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Sex allocation in Svalbard reindeer (Rangifer tarandus platyrhynchus); do gut parasites and maternal body condition determine the sex of the fetus?

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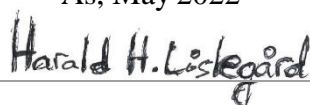
Master of Science in Natural Resource Management

Preface

This thesis is submitted as the final part of my master's degree in Natural Resource Management at the at the Faculty of Environmental Science and Natural Resource Management, Norwegian University of Life Sciences (NMBU).

I would like to thank my supervisor Professor Leif Egil Loe for his guidance and support, and for giving me the opportunity to participate in fieldwork on Svalbard. In addition, I would like to thank Professor Audun Stien for providing me with the dataset and giving me thorough and helpful feedback on the thesis. During my time on Svalbard, I worked closely with Samantha Paige Huset Dwinnell and Tirza Moerman and I would like to thank both for the time we spent together in the field and laboratory.

Finally, I would like to express my greatest appreciation to my friends in Ås and family back home for their good spirit and everlasting optimism and support. A special thanks goes out to my sister Åse Mari for her daily phone calls providing me with news from home.

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Ås, May 2022

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Abstract

Sex ratio is one of the most central demographic factors influencing species population dynamics. Intuitively, fetal sex ratio is a chance event resulting in 50 % males and 50 % females entering the population. However, in many wild birds and mammals this is not the case and sex ratios are skewed as a function of environmental and individual condition. Parasites have an ever-present influence on hosts populations and ecosystems reducing appetite, body condition and fecundity and even regulating host densities. New research has found that parasite-host interactions between a gastrointestinal nematode and a polygamous ungulate indirectly caused sex allocation through a negative effect on hosts body condition. Considering this, the present study examines fetus sex data from 80 individual Svalbard reindeer culled from 1995-2007 to explore if parasite-host interactions, body condition or age causes sex allocation in a novel polygamous ungulate. These relationships were analyzed using a principal component analysis, general linear models and partial least square path-modelling. This study found that fetal sex ratios of Svalbard reindeer followed the expected 1:1 sex ratio predicted from Fisher`s principle. Mothers showed no sign of favoring one sex over the other in relation with their individual age or fitness using back fat depth as a measurement of body condition. Neither of the two dominating abomasum larvae species (*M.marshalli* and *O.gruehneri*) had any direct nor indirect effect (through body condition) on the fetus sex. Furthermore, neither parasite species had a significant assossiation with body condition in Svalbard reindeer. Nevertheless, older animals decreased in body condition and increased in parasite abundance of *O.gruehneri*. The lack of fetal sex allocation in Svalbard reindeer may be caused by the harsh and unpredictable Arctic winter during pregnancy, with lower correlation between body condition in autumn and spring than in many other species. However, body condition and parasite burdens true effects on fetus sex ratios is uncertain in this study due to an offset of four to seven months between time of conception and sampling date. This study underlines the effect variating environmental stochasticity of winters can have on species living in Arctic ecosystems. In addition, it highlights the importance of timing the sampling period of sex allocation studies appropriately, if possible, around the specific specie`s time of conception.

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1 Introduction

Nearly a hundred years ago R.A. Fisher established that sex ratios in species should stabilize near equality due to a mechanism of natural selection leading to frequency-dependent selection (Fisher, 1930). His argument was that if one sex occurs at a lower frequency than the other sex in a population, the less frequent sex will have higher reproductive success due to their increased per capita contribution. The trait of producing the rarer sex will then become more common in the population`s gene pool (Carvalho et al., 1998), leading to selection for individuals producing more of the less frequent sex. This results in the sex ratio approaching and stabilizing at a 1:1 ratio (Fisher`s principle) and is common for sexually reproducing species. This equilibrium is predicted regardless of the species sex-determining system (e.g., sex chromosomes) (Carvalho et al., 1998) and deviations from it are expected to correct themselves within populations (Eshel, 1975). Conversely, skewed sex ratios are found in several vertebrate species (Clark, 1978; Ellegren et al., 1996; Hewison & Gaillard, 1996) and sex allocation theory suggests skewed sex ratios may evolve in situations where the relative fitness of one sex is higher than the other (Charnov, 1982; Ellegren et al., 1996). For vertebrates, the main hypotheses for the evolution of skewed sex ratios focus on situations when the maternal cost of producing a male and a female offspring of high quality differ. In such situations, environmental factors that affect the body condition of adult females may cause skewed sex ratios.

Offspring`s fitness is influenced by parents' ability to nurture, and it may be advantageous to adjust the sex of the offspring to fit the extent that nurture can be provided (Ellegren et al., 1996). All investment made by parents that increases the offspring's survival and reproductive success is called parental investment (Campbell, 1972). The Trivers-Willard hypothesis (TWH) postulates that a male will outproduce a female if both are in good condition at the end of this period (Trivers & Willard, 1973). Using both theory and data the hypothesis demonstrates that mothers in good condition will benefit from investing in the sex with higher variation in reproductive success as natural selection favors a skewed sex allocation. In polygynous ungulates, the males` reproductive success varies to a higher degree than females and depends on its condition and body size compared with the other males as intrasexual fighting over females occur frequently (Andersson, 1994; Hewison & Gaillard, 1999; McElligott et al., 2001). Wild polygynous ungulates often have body size dimorphism as a result of this sexual selection favoring larger body sizes for males (Andersson, 1994; Weckerly, 1998). Maternal

care will therefore benefit the males and mothers in good body condition will produce more sons and mothers in poor condition will produce more daughters (Trivers & Willard, 1973). Empirical support for the TWH have been found in polygynous ungulate species (Kojola & Eloranta, 1989; Kucera, 1991), but contesting results have also been reported (Clark, 1978).

Like the TWH, the Local Resource Competition (LRC) hypothesis also operates through maternal body condition but predicts the opposite sex ratio skew caused by offspring dispersion patterns. In general, mammals exhibit male-biased natal dispersal and this can be caused by resource competition (Greenwood, 1980). This is also frequent among polygamous species and leads to daughters being the more competitive offspring as feeding grounds and mating territories more frequently will overlap. The LRC hypothesis postulates that for philopatric species, mothers in good body condition can afford the potential competition from offspring of the less dispersing sex. Therefore, mothers in poor body condition under environmental stress will benefit from having sons and this leads to male-biased sex allocation (Clark, 1978; Silk, 1983). This skewed sex ratio has been recorded in several polygamous species as a result of environmental stress and body condition (Hewison & Gaillard, 1996; Skogland, 1986; Verme, 1983).

Environmental stress can be caused by parasites, and they have an ever-present influence on wild populations in nature. Biological processes in the animals are altered by parasites and negative effects on host condition and fitness has been demonstrated in empirical studies. Gastrointestinal parasites typically alter their hosts' gut functions and reduce appetite (Marilyn, 1994), may affect host body condition and fecundity (Stien et al., 2002) and even regulate host densities (Albon et al., 2002) as demonstrated for Svalbard reindeer (*Rangifer tarandus platyrhynchus*) infected by the gastrointestinal parasite *Ostertagia gruehneri* (*O.gruehneri*). Recently, Aleuy et al. (2020) demonstrated for the first time that the sex ratio in a large vertebrate was female-biased as a result of a parasite-host interaction. The authors found that the body conditions of ewes of Dall sheep (*Ovis dalli dalli*) was negatively related to the infection intensity of the gastrointestinal nematode *Marshallagia marshalli* (*M.marshalli).* The study concluded that this effect on maternal body condition indirectly influenced the fetal sex ratio in Dall sheep. Females in good body condition and with fewer nematodes of *M.marshalli* were more likely to have female fetuses, in agreement with the LRC hypothesis. Parasite-host interaction and sex allocation studies extend our knowledge of parasite`s ecological impact on animals` population dynamics and their life-history strategies. This is a field that lacks empirical records, and replicating the study done on Dall sheep with a novel species is therefore desirable.

