Body weight, body condition and structural size of Scandinavian wolves

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Body weight, body condition and structural size of Scandinavian wolves

Kroppsvikt, kondition och storlek hos varg i Skandinavien

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Abstract

Large carnivours are suffering from population declines all over the world, but many have also recolonized parts of their previous habitats. However, recovery by these species is usually slow and challenging. The population sizes are therefore often small and semi-isolated which can lead to lowered health, fitness and survival for these individuals. The objective of the present study was to investigate the effects of age, sex, inbreeding, conditions in natal territory (wolf density and food availability) as well as season on three body size measurements; body weight, body condition (residuals from a regression of body weight and body length) and structural size (a principal component analysis of body length, ear length and tail length) in the Scandinavian wolf (*Canis lupus*) population. Two different data sets were used, alive wolves measured when captured (1998 – 2014, n = 159), and dead wolves measured during necropsy (1999 – 2020, n = 329). Males were larger than females and older wolves were larger than younger. Increased level of inbreeding had a negative effect on both body weight and structural size but not on body condition. An increase with 0.1 of the inbreeding coefficient resulted in 1 kg decrease in body weight. The lack of effect on body condition could possibly be due to external circumstances rather than to congenital inbreeding. Food availability in natal territory did not have an effect on any of the size measurements, while wolf density had a positive effect on all three body size measurements. This could possibly be due to the surplus of food seen for this population and may be due to younger wolves are shown to stay with with their parents for longer when wolf densities are high and therefore maybe gaining more food per wolf per day. Body weights were mainly larger in winter than in summer. These results provide knowledge about factors affecting both body size and body condition, and therefore also indications of the health and fitness of the Scandinavian wolf population. This is important for future conservation, as this study shows the importance of management aimed to reduce inbreeding to achieve a more healthy wolf population eventhough the population is growing.

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1. Introduction

Factors such as habitat loss and overexploitation has caused population declines in large carnivores all over the world (Murphy et al., 2016). However, many large mammalian species have also recolonized parts of their previous habitats in the last couple of decades (Chapron et al., 2014; Ripple et al., 2014). But recolonization by large carnivores is relatively slow (Murphy et al., 2016) and the conservation management is often challenging (Cardillo et al., 2004), which ultimately results in many of these populations remaining small and semi-isolated (Åkesson et al., 2016; 2022). This is problematic since small and semi-isolated populations often suffer from lowered fitness (Reed, 2005; Labar & Adami, 2017; Haanes et al., 2013). Individual fitness is of importance since it is directly vital for species or population long term persistence (Reed, 2005).

1.1 Body size and body condition

1.1.1 The importance of body size and body condition

Body size and condition are commonly used indices to study how different factors affect fitness and vitality of populations (Rode et al., 2020). Both body size and body condition reflect an individuals' fitness, health and survival (Rode et al., 2020; Casas et al., 2013). Even though these measurements are different they are often related (Schulte-Hostedde et al., 2005) and are therefore hereafter referred to as body size. An individuals' body size can be important for its social rank, for example, Holand et al. (2004) showed that body size and age of female reindeer (*Rangifer tarandus*) affect their social rank within the herd. Body size can also be important for reproduction. Mysterud et al. (2004) found that reproductive effort increased with body size in male ungulates. Hence, body size can affect an individuals' survival and viability, for instance, a study on cane toads (*Rhinella marina*) by Cabrera-Guzmán et al. (2013) showed that larger body size during metamorphosis enhanced individual survival, growth and performance. According to Brzeski et al. (2014) body size can also affect other traits connected to fitness, such as ability to secure a mate, hunting success, or defending a territory. Both genetic as well as environmental factors, such as sex (Isaac, 2005), inbreeding

(Brzeski et al., 2014) and seasonal conditions (Geffen et al., 1992), can affect changes and variations in body size (Ibáñez et al., 2011).

1.1.2 Factors that may affect body size

Age and sex

Sexual dimorphism in body composition is found in many species and may be the result of differences in reproductive roles between males and females (Schulte-Hostedde et al., 2011). Larger body size and weight in males is common among mammal species and is due to sexual selection favoring larger males (Isaac, 2005). Body size also vary with age, which is an important fitness trait in many species, including the endangered red wolves *(Canis rufus)* (Rabon, 2014).

Inbreeding

Inbreeding often lowers individual fitness and impedes population growth (Hasselgren et al., 2021). Inbred individuals usually possess a more frequent occurrence of homozygous alleles, which are identical by descent in inbred individuals (Keller & Waller, 2002). Such events usually lead to a decreased fitness which is often referred to as inbreeding depression (Keller & Waller, 2002). Several studies have shown an association between inbreeding and a loss of phenotypic traits related to fitness in both captive (Fredrickson & Hedrick, 2002; Tao et al., 2021) and wild populations (Keller & Waller, 2002; Brzeski et al., 2014; Hasselgren et al., 2021). For instance, a study on red wolves by Brzeski et al. (2014) showed that an increased level of inbreeding result in smaller body sizes. Similarly, captive Mexican wolves (*Canis lupus baileyi*) showed a decrease in body weight of adults when the level of inbreeding increased (Fredrickson & Hedrick, 2002).

Conditions in natal territory

Studies have shown that characteristics of an animals’ natal territory can influence certain parts of its adult life (Gicquel et al., 2022; Millon et al., 2011). A study on Seychelles warblers (*Acrocephalus sechellensis*) by Brown et al. (2022) showed that individuals born in seasons with higher food availability and less competition were heavier. Gicquel et al. (2022) studied spotted hyenas (*Crocuta crocuta*) and found that different early life conditions such as maternal care and access to resources had an effect on performance measures later on in life. Similarly, in a study on tawny owls (*Strix aluco*) by Millon et al. (2011), prey density in the natal territory influenced female reproductive performance. Furthermore, Støen et al. (2006) studied brown bears (*Ursus arctos*) and found that natal dispersal probability and distance are density dependent, suggesting that increased female-female competition for space influenced female bears to disperse shorter distances (Støen et al., 2006).

