were shot in October and brought back to Longyearbyen where they were measured and weighed. Live weight was measured first before the reindeer were dressed and weighed again. I collected four measures of fat from the reindeers: subcutaneous fat (SUBCUT), Maximum fat (Maxfat), Ingesta free body fat (IFBfat) and loin fat (Loinfat). SUBCUT measures the depth of the fat with a calliper “slightly medial of the sacrotuberous ligament and the third corner in an equilateral triangle with the other corners being Tuber ischiadicum and Trochanter major of the femur” following method described in Stien et al. (2003). Maximum fat is the depth of the thickest subcutaneous rump fat and loin fat is a measure of thickness of longissimus dorsi fat taken between the 12th and 13th rib adjacent to the backbone. Lastly, the IFBfat is calculated using equations developed in Cook et al. (2021) to predict ingesta free body fat in caribou.

GPS data

The ten focal individuals were equipped with GPS-collars (Vectronic aerospace, Berlin, Germany). The GPS-collars recorded four positions every hour and the GPS-data were downloaded from the collars after culling in October. In addition to GPS-locations for 2022, I used GPS data from 307 individual years from 2009 to 2022 mostly with one position every hour with some exceptions, especially for 2017 where there were locations only every eight hours for most individuals.

April data of live captured individuals

To analyse carry-over effect of patch residence time on spring body mass I used a larger database of GPS- and capture-data running from 2009-2022, including the climate and environmental measures ground ice and snow water equivalent measure as described in Loe et al. (2021).

Behavioural observations

Together with fellow master students I also undertook visual observations of the GPS-marked individuals from 28 July to 13 October. These behavioural observations were collected by visiting the most recent locations of target GPS-animals (typically a few hours old), accessed by using a satellite phone as modem for a field computer and transferred to a handheld GPS. The GPS-marked reindeers were identified from their collar number and ear tag with spotting scopes and binoculars before observations began. Behavioural observations were carried out by categorizing behaviour type as for example walking grazing (WG), standing grazing (SG) and searching (S) (Appendix 1). Firstly, the GPS position, distance to the reindeer and time were noted down. Then behaviour type displayed by the reindeer were noted down every 10 seconds for 20 minutes by observing the reindeer through a spotting scope. This produced a dataset with 120 observations of behaviour type for each observation. In my case, the purpose of these data was to see if they correlated with PRT.

Temperature data.

Annual summer temperature for June - September were obtained from the meteorological station at Longyearbyen airport, 30 km north of the main study area (klimaservicesenter, 2023).

Statistical analysis

All statistical analyses were conducted using R software version 4.1.2 (R Core Team, 2021). Patch residence time (PRT) was analysed with the `adehabitatLT` package as a trajectory analysis based on the method created by Barraquand and Benhamou (2009). The calculation produces a patch residence time for every GPS point by estimating how long a reindeer uses to break out of a circle of a chosen radius. Because of lack of a priori expected radii of interest, I used an exploratory approach and computed PRT for circles from 50 to 1000 meters, with 50-meter increments. In addition, the `maxt`-function (Calenge, 2023) sets a time interval for the duration of time the reindeer is allowed to be outside the set radius without ending the time for the patch residence time, typically to account either for GPS-errors (for

small circles) or occasional movements regarded to not reflect the movement mechanism of primary interest. This time was set to 1 hour (four GPS points).

I first focused on the ten study individuals culled in October to investigate relationships between patch residence time for all radiuses and October body mass adjusted for lactation status. Body mass was adjusted by calculating the mean difference in weight (2.84 kg) between lactating and nonlactating females from another 116 reindeers shot in October in years 1998-2009, and 2021, for a more robust estimate that was independent from the focal individuals. The relationship between PRT and October mass was tested by using a simple linear model (lm) with mean PRT as predictor and adjusted live weight as response variable. In addition, a time series of weekly mean PRT were plotted to visualize how PRT changes throughout late summer and autumn. The slope of weekly PRT differed among individuals and display individual change in PRT through the season (Figure 1). Because of the development of PRT throughout the season, cumulative sum was used in the later analysis. I assumed that the cumulative sum of the daily average PRT for the period between 1st July and 30th September better accounts for changes in PRT during the summer and autumn (Figure 1) and better picks up on differences in PRT development over the season compared to using mean PRT.