My thesis will explore the fetal sex ratio in Svalbard reindeer in relation to maternal body condition and parasite infection intensities. I will explore if male- or female-biased sex allocation can be found in Svalbard reindeer as a result of maternal parasite intensity, and to which extent such an effect operates through body condition and depend on age. The dominant gastrointestinal parasitic nematodes in Svalbard reindeer are *M.marshalli* and *O.gruehneri*. *M.marshalli* was found to be significant for sex allocation in the Dall sheep study (Aleuy et al., 2020), and *O.gruehneri* has been shown to depress body mass and reproduction in Svalbard reindeer (Albon et al., 2002; Stien et al., 2002). Typically the two species make up more than 95 % of the adult worm burden in Svalbard reindeer (Irvine et al., 2000). Following the strategy in Aleuy et al. (2020) I will evaluate whether the fetal sex ratio in Svalbard reindeer deviates from a 1:1 relationship, and whether fetal sex ratio varies in relation to maternal body condition and parasite intensity. In addition, I will incorporate maternal age as a possible effect on sex allocation as it is expected to depress body condition (Milner et al., 2003). I will test two hypotheses:

H1 – Females in poor body condition will have more female than male offspring

This hypothesis is in line with prediction from the Trivers-Willard hypothesis. Natural selection will drive mothers in poor body condition with fewer resources during parental investment to adjust their sex ratio towards females because a daughter in poor body condition is expected to outproduce a son in similar condition (Trivers & Willard, 1973).

H2 – Females in poor body condition and with high parasite intensity will have more male than female offspring

This is in line with prediction from the Local Resource Competition hypothesis and the results found in the Dall sheep research. To avoid the postweaning cost of a competing offspring, mothers in poor body condition are more likely to adjust their sex ratio towards males, which are more likely to disperse (Clark, 1978). Parasite intensity of *M.marshalli* will influence sex allocation indirectly through a negative effect on maternal body condition and females in good body condition and with fewer gastrointestinal nematodes are more likely to have female fetuses (Aleuy et al., 2020).

2 Materials and method

2.1 Study area

The study was conducted in Nordenskiöld Land, Svalbard, at approximately 78 degrees north and 16 degrees east. The 3500 km^2 area is latitudinally centered in the 61000 km^2 archipelago of Svalbard (figure 1). Nordenskiöld Land`s climate is milder compared to similar latitudinal located areas. This is a result of the warm water provided by the West Spitsbergen Current (Vickers et al., 2021). The southwestern (SW) region of Svalbard including Spitsbergen south of Isfjorden has an annual average temperature of -6.7 °C, with wintertime (Dec–Jan-Feb) averaging at -13.4 °C and summertime (Jun-Jul-Aug) at 1.8 °C (Hanssen-Bauer et al., 2019). The average annual precipitation is 791 millimeters (mm) for the SW region. The autumn/winter season is the wettest with an average precipitation of 453 mm, compared with 339 mm in the spring/summer season. Precipitation is on average highest in September-October and lowest in May-June (Hanssen-Bauer et al., 2019). Snow covers the study area two-thirds of the year (October-June) (Loe et al., 2007).
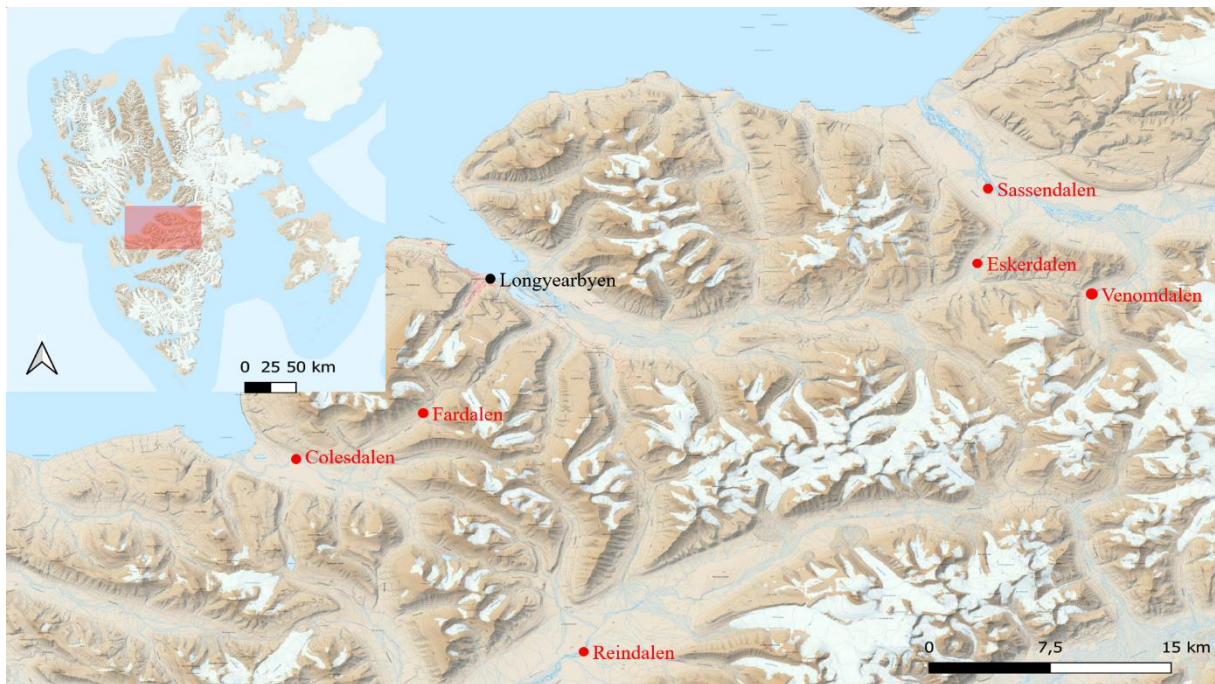

Figure 1. Study area, Svalbard. The six red dots show the location and names of the valley systems where animals were culled. Map data is provided by the Norwegian Polar Institute (Institute, 2020) and the map was created in QGIS.

2.2 Study species

The Svalbard reindeer is a subspecies of reindeer (*Rangifer tarandus*), and only found at the Arctic Archipelago of Svalbard. The Svalbard reindeer are known for their short necks and ears, stubby legs, short round heads and compact torsos (figure 2). They are the only wild large mammalian herbivore on Svalbard and do not experience any intraspecies competition (Loe et al., 2016). Predation from polar bears is minimal (Derocher et al., 2000). The estimated population size of Svalbard reindeer on Nordenskiöld Land during the time of the study (1989 – 2009) was 4000 animals (Le Moullec et al., 2019). Svalbard reindeer`s social system differs from their mainland relatives. In contrast to other Rangifer subspecies, Svalbard reindeer do not live in large herds but occur alone or in small unstable social groups (Alendal, 1974). They are seasonally sedentary, unlikely to migrate out of their own, relatively small, home ranges (Tyler & Øritsland, 1989) and experience minimal human activity (Loe et al., 2007). Natal dispersal rates in females and males are not known due to lack of GPS-marking of calves, but it is assumed that they follow the male bias seen in other *Rangifer* populations (Skogland, 1986; Sørensen, 2021). Late winter body condition and fecundity is primarily determined by interacting effects of Rain-On-Snow events and population density (Hansen et al., 2019a; Hansen et al., 2019b), as well as autumn condition, where warm Octobers and late snowfall has a positive effect (Albon et al., 2017; Loe et al., 2021). In addition there is an approximately 4 kg cost of reproduction of having weaned a calf the previous year (Pigeon et al., 2022). Svalbard reindeers main gut nematodes have a direct life cycle without any additional hosts. *M.marshalli* is considered a "winter parasite" and abundance builds up from October–April. *O.gruehneri* is a more common "summer parasite" peaking in abundance mid-summer (Irvine et al., 2000).

Figure 2. Svalbard reindeer (Rangifer tarandus platyrhynchus). Photo: Leif Egil Loe, 2021

2.3 Data collection

The data set contains information from 80 culled animals from six different valley systems (figure 1). They were culled in a timespan from February to May 1995-2007 with 19 individuals culled in February, 20 in Mars, 27 in April and 14 in May. The majority of animals were culled in Sassendalen (n = 32) and Colesdalen (n = 35) in 1997 (n = 29) and 1998 (n = 29). These valleys are located approximately 40 km East and 20 km Southwest of Longyearbyen (figure 1), still the populations differ in genetic composition (Cote et al., 2002).