Seasonal changes

Body size has been found to vary seasonally in some canids, such as the Blanford's fox (*Vulpes cana*) (Geffen et al., 1992). According to Geffen et al. (1992), body weights of adult Blanford's foxes increased towards winter and decreased during summer. Sparkman et al. (2011) showed that red wolves living in temperate climates show a variable seasonal predation pattern. These patterns seem to be influenced by the availability of small prey as well as the nutritional condition of larger prey (Sparkman et al., 2011). It is possible that the observed seasonal predation patterns also cause a change in the body weight of red wolves.

1.1.3 Measurements of body size

Body size can be measured in different ways, one way is to use an animals' body weight, similarly to what was done by Fredrickson & Hedrick (2002). Another way is by structural size, which can be done by merging several morphological measures and reducing them into a single index, for example by carrying out a principal components analysis (hereafter: structural size) (Sparkman et al., 2011; Brzeski et al., 2014). One can also measure an individuals body condition. This can be done through the residuals from a regression of body weight and a linear measure of body size (hereafter: body condition) (Schulte-Hostedde et al., 2005; Dobson, 1992). Through these residuals body size will be adjusted so that the relationship between body weight and body size is accounted for (Dobson, 1992).

1.2 The Scandinavian wolf population

After going extinct and later recolonizing the Scandinavian Peninsula, the Scandinavian population of the grey wolf (*Canis lupus*) has suffered from small population size (Åkesson et al., 2016; Liberg et al., 2005). Even though the population has been increasing in numbers, there is a high level of inbreeding following the small number of founding individuals (Åkesson et al., 2016; Liberg et al., 2005). The high level of inbreeding within the Scandinavian wolf population has been found to have negative effects on several traits, such as age at first reproduction (Wikenros et al., 2021), litter size, pup survival (Liberg et al., 2005) as well as breeding success (Åkesson et al., 2016). However, how and to what extent inbreeding affects body size is not known. Previous studies on wolves have found that age, sex, conditions in natal territory and season effects body size or other traits connected to fitness. For example, Sand et al. (2006) showed that hunting success was related to age in breeding male wolves, where older wolves had greater hunting success, most probably due to both experience and older wolves having a larger body size. Furthermore, male wolves had a 25-30% larger body size than female wolves, which could be reason to assume sexual differences in for example hunting success. Sanz-Pérez et al. (2018) studied natal conditions and found that some wolves display a natal habitat-biased dispersal behavior, this was seen for individuals dispersing shorter distances. Similarly, Milleret et al. (2019) found that female wolves reared in territories with a high anthropogenic influence tended to choose areas further away from humans when establishing as a breeding pair with a male. Additionally, according to Sand et al. (2006) it is possible that environmental changes such as seasons influences hunting success and kill rates in Scandinavian wolves.

To better understand how different intrinsic and extrinsic factors affects an individuals' body size, this study focused on the Scandinavian wolves, a population that has been monitored regarding body size, numbers and genetic status of individuals during the last 40 years.

2. Objectives

The objectives of this study were to investigate the effect of age, sex, inbreeding, conditions in natal territory (number of neighbouring territories (hereafter: wolf density) and number of hunter harvested moose (hereafter: food availability)), as well as seasonal changes on three different measurements; body weight, body condition and structural size, in the Scandinavian wolf population. In addition, the known effect of age and sex (Schulte-Hostedde et al., 2011; Isaac, 2005; Sand et al., 2006), were accounted for in the analyses. The following hypothesizes (H) and predictions (P) were made prior to the study;

H1. The level of inbreeding affects body weight, body condition and structural size.
P1. An increase in the individual inbreeding coefficient would be linked to a decrease in body weight, body condition and structural size (Fredrickson & Hedrick, 2002; Brzeski et al., 2014).

H2. Conditions in the natal territory affects body weight, body condition and structural size.
P2. An increase in wolf density in the natal territory would result in smaller wolves due to intra-specific competition.
P3. An increase in food availability in the natal territory would result in larger wolves (Brown et al., 2022).

H3. Season affects body weight, body condition and structural size.
P4. Wolves would be larger during winter months and smaller in warmer seasonal conditions in summer (Geffen et al., 1992).

3. Methods

3.1 Study area and study population

The wolf was hunted to very low numbers in Scandinavia (Norway and Sweden) during the first part of the 20th century (Laikre et al., 2013) and became functionally extinct in the end of the 1960s (Wabakken et al., 2001). During this time, the wolf still existed at higher numbers in the large Finnish/Russian population to the east (Wabakken et al., 2001). In 1978 a known successful reproduction took place in northern Sweden, probably by individuals from the Finnish/Russian source population (Wabakken et al., 2001). In 1983, two more individuals immigrated into south-central Scandinavia and reproduction occurred in one territory during the 1980s (Liberg et al., 2005; Wabakken et al., 2001). In 1991, successful breedings took place in two different places in Scandinavia during the same year, this for the first time since the 1950s (Wabakken et al., 2001). Following these events, the Scandinavian population was slowly reestablished.