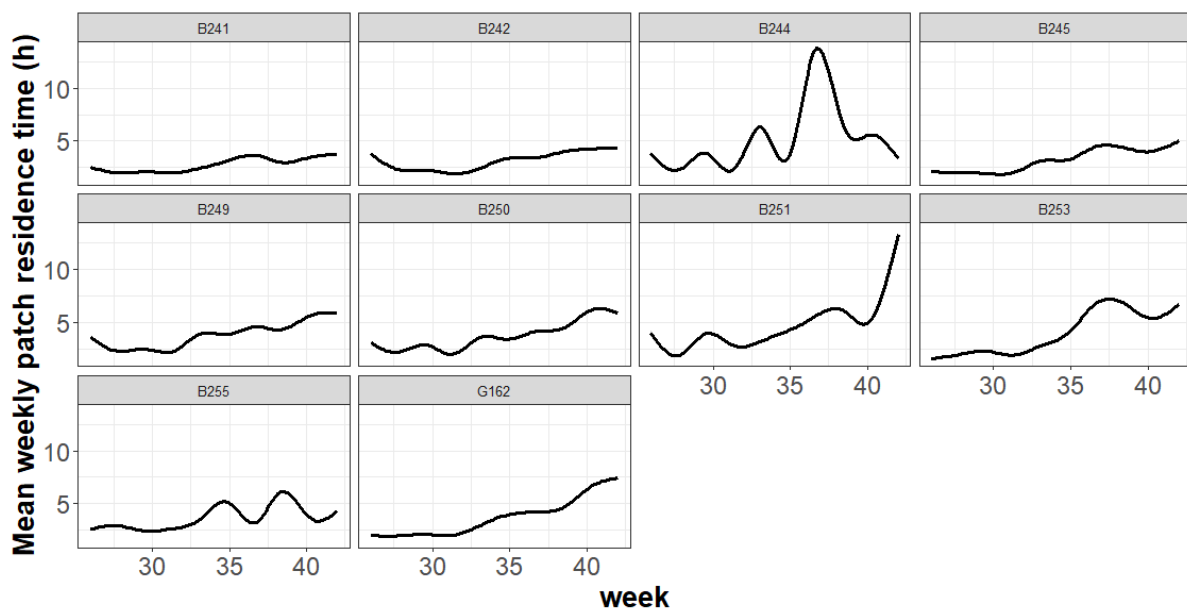


Figure 1 Time series of the development of mean weekly patch residence time from week 26 to week 42 for the ten Svalbard reindeer shot between 18th and 21st of October.

To test for any carry-over effect of cumulative summer and autumn PRT on late winter body mass I matched Cumulative PRT to the following late winter body mass. From the 307 individual-years with GPS-data I only got capture-data with late winter body mass on 156

individual-years. The matching of Cumulative PRT and late winter body mass then created a new dataset with 72 female reindeer over 11 years making up a total 156 individual-years. In addition, I added two other covariables known to affect late winter mass (Loe et al., 2021); subsequent winters ground ice and snow water equivalent. I used a linear mixed model (lmer) with cumulative PRT, Ground Ice and snowwater equivalent as fixed effects with reindeer id and year as random effects. The response variable was April body mass which had been adjusted according to reproductive status last year (factor variable), age (spline function), and which day the individual reindeer were weighed (linear variable) using the same approach as in Loe et al. (2021).

To test if annual plant biomass influences foraging behaviour among Svalbard reindeer, I fitted cumulative PRT (response) to mean summer temperature (predictor) a proxy for plant biomass (Van Der Wal and Stien, 2014) in a linear mixed model, with reindeer id as random effect. The relationship between PRT and visually assessed foraging behaviour was tested by calculating the mean PRT for the exact day of the respective foraging behaviour observation. Then the number of observations of one specific behaviour (Predictor) was fitted against daily mean PRT (Response) in a linear mixed effect model (lmer) with reindeer id as random effect.

Individual home ranges were calculated using the kernel method from the adehabitatHR package in R (Calenge, 2023), which produces accurate estimates of home ranges (Seaman and Powell, 1996). Home ranges were calculated for the period from 1st July to 30^h September. I used the 95% home range, which is a common choice to exclude extreme locations (Seaman and Powell, 1996). This method defines an area in which the individual is located with 95% certainty based on the geographical positions from GPS-collars. The relationship between home range and PRT were tested by a simple linear model (lm) between cumulative PRT (predictor) and the size of home range (response) for the respective reindeer.

3 Results

The effect of Patch residence time on October body mass

As expected, October body mass decreased with lower PRT (Figure 2, Figure 3). Patch residence time (PRT) had a significant effect on body mass for radii spanning from 50 to 400 m (Figure 2), and was most significant at 100 m (largest effect size). Adjusted October body mass varied from 64.2 kg to 75 kg, and mean PRT ranged from 2.9 to 5.8 hours across individuals when radius was set to 100 m. For this radius, the estimated effect of one hour increase in mean PRT was a decrease in 2.19 kg adjusted liveweight (SE = 0.9 and $p = 0.041$). After determining that PRT with 100 m radius had a significant effect on body mass all subsequent analyses were performed with 100 m as the patch radius.