Parasite burdens were estimated from counts of adult larvae in the abomasum of culled reindeer. The abomasum was extracted and frozen within three hours of death. It was then thawed, opened, and washed out in water. Adult nematodes were identified (Dróżdż, 1995) and counted from filtered subsamples of the washed-out abomasum content. Male nematodes were speciated and species specific parasite burdens were estimated as twice the number of adult male nematodes of the species (Irvine et al., 2000). The species included in this analysis are *M.marshalli* and *O.gruehneri*. The age of culled reindeer were determined by counting tooth cementum annuli from their incisor teeth (Reimers & Nordby, 1968). Subcutaneous back fat

depths were measured in millimeters measured on the carcass using a ruler (A. Stien Pers. Com.). Fetal sex in utero was determined by visual identification of the reproductive organs of the fetus (L.E. Loe Pers. Com.).

2.4 Data handling

All data manipulation were performed using RStudio Version 1.41103 (RStudio Team, 2021) and the tidyverse package (Wickham et al., 2019).

To correct for seasonal trends in both back fat depth and parasite intensity counts (Appendices; S1A, S1B, S1C, T1), both measures were corrected for sampling date in linear models using the lm() function from the base R package (RStudio Team, 2021). Back fat depth was used as response variable and julian day as the explanatory variable in one model. Original values of the *M.marshalli* and *O.gruehneri* counts were used as response variables and month of culling as the explanatory variable in two other models. I then extracted the residuals from the models as well as the predicted values from the median julian day (98) and the median month (Mars). The residuals were then added to the predicted constants from the median day and month to create the adjusted values for back fat depth and parasite intensities. The resulting dataset for each culled female reindeer included adjusted back fat depth (mm), adjusted abundance of adult *O.gruehneri* and *M.marshalli* in the abomasum, maternal age, fetuses' sex in utero, culling date and culling location. For one reindeer age was missing, so the dataset contained only 79 observations with respect to age. Adjusted back fat depth was used as the measure of female body condition.

2.5 Statistical analysis

All statistical analyses were performed using RStudio Version 1.41103 (RStudio Team, 2021).

2.5.1 Body condition

To analyze if maternal age or parasite burden influenced body condition, I constructed a generalized linear model (GLM) with the glm() function. Back fat depth was used as the response variable, and parasite intensities and age was put as the explanatory variables. The

GLM "family" argument was set to gaussian where "family" describes the error distribution and link function used. Gaussian is the standard "family" with data that has normal error distribution. To confirm normality I ran residual diagnostics using the olsrr package (Hebbali, 2020). Thereafter, I visualized the correlation between back fat depth and parasite intensity of the *M.marshalli* and *O.gruehneri* abundance and age in separate plots. Visualization of the spread and trend of the data was provided by adding data points, trendlines, confidence intervals and correlation coefficients with corresponding p-values to the scatter plots. I used the "pearson" correlation method that runs a parametric test producing Pearson`s correlation coefficient (Akoglu, 2018).

2.5.2 Parasite abundance

To test if animals age influenced their parasite abundance, I put *M.marshalli* and *O.gruehneri* as response variables and age as the explanatory variable in two negative binomial generalized linear models using the glm.nb() function from the mass package (Venables & Ripley, 2013). These models do not allow for negative values, therefore I set the negative adjusted parasite values of *O.gruehneri* (n = 9) and *M.marshalli* (n = 1) to zero using the pmax() function. Furthermore, to explore the correlation between maternal age and parasite intensity I made two plots with *M.marshalli* and *O.gruehneri* counts separately.

2.5.3 Sex allocation

To establish and visualize the associations between the extra uterine characteristics (parasite intensity, maternal age, body condition) and fetus sex, I performed and visualized a principal component analysis (PCA). This allowed me to observe trends, clusters and reduce dimensionality, while at the same time conserving the variance in the dataset (Jolliffe & Cadima, 2016). The analyses was done with the age, back fat depth, *M.marshalli* and *O.gruehneri* counts variables using the prcomp() function. The function allows for scaling of the data and because of the major difference in scales between age, back fat depth and parasite intensity, I saw it advisable to standardize them. All variables were scaled to have a mean of 0 and a variance of 1. This reduces the chance of one of the variables dominating the association in the analysis. The PCA analysis produced four principal components where the two first were used in further analysis. I visualized the PCA with the ggbiplot package (Q.Vu, 2011). I created

normal data ellipses for the distribution of male and female fetuses and vector arrows for the variables. The vectors visualized the strength of each variable, their influence on the principal components (PC) and the correlation between the variables themself. Vectors being more adjacent suggests a positive correlation, orthogonal (90°) suggest uncorrelation and vectors opposite of each other (180°) a negative correlation (Buehler et al., 2011). To test if the principal components had a significant effect on fetus sex, a new dataset was created with predicted PC-values using the predict() function and I ran a GLM. Fetus sex was coded as 0 = female and 1= male and used as the response variable in the GLM, with the GLM "family" argument set to binomial as the model only had two outcomes, male or female. The predicted PC-values were set as explanatory variables.

To determine if fetus sex was evenly distributed, I ran a chi-squared test with the chisq.test() function. Furthermore, to establish if maternal age, parasite burden or body condition influenced fetus sex, I constructed a GLM. I fitted the *M.marshalli* and *O.gruehneri* counts, back fat depth and maternal age as explanatory variables and fetus sex as the response variable in the same GLM. I visualized the correlation between proportion of male fetuses and body condition, parasite intensity of the *M.marshalli* and *O.gruehneri* counts and age in separate plots.

In line with the approach adopted in Aleuy et al. (2020) I fitted a partial least square path-model (PLS-PM) using the plspm package (Sanchez, 2015). Preliminary analyses did not find any effect of *O.gruehneri* on fetus sex. Therefore, in line with Aleuy et al. (2020), I only tested for the effect of *M.marshalli* in my final model. The main goal was to build a model imagining the cause-effect relationship of body condition, maternal age, parasite intensity and fetus sex as a network of variables. PLS-PM allows for calculating the relationships between the variables of the network and quantifying the connections using linear regression (Sanchez, 2013). Running a PLS-PM analysis requires you to set latent variables (LV), and they were defined in the inner model. It was built to measure the direct effect of maternal age on body condition, parasite intensity and fetus sex. In addition, the effect of parasite intensity on body condition and fetus sex. Also, body condition`s effect on fetus sex. It also detects any indirect association between parasite intensity and sex ratio working through body condition. The LV are measured using

manifest variables (MV) as indicators and was defined in the outer model. In my model, only one MV is used for each LV (table1).

Table 1. Latent and manifest variables of the final path model for sex allocation in Svalbard reindeer. Sample number = (n)

Laten variables	Manifest variable	n
Parasite intensity	M.marshalli abundance	*80*
Age	Age (years)	79
Body condition	Back fat depth (mm)	80
Fetus sex	Fetus sex (male or female)	80

Defining the cause-effect relationships in the model was done by creating the vectors of modes. This tells the model if the LV are the cause of the MV (reflective mode) or vice versa (formative mode). In my model formative modes were chosen for all four measurements of the LV. Having built the inner model, the outer model and defined the vector of modes I ran the PLS-path model with the plspm() function. Then I plotted the results with the plot() function and did the visualization in Microsoft Power Point version 2112. Finishing the PLS-PM, I ran a bootstrapping validation to get the necessary data for assessing the associations between the LV.

3 Results

3.1 Body condition

The GLM model incorporating all three variables in the same model showed that parasite intensity did not have any significant effect on body condition (table 2). However, *M.marshalli* had a near-significant p-value (table 2, p = 0.085). Age did have a significant negative association with body condition (table 2, p = 0.023).

Table 2. Parameter estimates for GLM model summarizing the effects of terms on body condition for Svalbard reindeer culled February – May (*n = 79*). SE = Standard error. Degrees of freedom = 78. Near-significant results** = p < 0.1. Significant results* = **p < 0.05**.