3.2 Measurements of body size

In this study two different data sets were used, one from capture events of alive individuals (hereafter: captured individuals) and one from dead individuals which were sent in to the National Veterinary Institute for examination (hereafter: necropsied individuals). As response variables, three different measurements were used; body weight, body condition and structural size. Body weight has been used as a measure of body size in previous studies on wolves (Fredrickson & Hedrick, 2002) and was chosen as a measure to be able to compare results with previous studies. Body condition was calculated from the residuals of a linear regression of body length (without tail) and body weight. This practice is recommended by Jakob et al. (1996). Lastly, a structural size measurement was also used, here a PCA of the measurements body length (without tail), tail length and ear length was carried out. These measurements were chosen since they have been used in similar studies (Sparkman et al., 2011; Brzeski et al., 2014). Those studies also included length of the hindfoot as well as shoulder height, however many individuals in this study lacked these measurements and therefore the PCA was conducted without those measurements.

3.2.1 Captured individuals

The first data set consists of measurements of wolves that have been immobilized and captured by helicopter in Sweden and Norway. For more capture details, see Sand et al. (2006). These captures were done by the Scandinavian Wolf Research Project (SKANDULV) between December and March every year since 1998. Body weight as well as different body measurements were taken when wolves were sedated. When preparing the data from all captured individuals (n = 297) for the analysis, some individuals had to be excluded from the study; all individuals that; lacked any of the measurements for the explanatory variables used in the study (n = 138), lacked a body length measure (n = 19) and lacked a measure for ear or tail length (n= 10). Hence, resulting in a total of 159 individuals for the body weight analysis, 140 individuals for the body condition analysis and 130 individuals for the analysis of structural size.

3.2.2 Necropsied individuals

For the second data set used in the study, the same measurements and variables which were collected during the capture events were here collected from deceased individuals. This data set was based on individuals which died in Sweden and was sent to the National Veterinary Institute (hereafter: SVA). Some individuals were measured by the County Administrative Board staff in field and other by SVA during necropsy. To prepare the data from the necropsied individuals (n = 873), some individuals had to be excluded; all individuals that; lacked any of the explanatory variables used in the study (n = 474), were in a condition that could have influenced their weight or size (i.e. causes such as signs of sarcoptic mange) (n = 25), were emaciated or had the highest grade of decomposition when they arrived at the National Veterinary Institute (n = 15), layed for a longer amount of time in water (assessed by the National Veterinary Institute) or were missing any body parts (n = 30), lacked a body length measure (n = 18) or tail length and ear length (n = 95). Hence, this resulted in a total of 329 individuals in the body weight analysis, 311 individuals in the body condition analysis and 216 individuals for the analysis of structural size.

3.3 Explanatory variables

3.3.1 Age and sex

To account for the change in body size during different life stages, individuals were divided in three different age groups, pups (until 1 year of age), yearlings (between 1 and 2 years of age) and adults (2 years and older). Within the adults, age did not influence body size, as tested by linear regressions of body size and age, similarly to Fredrickson & Hedrick (2002). This was done for all three body size measurements in both data sets (Appendix 1).

3.3.2 Inbreeding coefficient

The Scandinavian wolf population has been monitored every year since 1978. During the first 20 years the monitoring was based on snow tracking only, but thereafter snow-tracking in combination with DNA-sampling is the main method (Åkesson et al., 2022). Biological materials such as faeces, oestrous blood, blood samples and hair have been used for DNA-analyses. From these samples scent-marking individuals has been identified within territories as well as if they reproduced or not. Through snow tracking and DNA-sampling, previous studies have identified breeding pairs which enabled a reconstruction of the pedigree for the Scandinavian wolf population. Through this pedigree, calculations of the inbreeding coefficients for each individual were possible. For a more in-depth description see Liberg et al. (2005) for pedigree reconstruction and Åkesson et al (2016) for DNA-analysis and inbreeding coefficient calculations.

3.3.3 Conditions natal territory

The first variable chosen to represent natal territory conditions was wolf density as a measure of intra-specific competition for resources. The second variable was food availability in terms of moose density in the natal territory. For wolf density, the number of territories surrounding a target territory at a certain year was calculated using data from the annual monitoring of the Scandinavian wolf population (Wabakken et al., 2001). All territories were assigned a radius buffer of 18 km from the territory centroid, representing an average wolf territory size (Mattisson et al., 2013). The number of neighbouring territories were then calculated as the number of overlapping buffers with each territory buffer. Similarly, food availability was based on the same radius buffer from a territory centroid, where the number of hunter harvested moose within this buffer was calculated. The annual number of moose harvested was available at www.algdata.se. It is compulsory for hunters to report their annual harvest of moose.

3.3.4 Season

To account for changes in body weight throughout the year, season was used as a variable in this study. Season was divided into four quarters, quarter 1 (January – March), quarter 2 (April – June), quarter 3 (July – September) and quarter 4 (October – December). Only quarters 1 and 4 were represented in captured individuals due to the capture period only covering the months December – March every year. In necropsied individuals all four quarters were represented.

3.4 Statistical analysis

All statistical analyses were carried out in R version 4.2.1 (R Core Team., 2022). For the data from the captured individuals, Generalized Linear Mixed Models (GLMM) with wolf ID as a random factor were used to account for repeated measures when capturing the same individual more than once (56 repeated measures for the body weight analysis, 44 for body condition and 42 for structural size). Since there were no repeated observations in the data from the necropsied individuals, Generalized Linear Models (GLM) were used. Sex and age group (pups, yearlings and adults) were included in all models since it was assumed that they always had an influence on body size. Additional explanatory variables; inbreeding coefficient, wolf density, food availability and season (for ranges see Table 1) were included with all possible combinations (in total 17 models including the null model, see Tables 3 & 5). For both captured individuals and necropsied individuals, the three response variables body weight, body condition and structural size were used. The highest ranked model for each analysis was calculated using AIC corrected for small sample sizes (AICc). All models with ΔAICc ≤ 2 were considered equally important.