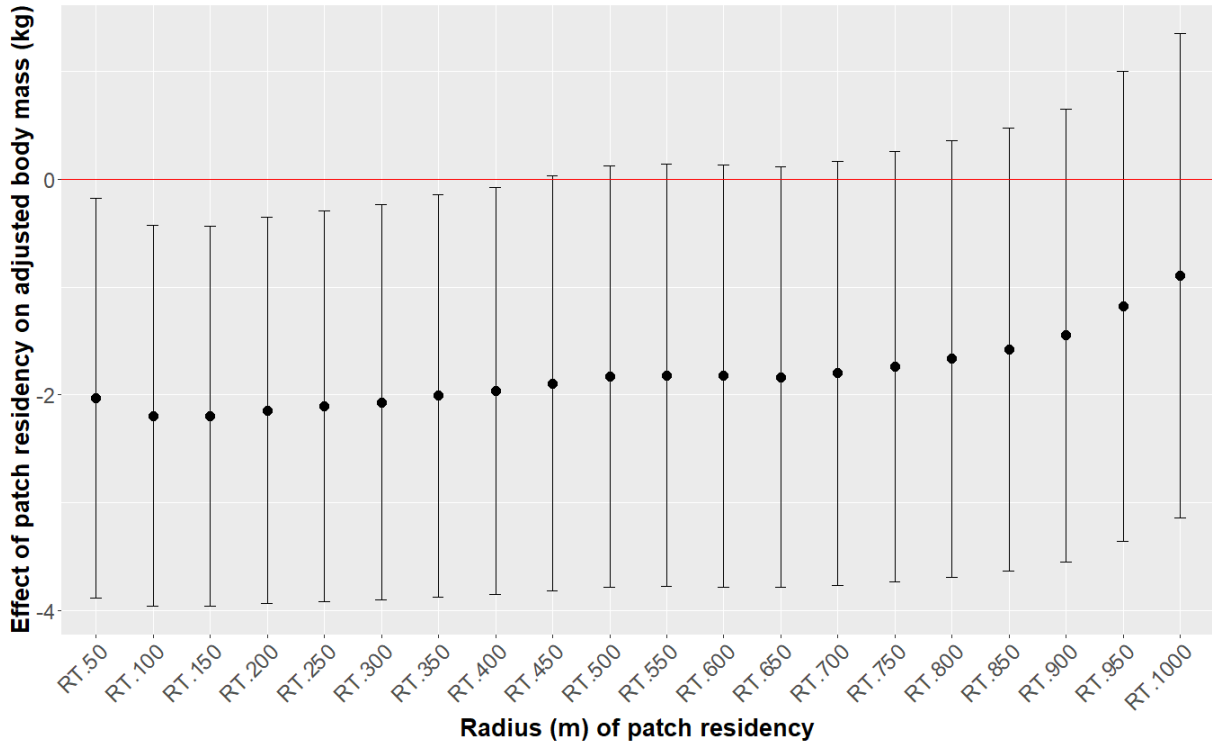


Figure 2 The effect of Patch residence time on body mass adjusted for calf status for the ten female reindeer shot between 18th October and 21st October 2022 for radii from 50 m to 1000 m with 50 m intervals.

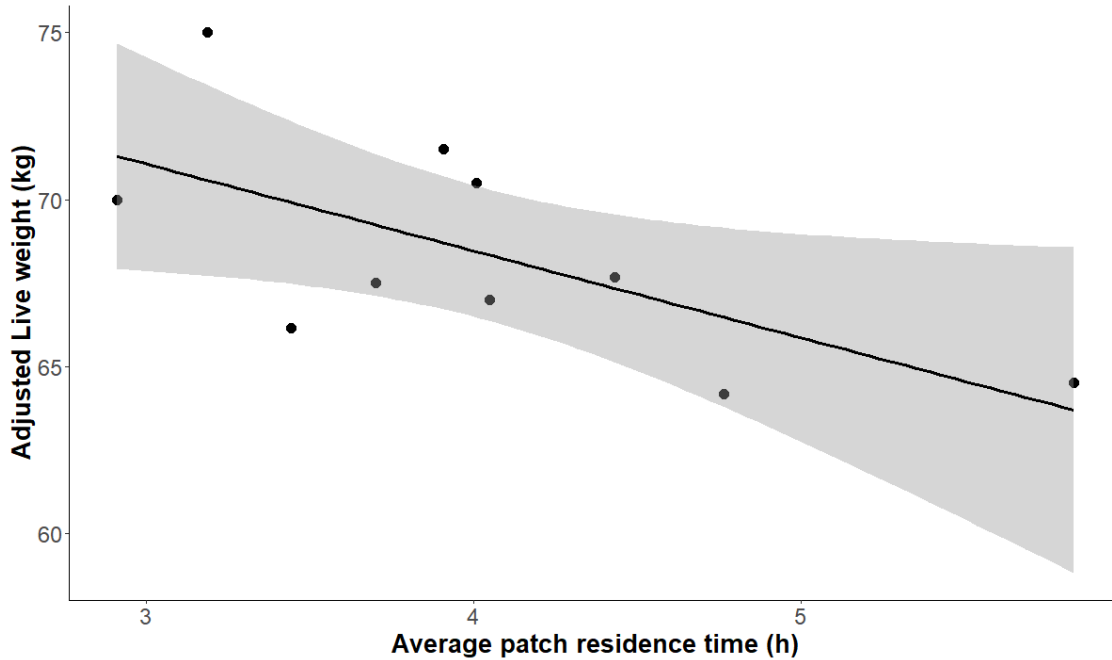


Figure 3 Live weight adjusted for calf status for 10 female Svalbard reindeer shot between 18th October and 21st October 2022 plotted against their average patch residence time with 100 m radius from 1st July to 17th October with fitted regression line and 95% confidence band.

The estimates for all body measures were negatively related to increasing patch residence time (Table 1). The effect size varied, and live weight and adjusted live weight were the only significantly affected measures (Table 1). Out of four fat measures only Loinfat showed signs of a correlation with mean PRT, but it was not significant ($p= 0.128$). The three other fat measures had no correlation with mean PRT (Table 1).

Table 1 Simple linear model (lm) outputs of seven models with scaled mean summer and autumn PRT.100m as predictor on seven body condition measurements (response variable) in 10 female Svalbard reindeer shot between 18th and 21st October 2022. Shown are the slopes (estimate), 95% confidence intervals (CI) and p-value of each estimate. Significant estimates in bold ($p<0.05$).