Term	Estimate	SE	P
M.marshalli	-0.00054	0.00031	0.085**
O.gruehneri	0.00042	0.0003076	0.12
Age	**-0.92**	**0.40**	**0.023 ***

The predicted back fat depth decreased from approximately 18 to 10 millimeters from minimum to maximum observed *M.marshalli* count, the correlation was low but near-significant (figure 3A, R = -0.19, p = 0.091). Furthermore, the predicted back fat depth increased with a few millimeters from minimum to maximum measured *O.gruehneri* count, but the correlation was minimal and far from significant (figure 3B, R = 0.055, p = 0.63). Predicted back fat decreased from approximately 18 to 10 millimeters from minimum to maximum maternal age, the correlation was near-significant (figure 4, R = -0.21, p = 0.06).
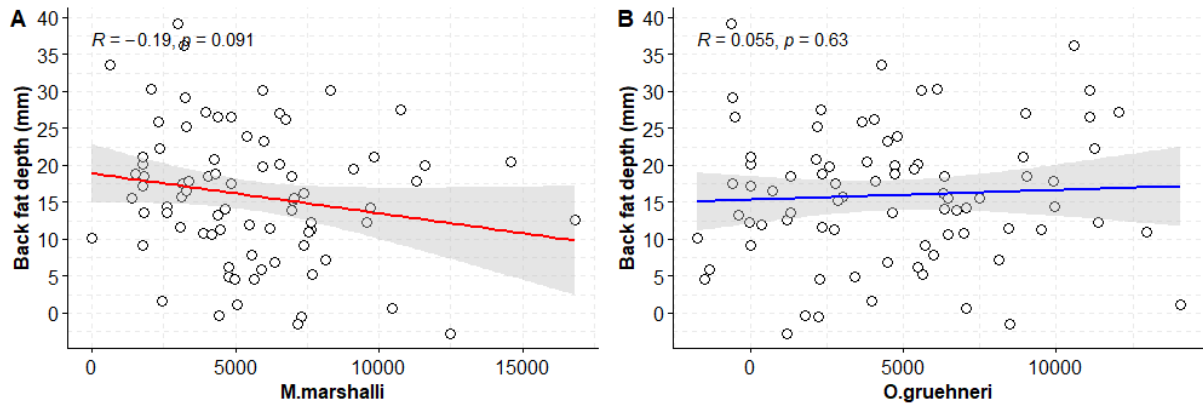
Figure 3. Predicted correlation (R) and p-value (p) between (A) seasonally adjusted *M.marshalli* and (B) *O.gruehneri* counts and seasonally adjusted back fat depth (mm), individuals represented with white circles (*n = 80*). Red and blue linear trend lines with corresponding confidence intervals regions (95 %) in grey.
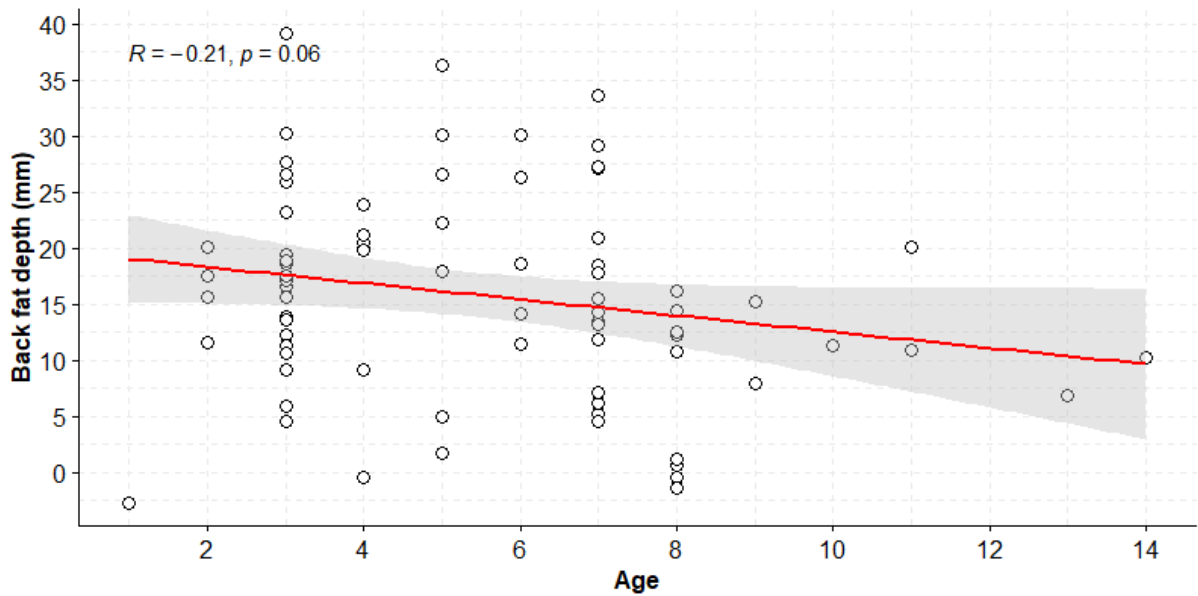

Figure 4. Predicted correlation (R) and p-value (p) between maternal age and seasonally adjusted back fat depth (mm), individuals represented with white circles (*n = 79*). Red linear trend line with corresponding confidence intervals regions (95 %) in grey.

3.2 Parasite abundance

There was a significant association between maternal age and *O.gruehneri* abundance found in the negative binomial generalized linear model (table 3, p = < 0). This was not found for *M.marshalli*.

Table 3. Parameter estimates for negative binomial generalized linear models summarizing the effects of age on parasite counts of *M.marshalli* and *O.gruehneri* for Svalbard reindeer culled February – May (n = 79). SE = Standard error. Degrees of freedom = 78. Near-significant results** = $p < 0.1$. Significant results* = **$p < 0.05$**.

Parasite	Estimate	Term	SE	P
M.marshalli	0.0057	Age	0.029	0.85
O.gruehneri	**0.098**	**Age**	**0.00056**	**< 0***

M.marshalli counts increased in a small and not significant degree with increasing maternal age (figure 5A, R = 0.025, P = 0.83). *O.gruehneri* counts increased significantly with increasing maternal age (figure 5B, R = 0.35, P = 0.0013).
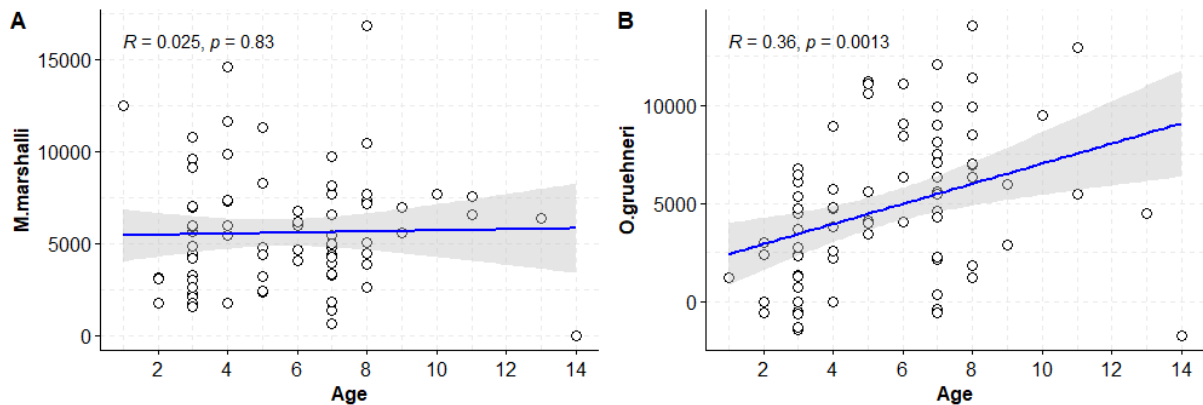

Figure 5. Predicted correlation (R) and p-value (p) between maternal age and seasonally adjusted (A) *M.marshalli* and (B) *O.gruehneri* counts, individuals represented with white circles (*n = 79*). Red and blue linear trend lines with corresponding confidence intervals regions (95 %) in grey.

3.3 Sex allocation

Variation in fetus sex was not explained by either PC1 or PC2 (table 4). The results from the PCA showed that PC1 and PC2 explained 64 % of the variation of the variables, where PC1 explained 37 % and PC2 explained 27 %. *O.gruehneri* is uncorrelated with both *M.marshalli*

and back fat depth, *M.marshalli* and age appears negatively correlated with body condition while age and *O.gruehneri* appears to be positively correlated (figure 6). Sex allocation is not apparent based on lack of any clustering of the fetus data points and data ellipses overlapping each other in the center of the graph (figure 6).