Table 1. Ranges of explanatory variables; age (years), inbreeding coefficient, wolf density (number of neighbouring territories), food availability (number of hunter harvested moose) and season (quarters 1 – 4), for all three response variables; body weight, body condition and structural size, for captured and necropsied wolves in Scandinavia, 1998 – 2020. Also showing the number of models that each explanatory variable (also sex) was included in out of the total number of highest ranked models within ΔAICc ≤ 2 (Models).

Data set	Response variable	Explanatory variable	Models	Range
Captured individuals	Body weight	Sex	4/4	–
		Age	4/4	0 – 9
		Inbreeding coefficient	3/4	0 – 0.44
		Wolf density	1/4	0 - 5
		Food availability	0/4	2.2 – 5.7
		Season	2/4	1, 4
	Body condition	Sex	4/4	–
		Age	4/4	0 – 9
		Inbreeding coefficient	0/4	0 – 0.44
		Wolf density	2/4	0 - 5
		Food availability	0/4	2.2 – 5.7
		Season	2/4	1, 4
	Structural size	Sex	6/6	–
		Age	6/6	0 – 9
		Inbreeding coefficient	2/6	0 – 0.44
		Wolf density	1/6	0 - 5
		Food availability	1/6	2.2 – 5.7
		Season	2/6	1, 4
Necropsied individuals	Body weight	Sex	4/4	–
		Age	4/4	0 – 10
		Inbreeding coefficient	2/4	0 – 0.49
		Wolf density	0/4	0 - 7
		Food availability	0/4	1.8 – 5.5
		Season	2/4	1, 2, 3, 4
	Body condition	Sex	3/3	–
		Age	3/3	0 – 10
		Inbreeding coefficient	1/3	0 – 0.49
		Wolf density	1/3	0 - 7
		Food availability	0/3	1.8 – 5.5
		Season	0/3	1, 2, 3, 4
	Structural size	Sex	1/1	–
		Age	1/1	0 – 10
		Inbreeding coefficient	1/1	0 – 0.49
		Wolf density	1/1	0 - 7
		Food availability	0/1	1.8 – 5.5
		Season	0/1	1, 2, 3, 4

4. Results

4.1 Captured individuals

A moderate to strong correlation was seen between both body weight and body condition as well as between body weight and structural size. Only a weak correlation was seen between body condition and structural size (Table 2).

Table 2. Correlations between the three body size measurements (Response variables); body weight, body condition and structural size, for captured and necropsied wolves in Scandinavia, from 1998 to 2020. Pearson correlation coefficient (r), degrees of freedom (df) and a 95% confidential interval (CI) fram a Pearson correlation analysis are shown.

Data set	Response variables	r	df	95% CI
Captured individuals	Body weight – Body condition	0.756	128	0.671 – 0.821
	Body weight – Structural size	0.663	128	0.554 – 0.750
	Body condition – Structural size	0.210	128	0.039 – 0.369
Necropsied indiciduals	Body weight – Body condition	0.817	214	0.767 – 0.857
	Body weight – Structural size	0.631	214	0.543 – 0.705
	Body condition – Structural size	0.291	214	0.163 – 0.408

4.1.1 Body weight

For the body weight ($n_{observations}$ = 159, $n_{individuals}$ = 103), males (n = 77) had a 26% larger body weight than females (n = 82). Adults (n = 84) had a 5% larger body weight than yearlings (n = 28), and a 25% larger body weight than pups (n = 47). Yearlings had a 19% larger body weight than pups (Fig. 1).

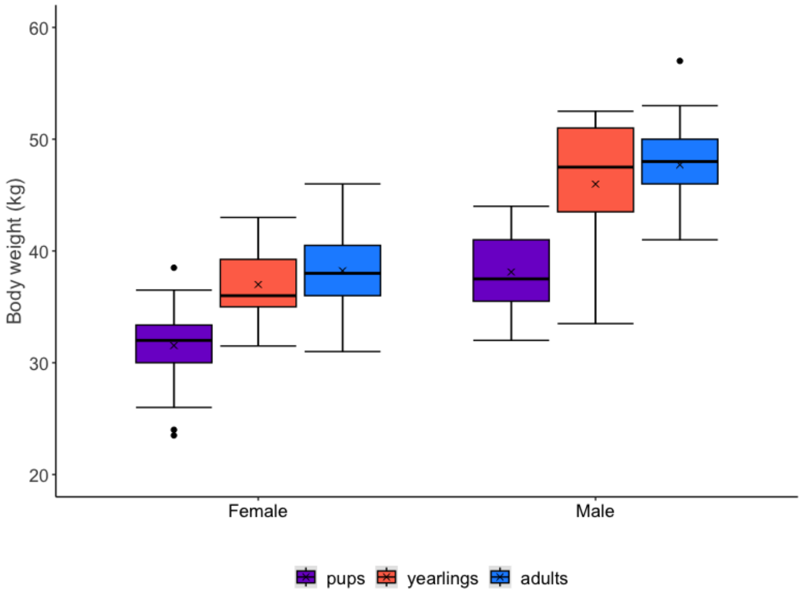

Figure 1. Body weights (median, mean (x), lower error-whisker (Q1 - 1.5 x IQR) and upper error-whisker (Q3 + 1.5 x IQR) and outliers) of captured individuals (n = 159) of the Scandinavian wolf population from 1998 to 2014, in relation to age groups; adults (n = 62), yearlings (n = 50) and pups (n = 47), as well as by sex, female (n = 82) and male (n = 77). Note that the Y-axis start at 20 kg.