	Mean PRT 100 m (h)		
<i>Response variable</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
LIVEWT.ADJ (Kg)	-2.19	-4.27 – -0.12	0.041
LIVEWT (Kg)	-1.98	-3.75 – -0.21	0.032
DRESSWT (Kg)	-0.70	-2.61 – 1.21	0.423
SUBCUT (mm)	-1.87	-8.05 – 4.31	0.506
Maxfat (cm)	-0.19	-0.84 – 0.45	0.504
IFBFat. (%)	-1.36	-4.69 – 1.97	0.374
Loinfat (cm)	-0.2	-0.47 – 0.07	0.128

The carry-over effect of cumulative patch residence time on late winter body mass

Late winter body mass was negatively related to cumulative PRT (Figure 4. An increase in one standard deviation of cumulative PRT reduced body mass by 1.34 kg \pm 0.47SE (P=0.005). In addition, ground ice negatively affected late winter body mass with a 1.9 kg decrease in body mass per standard deviation, whereas snow water equivalent did not affect late winter body mass (Table 2). The random effects id and year effected the model showing how the influence of PRT differs between years (Table 2).

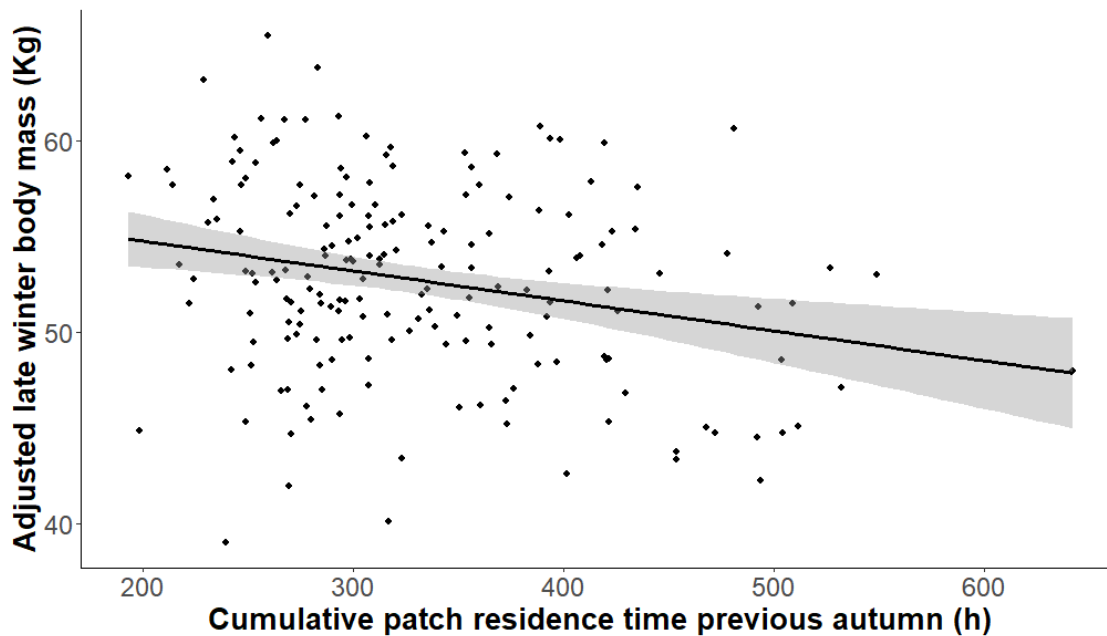


Figure 4 Adjusted late winter body mass for 156 id-years of 72 female Svalbard reindeers plotted against previous summer-autumn cumulative patch residence time with regression line with 95% confidence band.

Table 2 Generalized mixed model (Glm) with factors influencing adjusted late winter body mass of GPS collared female Svalbard reindeer captured between 2009 and 2021 with Reindeer id and year as random effects. Late winter body mass was adjusted according to reproductive status last year (factor variable), age (spline function), and which day the individual reindeer were weighed (linear variable). Shown are the variance and standard deviation for random effects and slopes (estimates), Standard errors (SE), degrees (df), t-value (t) and p-value for fixed effects. Significant estimates in bold $p < 0,05$.

Random effects

Groups	Name	Variance	Std.Dev
Id	(Intercept)	8.460	2.909
Year		4.698	2.167
Residual		9.493	3.081

Number of observations: 156, Groups: id, 72; year, 11

Fixed effects

	Estimates	SE	df	t	P
Intercept	52.4	0.80	13.7	65.2	<0.001
Cumulative PRT 100 m (Scaled)	-1.34	0.47	121.2	-2.89	0.005
Snowwater equivalents (scaled)	0.11	0.49	81.2	0.22	0.82
Ground ice depth (Scaled)	-1.9	0.46	87.2	-4.17	<0.001

PRT in relation to mean summer temperature, foraging behaviour and home range size

The correlations between PRT and temperature depended on the period chosen and was strongest for July and August combined (Table 3). Mean July-August temperature ranged from 4.65 °C to 7.65 °C and mean cumulative PRT ranged from 145.5 h in 2012 and 227.6 h in 2020. Contrary to my prediction mean summer temperature had a positive effect on cumulative PRT, with an estimated increase of 5.5 h in PRT for each 1°C increase mean temperature (P =0.001).