Table 4. Parameter estimates for GLM model summarizing the effects of the principal components from the PCA-analysis on body condition for Svalbard reindeer culled February – May (*n = 79*). SE = Standard error. Degrees of freedom = 78. Near-significant results** = p < 0.1. Significant results* = **p < 0.05**.

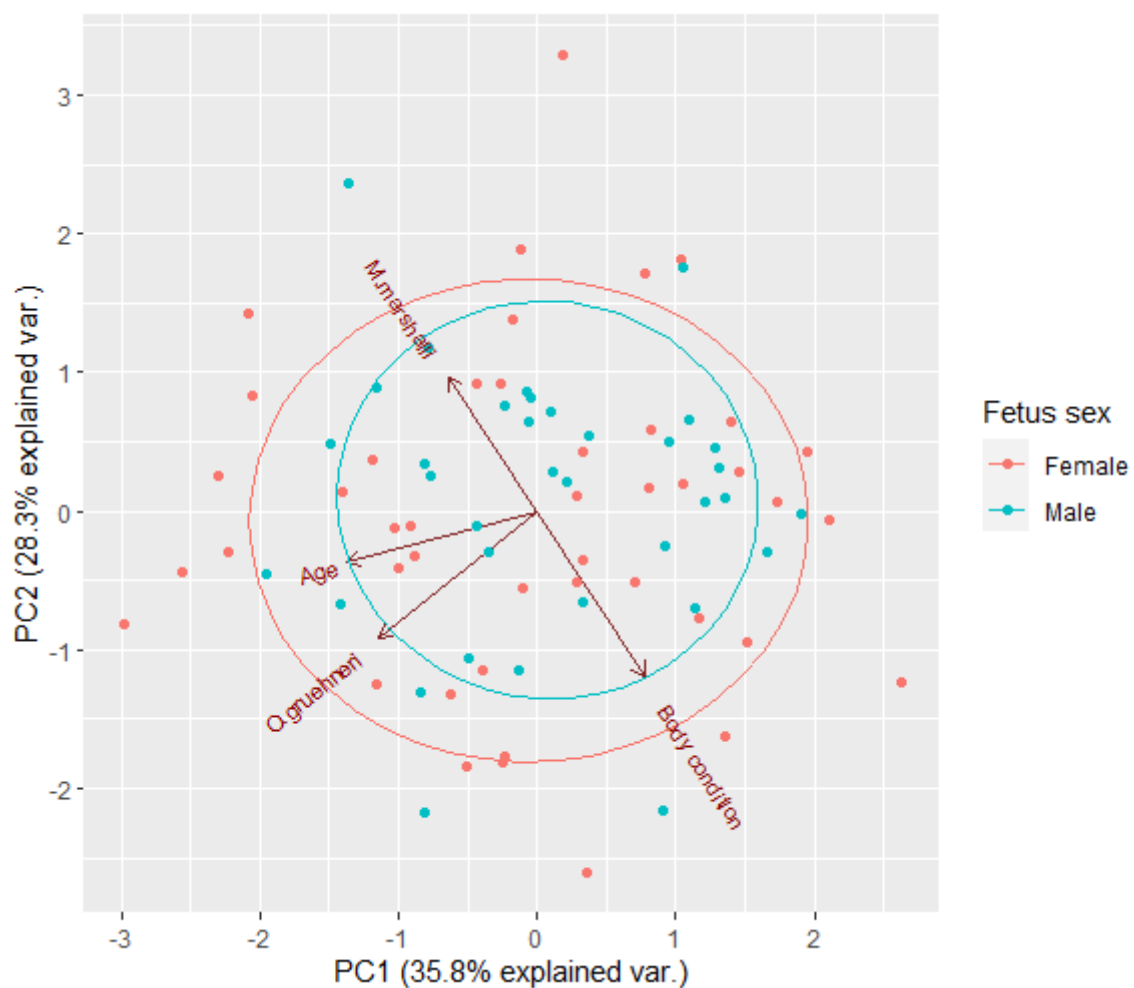| Term	Estimate	SE	P
PC1	0.000033	0.000073	0.65
PC2	-0.000023	0.000066	0.72

Figure 6. Visualization of the principal component analysis illustrating clustering of the fetus sex (red dots = females, blue dots = males), normal data ellipses for the distribution of male and female fetuses (blue and red circles) with vector arrows showing the correlation and strength between the seasonally adjusted variables and the principal components.

Overall, the dataset consisted of 44 female and 36 male fetuses. Therefore, the sex ratio did not deviate significantly from the expected 1:1 sex ratio ($\chi^2 = 0.8$ p = 0.37). The GLM model showed that body condition and parasite intensity did not explain any of the variations in fetus sex (table 5) and this supports neither of my hypotheses (H1 and H2). In addition, age had no effect on fetus sex.

Table 5. Parameter estimates for GLM model summarizing the effects of terms on fetus sex for Svalbard reindeer culled February – May (*n = 79*). SE = Standard error. Degrees of freedom = 78. Near-significant results** = p < 0.1. Significant results* = **p < 0.05**.

Term	Estimate	SE	P
M.marshalli	0.000033	0.00007	0.65
O.gruehneri	-0.000023	0.000066	0.72
Body condition	-0.0013	0.027	0.96
Age	-0.048	0.096	0.62

The predicted male ratio increased a few precent from minimum to maximum observed back fat depth, but the effect was far from significant (figure 7A, R = 0.0096, p = 0.93). The median value of back fat depth for the animals with female and male fetuses was almost identical, but the animals with female fetuses had a larger spread in back fat depth than the animals with male fetuses based on 25th and 75th percentiles (figure 7B). Although the predicted sex ratio increased from approximately 45 to 50 % males from minimum to maximum observed *M.marshalli* count, the effect of parasite burden on sex ratio was not significant (figure 8A, R = 0.038, p = 0.74). The predicted sex ratio decreased from approximately 50 to 35 % males from minimum to maximum observed *O.gruehneri* count, but also this effect was far from significant (figure 8B, R = -0.07, p = 0.54). Proportion of males dropped from approximately 50 to 30 % from minimum to maximum maternal age, but again only composed a non-significant trend (figure 9, R = -0.075, p = 0.51).
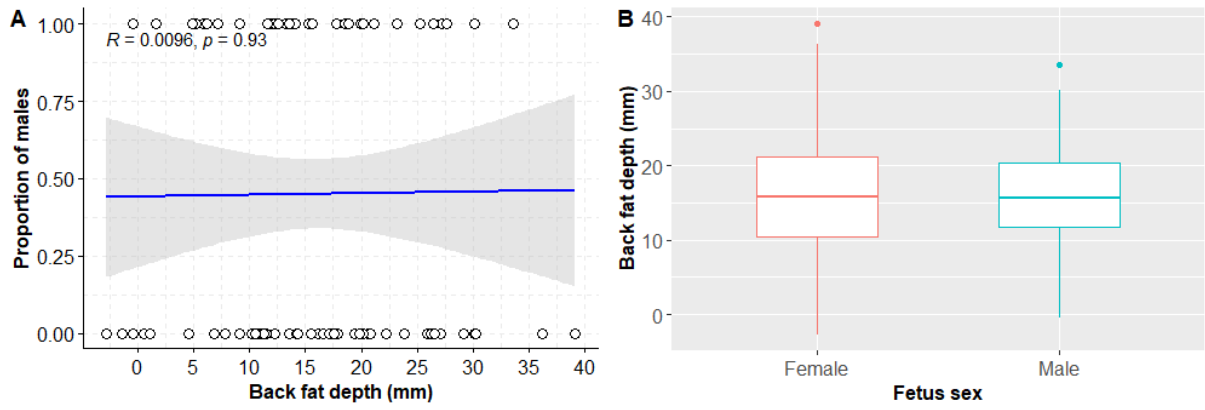
Figure 7. (A) Predicted correlation (R) and p-value (p) between seasonally adjusted back fat depth (mm) and proportion of male fetuses, individuals represented with white circles (*n = 80*). Blue linear trend line with corresponding confidence intervals regions (95 %) in grey. (B) Male and female fetuses' comparison with back fat depth (mm). The middle line through the box represents the median value for each group. The boxes represent the inner-quartile range (the 25th and 75th percentiles; IQR). Whiskers showing the range of data and dots representing outliers.
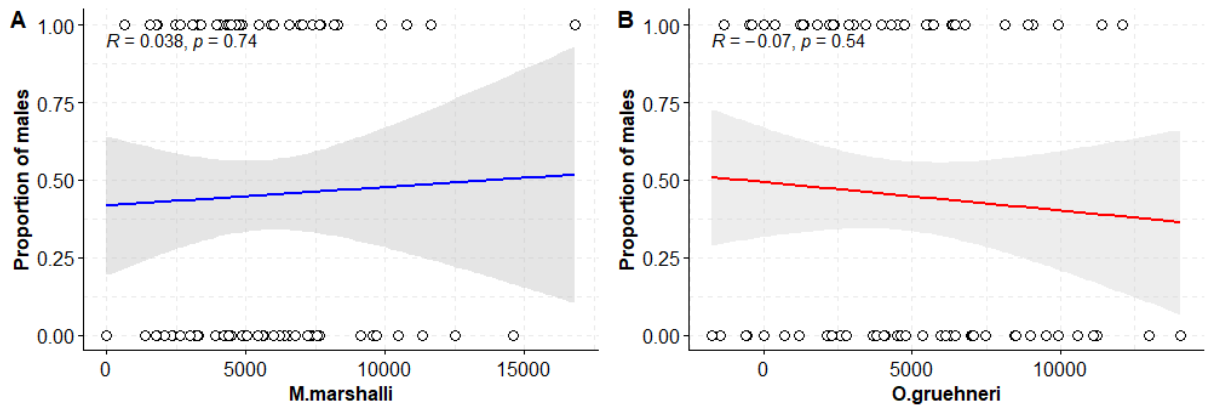
Figure 8. Predicted correlation (R) and p-value (p) between seasonally adjusted (A) *M.marshalli* and (B) *O.gruehneri* counts and proportion of male fetuses, individuals represented with white circles (*n = 80*). Red and blue linear trend lines with corresponding confidence intervals regions (95 %) in grey.