When carrying out the model analyses, four models had a $\Delta AICc \leq 2$. The highest ranked model included only inbreeding coefficient and season (apart from age group and sex, which were included in all models) (Table 3). For season, the 95% CI overlapped zero (Table 4), which hereafter will be referred to as weak effects. For a 0.1 increase in inbreeding coefficient the body weight decreased by 1 kg (Fig. 2). The difference in body weight between adults and yearlings was weak.

The second highest ranked model included only inbreeding coefficient, which here had a weak effect on body weight. In the third ranked model only age and sex were included (Appendix 2). In the fourth highest ranked model both inbreeding coefficient, wolf density and season were included. However, both wolf density and season showed weak effects on body weight (Table 4).

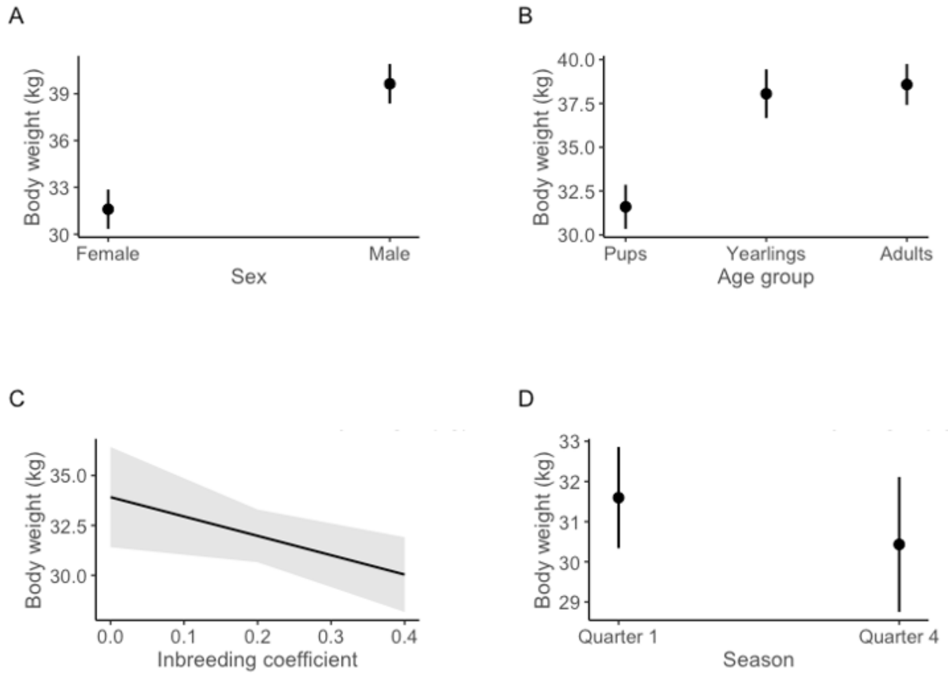

Figure 2. The result of the highest ranked model; the effect of A) sex, B) age, C) inbreeding coefficient and D) season on body weight in captured individuals of the Scandinavian wolf from 1998 to 2014 (n = 159). Note that the Y-axis do not start at zero and are different between the panels.

4.1.2 Body condition

For body condition ($n_{observations} = 140$, $n_{individuals} = 96$) (Appendix 3), males (n = 69) had a positive mean body condition while females (n = 71) had a negative mean body condition. This means that males on average had a larger weight in relation to length than females did. Both age groups adults (n = 73) and yearlings (n = 23) had positive mean body condition while pups (n = 44) had negative (Fig. 3).

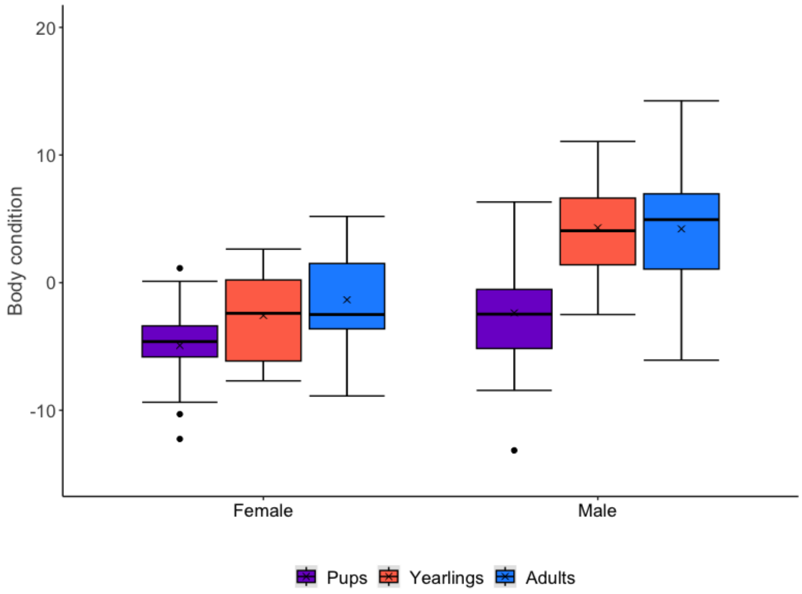

Figure 3. Body condition (residuals from a regression of body weight and body length) from captured individuals (median, mean (x), lower error-whisker (Q1 - 1.5 x IQR) and upper error-whisker (Q3 + 1.5 x IQR) and outliers) (n = 140) of the Scandinavian wolf population from 1998 to 2014, in relation to age groups adults (n = 73), yearlings (n = 23) and pups (n = 44) as well as by sex, female (n = 71) and male (n = 69).