Table 3 The effect of mean summer temperature on Cumulative PRT for different time periods. Shown are the slopes (estimates), confidence intervals (CI) and p-value for each linear model. Significant estimates in bold p<0.05

Mean summer temperatur (°C)			
<i>Response variable</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Csum July (h)	0.82	-0.80 – 2.43	0.320
Csum August (h)	3.04	0.47 – 5.62	0.021
Csum September (h)	1.62	-2.29 – 5.52	0.416
Csum July-August (h)	5.49	2.12 – 8.86	0.001
Csum August-September (h)	4.49	-0.84 – 9.82	0.098
Csum July-September (h)	6.56	0.61 – 12.51	0.031

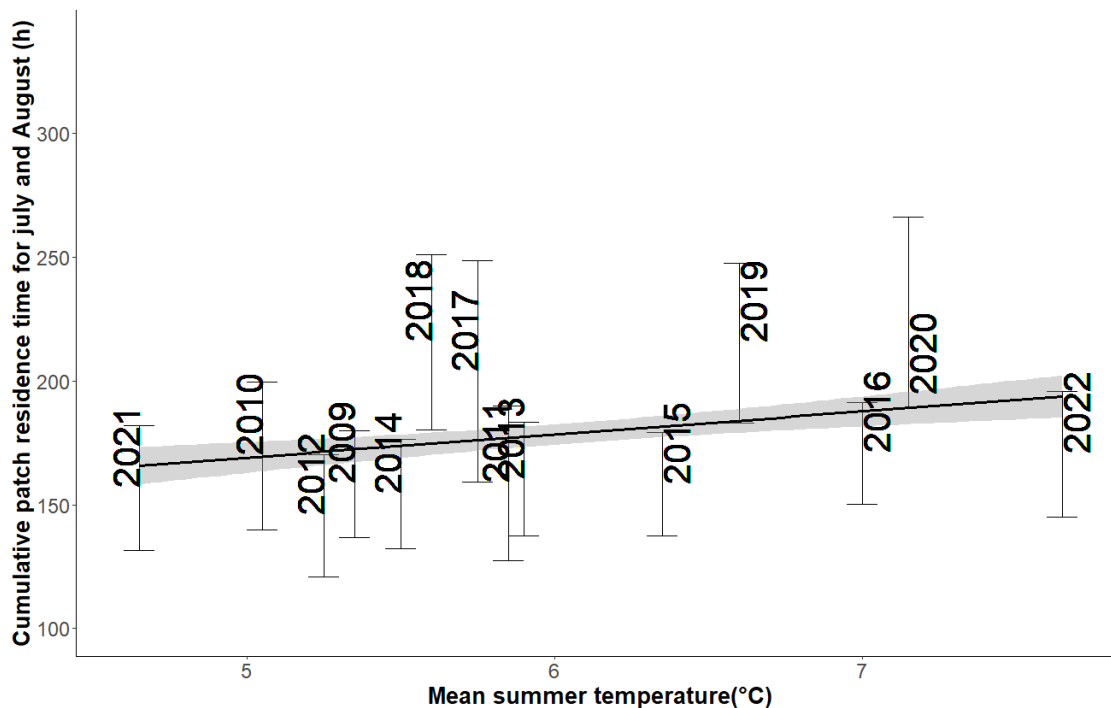


Figure 5 Mean cumulative patch residence time from 1st July and to 31st August with standard error bars plotted against the mean summer temperature (June and July) with fitted regression line and confidence band.

As predicted, daily mean PRT was significantly related to foraging behaviour observed in the field. Mean daily PRT decreased with 0.7 h as walking grazing increased with 1 standard deviation (Figure 6, SE= 0.18, P<0.001) and increased with 0.4 h as standing grazing increased with one standard deviation (Figure 7, SE= 0.19, P=0.05).