Figure 9. Predicted correlation (R) and p-value (p) between maternal age and back fat depth (mm), count size represented with different sized black circles (*n = 79*). Red linear trend line with corresponding confidence intervals regions (95 %) in grey.

The PLS-PM have the benefit of estimating the above-mentioned relationships in one analysis, including portioning in direct and indirect effects. However, no support for either of my hyp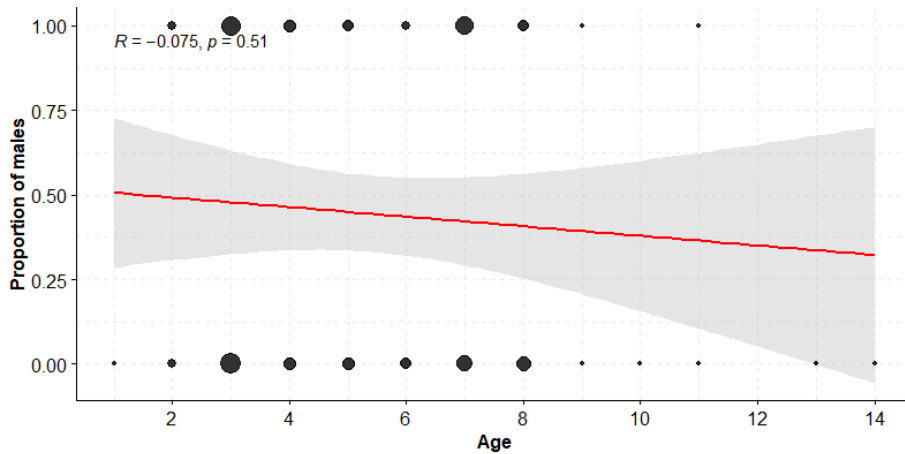otheses (H1 & H2) was found as no direct or indirect significant associations between body condition, parasite intensity and sex ratio were discovered (figure 10). Nevertheless, the negative effect of higher parasite load on body condition was significant in the PLS-PM framework (figure 10). The model confirmed the negative significant effect from the GLM of age on body condition and predicted a small non-significant positive effect of age on *M.marshalli* intensity. The PLS-PM predicted that older animals and animals with higher body condition has more female fetuses shown by the negative association between the variables (figure 10), but this association was not significant. Higher parasite intensity was positively correlated with the tendency of having more male fetuses, this was not significant either. The significance of the path model's associations and their direct and indirect effects on the other LV are illustrated in the tablature with the path coefficients bootstrap confidence intervals. The confidence intervals containing 0 are not significant at a 5 % confidence level (table 6) (Sanchez, 2013).
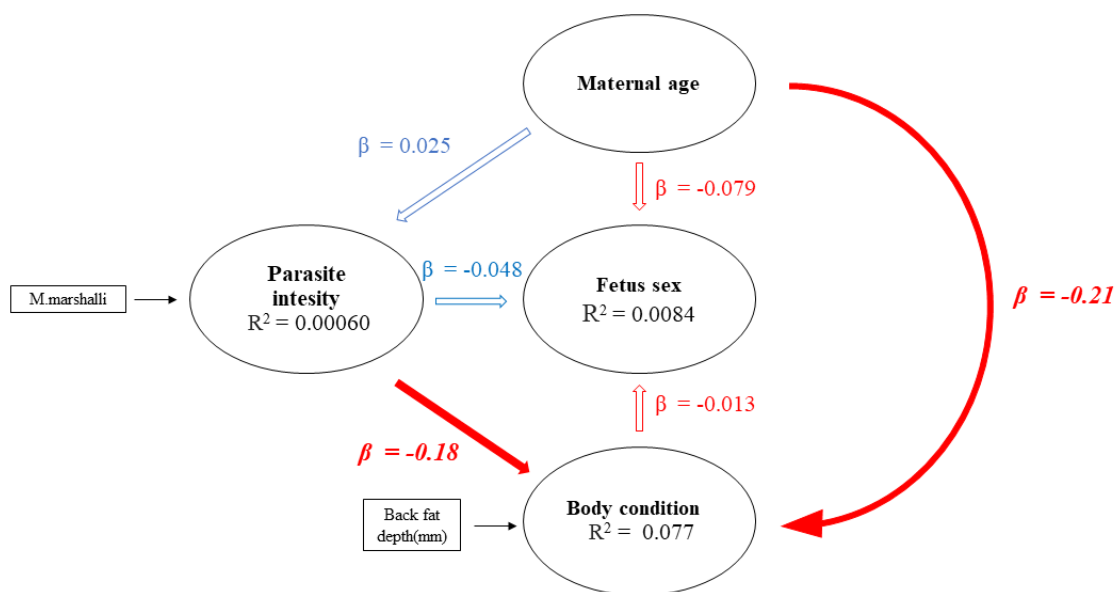
Figure 10. Partial least square path-model illustrating the relationship between the latent variables (maternal age, seasonally adjusted parasite intensity, seasonally adjusted body condition and fetus sex) for Svalbard reindeer (n = 79). R^2 = coefficients of determination for each latent variable (LV) and indicate the amount of variance explained by their independent latent variables. β = path coefficient between the LV. Filled arrows indicates a significant path coefficient confirmed by bootstrapping. Unfilled arrows are non-significant. Red arrows = negative association and blue arrows = positive. Blue arrow on fetus sex = more male fetuses and red arrow = more female fetuses.

Table 6. PLS-PM`s direct, indirect and total effect shown with path coefficients (β) linking the latent variables (LV) representing maternal age, seasonally adjusted parasite intensity, seasonally adjusted body condition and fetus sex. Bootstrapping validations 95 % confidence intervals used for testing statistical **significance***. If the 95 % CI includes 0 = no significant association.