Four models had a ΔAICc ≤ 2, the highest ranked model only included age and sex (Table 3, Fig. 4), however the difference in body condition between age groups adults and yearlings was weak (Table 4).

In the second highest ranked model, season was also included with weak effects, and in the third model, wolf density was included instead of season (Appendix 4). In the fourth ranked model, both wolf density and season were included. A positive relationship was seen between body condition and wolf density, where a greater wolf density was linked to greater body condition, but the effect was weak.

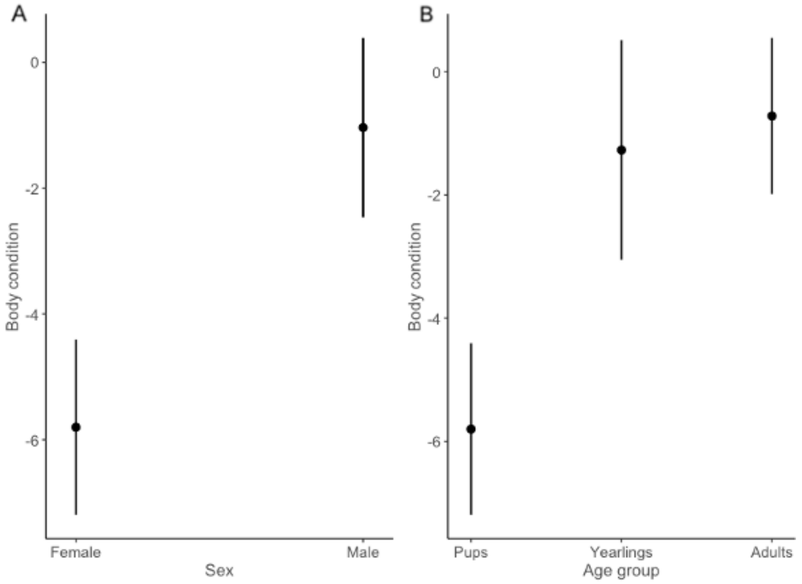

Figure 4. The result of the highest ranked model; the influence of A) sex and B) age on body condition (residuals from a regression of body weight and body length) in captured individuals of the Scandinavian wolf from 1998 to 2014 (n = 140). Note that the y-axis differ between the panels.

4.1.3 Structural size

When calculating structural size through a PCA, PC1 stood for 55% of the total variance and there was a substantial drop in the variance explained by PC2 and PC3 (24% and 21%). All three variables (body length, ear length and tail length) in PC1 were equally important and positively associated with each other (Appendix 5). Hence, PC1 was used as a measurement for structural size.

For structural size($n_{observations}$ = 130, $n_{individuals}$ = 88), males (n = 64) had larger mean structural size than females (n = 66). Adults (n = 67) had larger mean structural sizes than both yearlings (n = 19) and pups (n = 44) (Fig. 5).

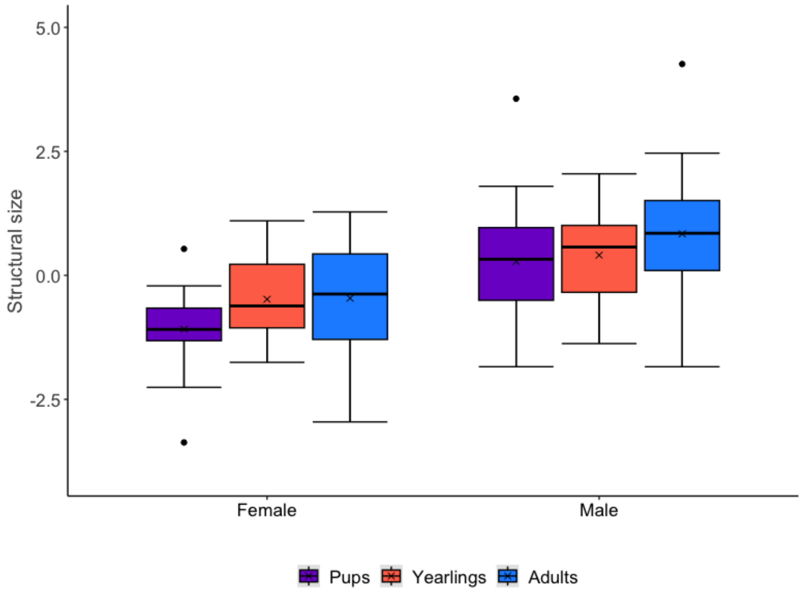

Figure 5. Structural size (PC1 from a PCA of body length, ear length and tail length) of captured individuals (median, mean (x), lower error-whisker (Q1 - 1.5 x IQR) and upper error-whisker (Q3 + 1.5 x IQR) and outliers) (n = 130) of the Scandinavian wolf population between 1998 to 2014, in relation to age groups; adults (n = 67), yearlings (n = 19) and pups (n = 44) as well as by sex, female (n = 66) and male (n = 64). Y-axis starting at -4.

For structural size, six models had a ΔAICc ≤ 2 and the highest ranked model included only age and sex (Fig. 6). The difference in structural size between age groups adults and yearlings was weak (Table 4).

In the second highest ranked model, inbreeding coefficient was also included (Table 3). There was a negative relationship between inbreeding coefficient and structural size, with a decrease of 0.2 in PC1 with a 0.1 increase in inbreeding coefficient (Appendix 6), but the effect was weak (Table 4). In the third model, season was included instead of inbreeding coefficient and in the fourth model, both variables inbreeding coefficient and season were included (Appendix 6). In the fifth model, wolf density was included and in the sixth model, food availability was included. All these variables had weak effects on structural size (Table 4).