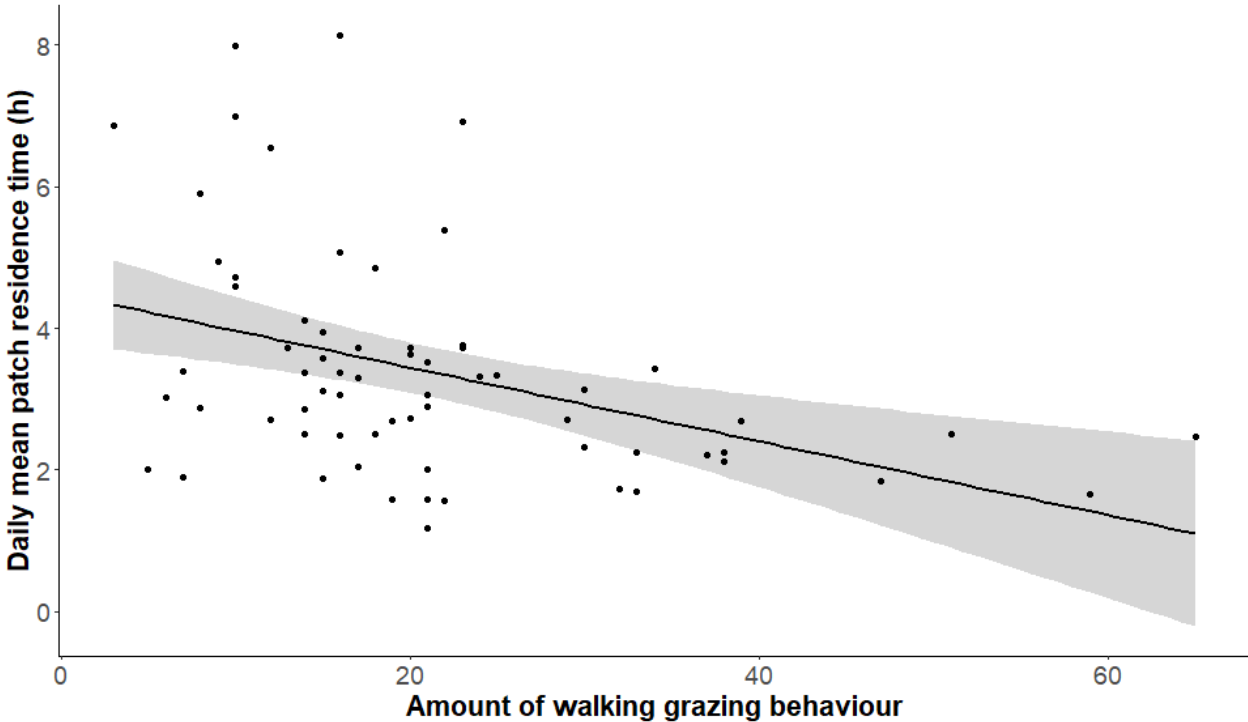


Figure 6 The mean patch residence time for the day of the observation plotted against the amount of walking grazing observations out of a total of 120 observations.

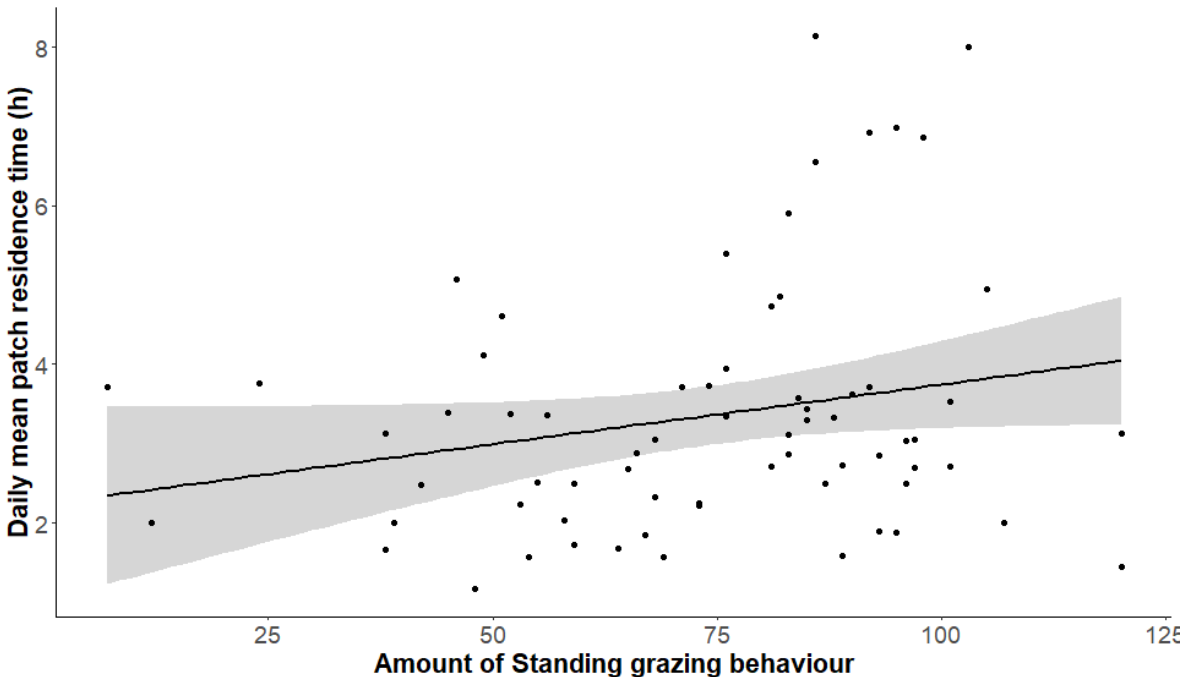


Figure 7 The mean patch residence time for the day of the observation plotted against the amount of standing grazing observations out of a total of 120 observations.

In accordance with my prediction, there was a negative relationship between cumulative PRT and home range from 1st July to 30th September (Figure 8). Home range decreased with 0.11 km² when cumulative PRT for summer and autumn increased by one standard deviation (SE= 0.02, P<0.01).