Relationships	Effects			95 % CI
	Direct(β)	Indirect(β)	Total(β)	
Age → Parasite	0.026		-0.26	-0.23 – 0.26
Age → Condition	**-0.21**	**-0.0044**	**-0.21**	**-0.36 – -0.015***
Age → Sex	-0.080	0.0040	-0.075	-0.30 – 0.16
Parasite → Condition	**-0.18**		**-0.18**	**-0.38 – -0.018***
Parasite → Sex	0.048	0.0024	0.050	-0.15 – 0.27
Condition → Sex	-0.013		-0.013	-0.29 – 0.23

4 Discussion

In this study, the relationships between gastrointestinal parasites, body condition, maternal age and fetal sex allocation in Svalbard reindeer were examined. The simplicity of the parasite-host system on Svalbard makes this an ideal species to study parasite-host interactions. A significant effect of maternal age on both parasite intensity and body condition was found as parasite numbers of *O.gruehneri* increased with age and body condition decreased. However, no significant effect of parasite intensity on body condition was found. Furthermore, body condition and parasite intensity caused no significant deviation from a 1:1 sex ratio in Svalbard reindeer fetuses. The results in this study are contrary with the local resource competition hypothesis, the Trivers-Willard hypothesis and the results found in the Dall sheep research. Sex allocation caused by maternal body condition may not occur in the extreme conditions of the stochastic arctic winter on Svalbard, and competition benefits may not apply due to low dispersal of males, although data on dispersal is weak. However, an offset between conception and sampling date might limit the results found in this study. Nevertheless, the findings of the present study build on existing evidence for populations approaching and stabilizing at a 1:1 sex ratio following Fisher`s principle.

4.1 Age, parasite abundance and body condition

In this study, maternal age influenced both parasite abundance and body condition and this supports previous findings. Parasite intensity had no significant association with body condition. However, *M.marshalli* had a near significant negative correlation with body condition, which lends partly support to a previous study done on another ungulate species.

4.1.1 Effect of age on parasite abundance

This study shows a clear linear increase in parasite abundance of *O.gruehneri* with age and this abundance has previously been shown to increase in Svalbard reindeer their second year of age (Irvine et al., 2000). No significant association between age and *M.marshalli* abundance was found in the current study and this also supports previous findings. Conversely, Aleuy et al. (2018) concluded that *M.marshalli* did increase significantly with age in Dall sheep.

M.marshalli on Svalbard has a strong contrasting seasonality compared to other parasitic nematodes, with high winter-transmission and abundance peaking in late winter and declining rapidly towards the summer (Carlsson et al., 2012; Irvine et al., 2000). This can be the result of *M.marshalli* adapting to the High Artic conditions on Svalbard (Carlsson et al., 2012) and *M.marshalli* displays less seasonality in Dall sheep where infection rates are high all year (Aleuy et al., 2018; Nielsen & Neiland, 1974). Carlsson et al. (2012) speculated that the different life-history strategies found in *M.marshalli* could be caused by a species complex within the genus *Marshallagia.* Age does effect parasite abundance, but this effect differs between host species and may be caused by differences in life-history strategies between the hosts parasite populations.

4.1.2 Effect of age on body condition

The reduction in body condition found in older animals in this study was significant and supports previous findings. In my thesis subcutaneous back fat depth measured in millimeters was used as the measurement for maternal body condition. Using back fat depth for assessing condition has its limitations, as it has a narrow range (0 – 42 mm) and it does not place different sized animals on the same comparable basis (Langvatn, 1977). Even so, it is a suitable indicator of total fat in ruminants (Cook et al., 2001; Milner et al., 2003) and used as a predictor for body condition in cervids (Langvatn, 1977). Body condition of Svalbard reindeer has been shown to decrease in older animals (Milner et al., 2003; Stien et al., 2002) and age is an important factor in determining how much food animals can masticate. This determines the rate winter pasture gets eaten as teeth become less effective with age. Mortality rates are higher in winter for reindeer with worn molar teeth and tooth wear increases linearly until the age of eight (Tyler, 1986). This study confirms that older animals will naturally decrease in body condition as they go through senescence.

4.1.3 Effects of parasites on body condition

In this study, which is based on cross sectional data, there was no significant correlation between parasite abundance and body condition and this result lends support to previous findings. Stien et al. (2002) found that anthelmintic treatments (parasite treatments) had no positive effect on body mass and back fat depth in Svalbard reindeer in cross-sectional data but

did find a negative association between worm burden and body condition in their experimental setup. Reduction in body mass and back fat depth in the experiment were mainly caused by *O.gruehneri*, and no negative impact was found for *M.marshalli*. Nevertheless, they theorized that the lack of detection of a negative effect by *M.marshalli* may have been due to the experimental design`s limitations in detecting potential effects caused by the seasonal patterns of *M.marshalli`s* population dynamics. The results from the current study indicates that there may be a biological significant relationship between *M.marshalli* abundance and back fat depth as a near significant correlation was found supporting this claim. *M.marshalli* has been found to have a negative effect on body condition measured in subcutaneous fat reserves in Dall sheep (Aleuy et al., 2018; Aleuy et al., 2020). Conversely, Carlsson et al. (2018) also found no strong improvement in body condition of Svalbard reindeer after anthelmintic treatment and postulated that *M.marshalli* might have evolved a low virulence on Svalbard due to the host experiencing environmental stress by the High Arctic winter. The effects of parasites on body condition seems to vary between ungulate species and *M.marshalli* continues to display an alternative life-history strategy in Svalbard reindeer.

4.2 Sex allocation

No skewed sex ratios were found in this study as a result of body condition, parasite intensity or age. These findings support Fisher`s principle and indicate that natural selection does not favor one sex over the other causing Svalbard reindeer to allocate their offspring's sex. The results found in this study may be caused by environmental factors, life-history strategies and/or data limitations.

4.2.1 The arctic winter may reduce the fitness benefits required for sex allocation

In this study body condition did not influence the fetus sex, and this may be caused by unpredictability considering individual`s energy loss during the winter. No other cervids live as far north as the Svalbard reindeer, and they do experience an unpredictable, extreme and adverse environment and climate (Reimers, 1977; Reimers, 1982; Solberg et al., 2008; Tyler, 1987b) that varies greatly between years (Aanes et al., 2000). Climate factors has been demonstrated to be significant for survival in several ungulate species (Picton, 1984). Furthermore, stochastic variations in winter climate negatively influence Svalbard reindeer`s

population growth by limiting food availability and increasing the energetic cost of movement through increase of snow cover (Aanes et al., 2000). Also, in my study area there has been four years with substantial population declines over the last 25 years as a combination of ROS (rain-on-snow) events and high population densities (Hansen et al., 2019a). Timing of Svalbard reindeer`s peak body condition and their consecutive loss of body mass and fat reserves (Reimers & Ringberg, 1983) correlates with their seven months of pregnancy during the winter (October-June). Despite high fat reserves compared with other *Rangifer* subspecies (Tyler, 1987a), Svalbard reindeer needs to acquire their main daily energy requirements through feeding during winter. Reimers (1982) and Tyler (1987b) found that winter mortality caused by starvation is substantial for Svalbard reindeer. Therefore, survival is more dependent on reindeers ability to sustain a high food intake during the winter than fat reserves in autumn, recently corroborated by Trondrud et al. (2021). These factors make the arctic winter uncertain for both females in good and poor body condition. For that reason, the fitness benefits of a high fat reserve in autumn may not be substantial to drive natural selection towards sex allocation and Svalbard reindeer maintains the expected 1:1 sex ratio of Fisher`s principle.

4.2.2 Low dispersal of young males may render the LRC hypothesis unlikely

Mothers in poor body condition had no male-biased sex allocation in this study and this can be explained by Svalbard reindeer not exhibiting a sex-biased dispersion pattern essential for the LRC hypothesis. This is not something that has been studied extensively in Svalbard reindeer. Nevertheless, it has been tested to a small degree where a tendency was found for young males marked with ear tags as calves to move between two valleys (Colesdalen and Reindalen) and the areas west for the valleys (figure 1) (Sørensen, 2021). Around twenty percent of males from the age of 1 to 3 years old (n = 14) moved between the valley systems, while the remaining 80 % (n = 72) remained faithful to their home valley. No adult males migrated between valleys. The fact that such a low proportion of males were found to disperse may render LRC a weaker driver of competition avoidance than in many other study systems. In addition, Svalbard reindeer exhibit a non-gregarious behavior unlike other *Rangifer* subspecies. They usually live in small seasonal home ranges and remain in small (2-3 animals) social groups (Alendal et al., 1979; Tyler, 1987b) where the mother calf pair form the only stable social bond (L.E. Loe Pers. Com.). It is likely that Svalbard reindeer have a social system where scramble/exploitation is the dominant form for competition, and where the presence/absence of a previous offspring in

your home range has a negligible contribution to the overall grazing pressure. As a result, natural selection will not drive mothers in poor condition towards a male-biased sex allocation if no considerable resource competition benefit is achieved by having more sons.