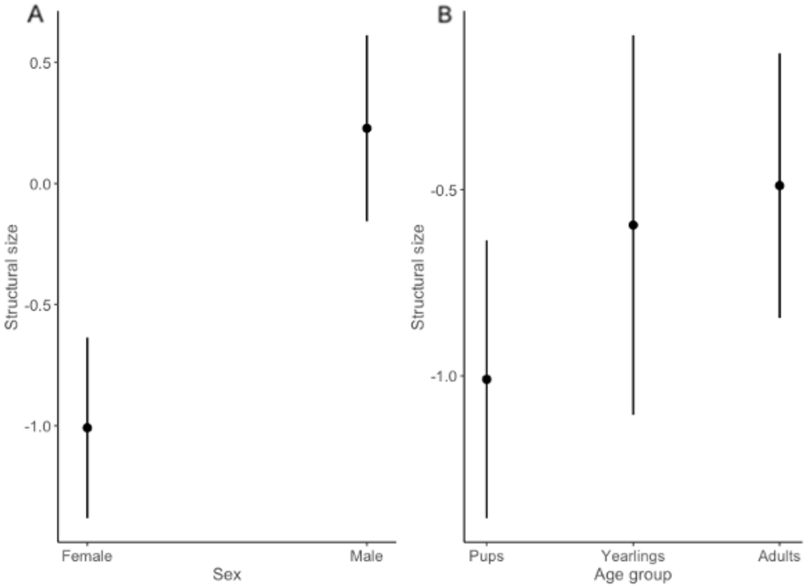

Figure 6. The result of the highest ranked model; The influence of A) sex and B) age group on structural size (PC1 from a PCA of body length, ear length and tail length) in captured individuals of the Scandinavian wolf from 1998 to 2014 (n = 130). Note that y-axis differ between the panels.

Table 3. Generalized linear mixed models to assess the effect of age group, sex, inbreeding coefficient (F), wolf density (number of neighboring territories in natal territory, Wolf) food availability (moose hunt data in natal territory, Moose) and season, on three different body size measures of captured wolves in Scandinavia, from 1998 to 2014,: Body Weight, body condition (body weight and body length residuals) and structural size (PC1 from a PCA of body length, ear length and tail length). For all models, degrees of freedom (df), AICc weight (AIC w.) and AICc relative to the highest ranked model (ΔAICc) are shown.

Response variable	**Model rank**	**Intercept**	**Age**	**Sex**	**F**	**Wolf**	**Moose**	**Season**	**df**	**AICc w.**	**ΔAICc**
Body weight	1	X	X	X	X			X	8	0.20	0
	2	X	X	X	X				7	0.18	0.15
	3	X	X	X					6	0.10	1.31
	4	X	X	X	X	X		X	9	0.07	1.99
		X	X	X	X		X	X	9	0.07	2.22
		X	X	X	X	X			8	0.06	2.25
		X	X	X	X		X		8	0.06	2.31
		X	X	X				X	7	0.06	2.33
		X	X	X		X			7	0.04	3.35
		X	X	X			X		7	0.04	3.46
		X	X	X	X	X	X	X	10	0.02	4.15
		X	X	X		X		X	8	0.02	4.30
		X	X	X	X	X	X		9	0.02	4.36
		X	X	X			X	X	8	0.02	4.53
		X	X	X		X	X		8	0.01	5.47
		X	X	X		X	X	X	9	0.01	6.46
		X							3	0	153.57
Body condition	1	X	X	X					6	0.21	0
	2	X	X	X				X	7	0.14	0.80
	3	X	X	X		X			7	0.10	1.50
	4	X	X	X		X		X	8	0.08	1.94
		X	X	X	X				7	0.08	2.03
		X	X	X			X		7	0.07	2.14
		X	X	X	X			X	8	0.06	2.48
		X	X	X			X	X	8	0.05	2.91
		X	X	X	X	X			8	0.04	3.61
		X	X	X	X	X		X	9	0.03	3.71
		X	X	X		X	X		8	0.03	3.75
		X	X	X	X		X		8	0.03	4.21
		X	X	X		X	X	X	9	0.03	4.23
		X	X	X	X		X	X	9	0.02	4.64
		X	X	X	X	X	X		9	0.01	5.89
		X	X	X	X	X	X	X	10	0.01	6.03

		X							3	0	60.99
Structural size	1	X	X	X					6	0.19	0
	2	X	X	X	X				7	0.18	0.09
	3	X	X	X				X	7	0.10	1.21
	4	X	X	X	X			X	8	0.07	1.91
	5	X	X	X		X			7	0.07	1.94
	6	X	X	X			X		7	0.07	1.99
		X	X	X	X	X			8	0.06	2.16
		X	X	X	X		X		8	0.06	2.17
		X	X	X			X	X	8	0.04	3.32
		X	X	X		X		X	8	0.04	3.34
		X	X	X	X		X	X	9	0.02	4.06
		X	X	X	X	X		X	9	0.02	4.09
		X	X	X		X	X		8	0.02	4.11
		X	X	X	X	X	X		9	0.02	4.37
		X	X	X		X	X	X	9	0.01	5.56
		X	X	X	X	X	X	X	10	0.01	6.36
		X							3	0	27.97

Table 4. Captured individuals of the Scandinavian wolf population from 1998 to 2014. Conditional model parameter estimates (β), with standard error (SE) and a 95% confidential interval (CI) (explanatory variables shown in bold are not overlapping zero) for each explanatory variable in the models within ΔAICc ≤ 2 (Table 1) for all three response variables. The reference for sex is female, for age group the reference is adults and for season it is “quarter 1”.