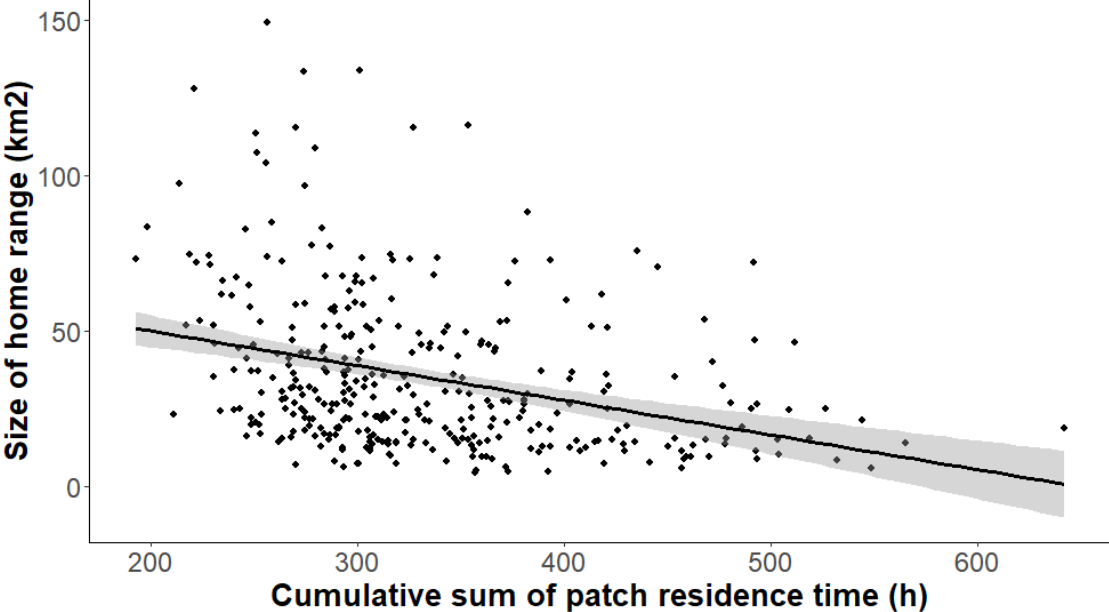


Figure 8 Size of home range and cumulative patch residence time for 303 id-years of female Svalbard reindeer from 2009 to 2022 including prediction line with 95% confidence band.

4 Discussion

My findings of how PRT relates to October and late winter body mass show how movement ecology influences recovery of mass and condition over the summer, known to influence subsequent survival and fecundity in female Svalbard reindeer (Albon et al 2017). The significant negative effect of increased mean summer and autumn PRT on October live weight indicates a benefit from selective grazing and more movement through the landscape. The significant carry-over effect of cumulative PRT on the subsequent late winter body mass in a much larger sample of reindeer (N=156 versus 10) further strengthens the evidence that increased movement has fitness benefits. An increase in PRT indicates that an individual stays longer in the same patch before choosing to move on, while the correlation PRT and mean summer temperature, a proxy for plant standing crop (Van der Wal & Stien 2014), suggests that forage abundance affects foraging behaviour. The relationship between PRT and foraging behaviour was established through the correlations with standing and walking grazing behaviour types. Lower daily mean PRT indicates more standing grazing, while a higher daily mean PRT indicates less walking grazing. Lastly, the correlation with home range size indicates how more movement through lower PRT influences habitat use and spatial exploration. This study demonstrates that movement ecology and foraging behaviour responses to the habitat influences fitness of an arctic herbivore.

Body mass as a nutritional condition measure

Energy reserves and nutritional condition in herbivores is found to be more closely related to fat storage compared to live weight (Cook et al., 2021, Parker et al., 2009). The lack of a significant effect on dressed weight and the four fat measures might contest the relationship between PRT and fitness following the evaluation of nutritional condition measures in Cook et al. (2021). Out of the four fat measures only loin fat displayed a trend in relation to PRT ($p=0.128$) with the three others showing no tendencies (Table 1). For Svalbard reindeer there is however found a strong correlation between October body mass and ovulation (Albon et al., 2017) and late winter body mass and reproduction (Veiberg et al., 2017). Svalbard reindeer also display a huge interannual variation in late winter body mass (Veiberg et al., 2017) and even though fat stores spare body protein oxidation (Barboza and Parker, 2008) there is variation in body protein (Chan-McLeod et al., 2000). This suggests that energy resources are mostly stored in fat reserves, but also in muscle tissue as body protein. Also, for the ten focal individuals culled in October all estimates on autumn body

condition were negative, strengthening the relationship between PRT and body condition. There were however only ten individuals which is a small sample size.

In addition to only ten individuals in the analysis, B244 showed a slope differentiating a lot from the other nine individuals (Figure 1). This individual did also display high body temperatures, indicating a fever, simultaneously as the peak PRT (L. M. Trondrud, unpublished data). With only ten individuals this might have had a severe effect on the model between PRT and body condition measures. The individual was included in the analysis because of the assumption that it represents the natural variation.

Plant biomass influences PRT

The effect of PRT on body mass suggests that individuals differ in utilization of habitat and responds differently to seasonal and annual fluctuations of forage. These responses might be small and seem neglectable, but small differences in patch use, grazing patterns, and forage selection result in a multiplier effect on body mass gain (White 1983). The relationship between cumulative PRT and mean summer temperature (Figure 5), a proxy for plant standing crop shows that PRT is bottom-up influenced from forage availability. The increase in PRT with higher levels of biomass is contrary to my prediction and suggests that Svalbard reindeer do not increase in their selectivity in years with more plant biomass. This may suggest that the search image of food for Svalbard reindeer doesn't change even if the availability of food is greater. Instead of foraging even more selective in years with more plant biomass, the threshold for moving to a new patch increases. Albon et al. (2017) found an increase in October body mass with higher annual plant biomass, the increase in PRT suggests that the underlying cause of this increase is not alternated foraging behaviour through even more selection of high-quality forage, but reduction search effort and movement. The increased PRT with higher level of plant biomass may be a result from higher density of forage leading to decreased need for search behaviour to access the same quality in years with higher plant biomass.