4.2.3 Effects of offset between conception and data sampling

No support for the TWH was found in this study, but the reliability of this data and the generalizability of the results may be limited by the time passed since conception to the actual measurements were conducted. Cameron (2004) conducted a meta-analysis of mammalian sex ratios studies exploring patterns in sex-allocation theory and found that the TWH was consistently supported in studies that measured female condition around time of conception. She theorized that glucose levels in utero near time of conception and early cell division of the blastocyst may contribute to deciding the fetus sex. A high-fat diet during early cell division has been found to cause male-biased sex allocation in mammals (Rosenfeld et al., 2003). Furthermore, animals with high fat diets demonstrates an increased circulating blood glucose level (Folmer et al., 2003) and high glucose levels during the early blastocyst stage suppresses the growth of female embryos in ungulates (Larson et al., 2001). Cameron et al. (2008) also confirmed a female-biased skewed sex ratio in a mammal with experimental lowered glucose levels at conception. The data used in the current study was collected from February until May, and Svalbard reindeer have a median time of conception around the 24th of October (Loe et al., 2006). If sex allocation is decided by diet around conception, then the approach in the current study is only valid if there is a strong correlation between body condition in February until May and fat-intake in October. Therefore, sampling date is a considerable possible source of error in this study and the available data may not be representable of fat levels around conception when sex allocation occurs.

The true infection rate of *M.marshalli* when the sex is decided may be different than measured due to over-winter transmission by infective larva and this may limit the results found in this study. Larvae and their eggs survive in feces during the winter and this life-history strategy is theorized to be the result of adaptation to long winters (Irvine et al., 2000). Limited grazing opportunities may lead to reindeer eating feces (coprophagy) and ingesting infective larvae leading to increased parasite intensity during the winter season (Carlsson et al., 2012). Irvine et al. (2000) found that Svalbard reindeer had a significant increase in *M.marshalli* abundance from October to April. The parasite intake is controlled by winter grazing opportunity and

feeding strategy for each individual animal or population. If sex allocation occurs shortly after conception as suggested, parasite intensity may have been measured to late in the season and the available parasite data may not be representative of parasite infection abundance around conception in October.

4.2.4 Differences between the Dall sheep research and the Svalbard reindeer data

There are considerable differences in the data used in the Dall sheep research compared with the data from the Svalbard reindeer. This may be why they find sex allocation and the current study do not. The reindeer dataset has a larger dataset, but it is more inconsistent. More individual reindeer were analyzed (n = 79), and they had higher parasite burden of *M.marshalli* (mean = 5185) compared with the sheep (n = 50, mean = 100). All their data was from several Dall sheep subpopulations and the same month, February, and two different years (1971 and 1972). This is a considerable difference between the data sets. The data in the current study is collected from seven different years over a time span of 12 years. The reindeer data was from two distinct populations (Colesdalen and Sassendalen) and four different months. Sampling variation associated with the design, including years that vary in harshness of winter and valleys and populations differ in dietary availability, parasite burden and transmission both in summer and winter limits my results.

5 Conclusion

Parasite-host interactions and fitness-dependent sex allocation changes population dynamics and therefore influences ecosystems and species themselves. I suggest that the unpredictability of the stochastic Arctic winter reduces the possibility for a female to determine the optimal sex of offspring in a given year and can explain the lack of sex allocation in Svalbard reindeer. In general, parasitic nematodes negative effect on hosts can hinder fat intake by altering appetite, reduce glucose concentrations around conception and with that mitigate the inhibiting effect of glucose on female blastocysts. This has the potential to influence sex allocation in accordance with the Trivers-Willard hypothesis leading to animals in poor body condition having more females than animals in good body condition. If there, this effect may not have been discovered in the current study due to the offset between conception period and sampling date. Future studies on sex allocation should consider this a possible source of error and sample their data as near conception as possible, although there are strong methodological challenges in this. Nevertheless, it is important to acquire deeper knowledge of the systems behind species population dynamics. Rapid warming of the arctic is occurring in an increasing degree and species as Svalbard reindeer may become more vulnerable in the long term. Studies like the one conducted in this thesis strengthen the scientific foundation necessary to understand a keystone species in a threatened arctic ecosystem.

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7 Appendices
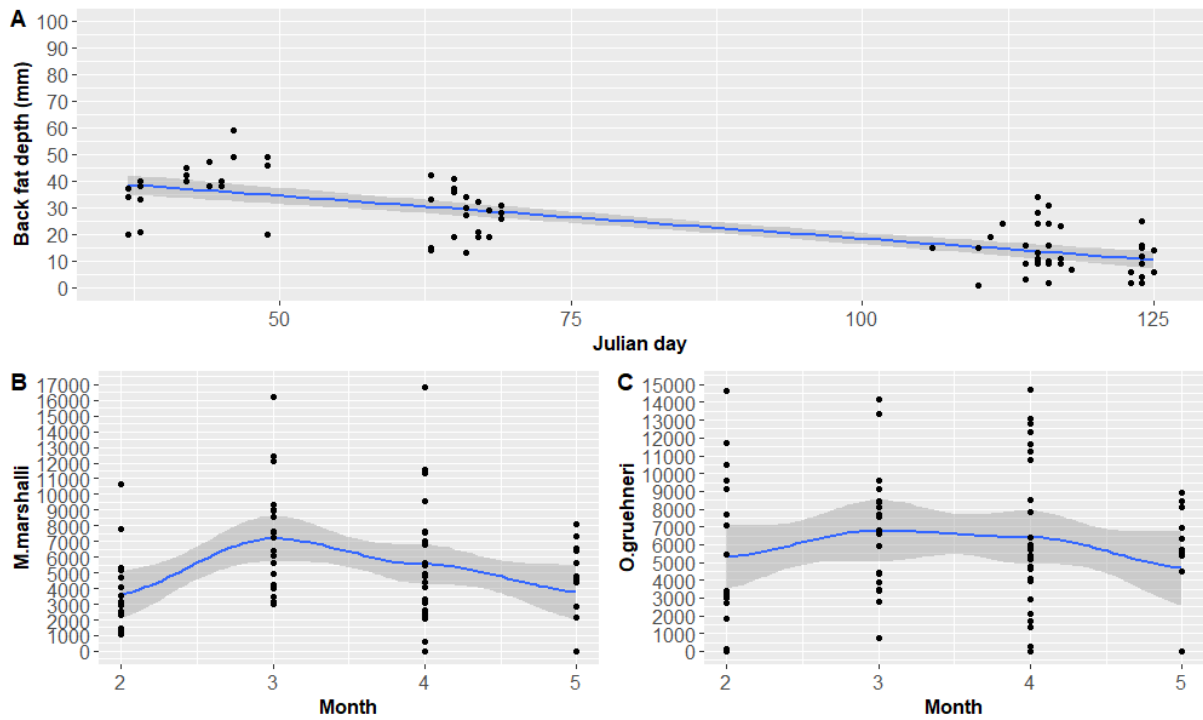
S1. (A) Unadjusted back fat depth measured in millimeters for Svalbard reindeer (n = 80) measured from February – May in relation to julian day. Blue linear trend line demonstrating a clear decrease in back fat depth with increasing julian day. (B) The original unadjusted *M.marshalli* count of Svalbard reindeer (n = 80) measured from February (2) – May (5). A blue trend line is fitted to illustrate the uneven trend throughout the four months. (C) The original unadjusted *O.gruehneri* count of Svalbard reindeer (n = 80) measured from February (2) – May (5). A blue trend line is fitted to illustrate the uneven trend throughout the four months.

T1. Parameter estimates of linear models for seasonally adjustment, SE = Standard error.

Explanatory variable	Response variable	Estimate	SE
Julian day	Back fat depth	-0.32	0.03092
Month	M.marshalli	1378	118
Month	O.gruehneri	1567	134