The effect of plant biomass on cumulative PRT varied between time periods and had only an effect on foraging behaviour in August, July and August and July to September with the strongest effect on cumulative PRT for July and August. This shows that the response on plant biomass level is related to late summer/early autumn grazing. The slopes for PRT are more similar around week 30 (figure 1), and the effect of cumulative PRT suggests an additive effect of selectivity later in the season. This indicates that individual foraging behaviour

differences increase from late summer to autumn. When plant senescences, tracking of high-quality forage gets more difficult, and it might be that the difference in October body mass comes from individuals' ability to target higher forage quality even when plant senescences.

PRT is a useful metric for grazing behaviour

There was a correlation between the foraging behaviour types and PRT as expected from the predictions. More WG were correlated with lower PRT, while the opposite relationship was found with SG. If we assume that more WG is a characteristic of more selective feeding where the reindeer are more discriminate in terms of what it eats. PRT provides a link between detailed grazing behaviour of how selective individuals are, in addition to how much they move around while foraging. Herbivores are expected to select for quality landscape level, but for quantity when foraging in a patch (Kaszta et al., 2016) and earlier studies on Svalbard reindeer have found that they select for quantity over quality when foraging (Van der Wal et al., 2000). My data on the benefit of more walking grazing compared to standing grazing suggests that selectivity even at a fine scale is advantageous, but what these individuals select for are outside the scope of this paper.

Foraging herbivores select plant species, specific plant within the same species, bitesize and plant part. We know from studies on other ungulates that they can determine which part of a plant is most nutritious (Hjeljord, 2008). Moose cut off branches at a very precise radius to only target this year's growth to avoid the tannins in the older parts of the branch (Hjeljord, 2008) and diet quality of herbivores is closely linked to what plant parts is clipped (Fortelius, 1985). Higher selectivity in when clipping plants makes up for better digestible food and increased fitness and Svalbard reindeer may have the ability to be as selective. Yoccoz et al. (1993) did however suggest that it may be more advantageous to increase intake rate and reduce search time, especially if discrimination errors are large and nutritional differences small. To further explain what drives PRT on a fine scale bite size and bite rate would have provided even more details in how Svalbard reindeer differ in foraging strategy in addition to species plant part selection. Generally, forage on Svalbard is of high quality (Staalnd et al., 1983, Staalnd, 1984), but following the multiplier effect small differences in daily forage quality intake adds up to an effect on fitness (White, 1983).

Low PRT scale up to a large home range size

The home range of a Svalbard reindeer is mostly decided by forage and tracking of resources (Hansen et al., 2009) since they have few limitations or constraints on their spatial use and movement (Derocher et al., 2000, Williamsen et al., 2019, Reimers, 1977). In accordance with the final prediction larger home ranges and lower PRT correlated suggesting that reindeers who move more and are more selective have a bigger home range. This supports optimal foraging theory in which individuals track high quality forage and utilizes more habitat to track better grazing conditions and more nutritious plants and habitats. Since home ranges are a function of forage quality and quantity (Van Beest et al., 2010, Dussault et al., 2005), individual variations suggest Svalbard reindeer have different requirements of forage abundance or different knowledge of where the best sites are in a seasonal and heterogenous landscape. In a habitat with few limitations, all reindeers can access the same habitat and patches, indicating that knowledge of the forage distribution is the only factor determining differences in home range sizes and search effort. Lower PRT and more search effort increases the home range to satisfy the required forage quality abundance within the home range (Van Beest et al., 2010, Saïd et al., 2009). Since home ranges are known to be regulated from the forage availability (Hansen et al., 2009), the strong relation to PRT provides a confirmation that PRT represents foraging behaviour and selectivity through search effort and movement.

Conclusion

In conclusion, PRT affects fitness of Svalbard reindeer, both as an imminent effect on October body mass and as a carry-over effect on late winter body mass. More selective grazing and subsequent targeting of better forage quality yields a higher energy return in a heterogenous habitat. The small differences between individuals in daily foraging behaviour have a multiplier effect over time and results in higher body mass and better nutritional condition both in the immediate October and as a carry-over effect. Most studies on carry-over effects are on population level or on nutritional condition and not from individual behavioural strategies (Moore and Martin, 2019, Monteith et al., 2014). Knowledge on how carry-over effects diversify within populations are lacking (Moore and Martin, 2019) but are important to improve understanding of species ecology and biology (Marra et al., 2015). My study is the first to document a carry-over effect of individual foraging behaviour in summer and autumn on late winter body mass for a large herbivore with impacts on population growth.

Overall, this study provides evidence of individual foraging benefits through a novel approach using GPS data to quantify the effect of patch use. My study provides a new way of quantifying individual foraging behaviour by using GPS data, and future research should go even more detailed into the grazing choices of plant choice, bite rate and bite size. If these fine scale choices can be related to PRT, GPS data can be used to quantify individual foraging behaviour to better understand within-population differences and individual movement ecology.

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Appendix

Appendix 1. All categories for behavioural observations

Behaviour types	
S	Standing head up
SG	Standing + grazing
SS	Standing + searching (head down)
SC	Standing + chewing (head up)
W	Walking head up
WG	Walking + grazing
WS	Walking + searching
WC	Walking + chewing (head up)
R	Running
SR	Standing and ruminating
WR	Walking and ruminating
LR	Lying and ruminating
SD	Standing and digging in gravel
SDG	Standing, digging and eating in gravel



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