Response variable	**Model number**	**Explanatory variable**	**β**	**SE**	**95% CI**
Body weight	1	**Intercept**	40.894	1.249	38.4 – 43.357
		Age group: yearlings	-0.526	0.651	-1.895 – 0.784
		Age group: pups	-6.982	0.597	-8.232 – -5.768
		Sex: male	8.037	0.728	6.591 – 9.475
		Inbreeding coefficient	-9.679	4.484	-18.535 – -0.796
		Season: quarter 4	-1.165	0.753	-2.675 – 0.322
	2	**Intercept**	40.41	1.218	37.979 – 42.812
		Age group: yearlings	-0.467	0.655	-1.841 – 0.84950
		Age group: pups	-7.126	0.594	-8.373 – -5.917
		Sex: male	8.066	0.733	6.609 – 9.515
		Inbreeding coefficient	-8.124	4.405	-16.838 – 0.594
	3	**Intercept**	38.432	0.6	37.224 – 39.621
		Age group: yearlings	-0.465	0.658	-1.847 – 0.857
		Age group: pups	-7.05	0.597	-8.299 – -5.839
		Sex: male	8.019	0.746	6.536 – 9.492
	4	**Intercept**	40.775	1.269	38.242 – 43.278
		Age group: yearlings	-0.574	0.657	-1.954 – 0.749
		Age group: pups	-7.0	0.598	-8.251 – -5.786
		Sex: male	8.021	0.727	6.577 – 9.458
		Inbreeding coefficient	-9.68	4.476	-18.52 – -0.812
		Wolf density	0.226	0.444	-0.653 – 1.102
		Season: quarter 4	-1.206	0.758	-2.73 – 0.289
Body condition	1	Intercept	-0.719	0.641	-1.986 – 0.565
		Age group: yearlings	-0.553	0.924	-2.383 – 1.271
		Age group: pups	-5.082	0.763	-6.588 – -3.575
		Sex: male	4.763	0.757	3.255 – 6.26
	2	Intercept	-0.625	0.644	-1.897 – 0.665
		Age group: yearlings	-0.601	0.919	-2.419 – 1.212
		Age group: pups	-4.922	0.771	-6.443 – -3.4
		Sex: male	4.767	0.756	3.261 – 6.262
		Season: quarter 4	-1.362	1.141	-3.615 – 0.893
	3	Intercept	-0.952	0.696	-2.326 – 0.438
		Age group: yearlings	-0.568	0.922	-2.392 – 1.251

		Age group: pups	-5.114	0.762	-6.618 – -3.61
		Sex: male	4.732	0.756	3.226 – 6.227
		Wolf density	0.42	0.494	-0.557 – 1.401
	4	Intercept	-0.905	0.694	-2.275 – 0.481
		Age group: yearlings	-0.629	0.915	-2.438 – 1.179
		Age group: pups	-4.941	0.768	-6.456 – -3.425
		Sex: male	4.729	0.754	3.229 – 6.221
		Wolf density	0.526	0.499	-0.458 – 1.517
		Season: quarter 4	-1.552	1.15	-3.823 – 0.722
Structural size	1	**Intercept**	-0.489	0.18	-0.85 – -0.134
		Age group: yearlings	-0.106	0.269	-0.648 – 0.43
		Age group: pups	-0.52	0.208	-0.937 – -0.104
		Sex: male	1.237	0.208	0.824 – 1.649
	2	Intercept	-0.009	0.369	-0.746 – 0.72
		Age group: yearlings	-0.133	0.268	-0.675 – 0.401
		Age group: pups	-0.516	0.207	-0.928 – -0.103
		Sex: male	1.211	0.206	0.803 – 1.619
		Inbreeding coefficient	-1.949	1.321	-4.56 – 0.672
	3	**Intercept**	-0.511	0.18	-0.874 – -0.155
		Age group: yearlings	-0.094	0.268	-0.636 – 0.44
		Age group: pups	-0.554	0.210	-0.974 – -0.134
		Sex: male	1.236	0.207	0.824 – 1.646
		Season: quarter 4	0.309	0.305	-0.293 – 0.91
	4	Intercept	-0.08	0.383	-0.847 – 0.677
		Age group: yearlings	-0.122	0.268	-0.664 – 0.413
		Age group: pups	-0.539	0.209	-0.957 – -0.121
		Sex: male	1.213	0.206	0.805 – 1.62
		Inbreeding coefficient	-1.721	1.362	-4.412 – 0.983
		Season: quarter 4	0.211	0.312	-0.406 – 0.828
	5	Intercept	-0.312	0.4	-1.112 – 0.478
		Age group: yearlings	-0.124	0.271	-0.671 – 0.416
		Age group: pups	-0.534	0.21	-0.953 – -0.114
		Sex: male	1.244	0.208	0.83 – 1.655
		Food availability	-0.046	0.093	-0.231 – 0.14
	6	**Intercept**	-0.528	0.194	-0.913 – -0.145
		Age group: yearlings	-0.118	0.27	-0.662 – 0.419
		Age group: pups	-0.529	0.208	-0.946 – -0.112
		Sex: male	1.232	0.207	0.822 – 1.641
		Wolf density	0.074	0.135	-0.2 – 0.341

4.2 Necropsied individuals

A moderate to strong correlation was seen between both body weight and body condition as well as between body weight and structural size. A weak correlation was seen between body condition and structural size (Table 2).

4.2.1 Body weight

For the overall body weight (n = 329), males (n = 186) had a 24% larger mean body weight than females (n = 143). Adults (n = 106) had a 8% larger mean body weight than yearlings (n = 154), and a 32% larger mean body weight than pups (n = 69). Yearlings had a 22% larger mean body weight than pups (Fig. 7).

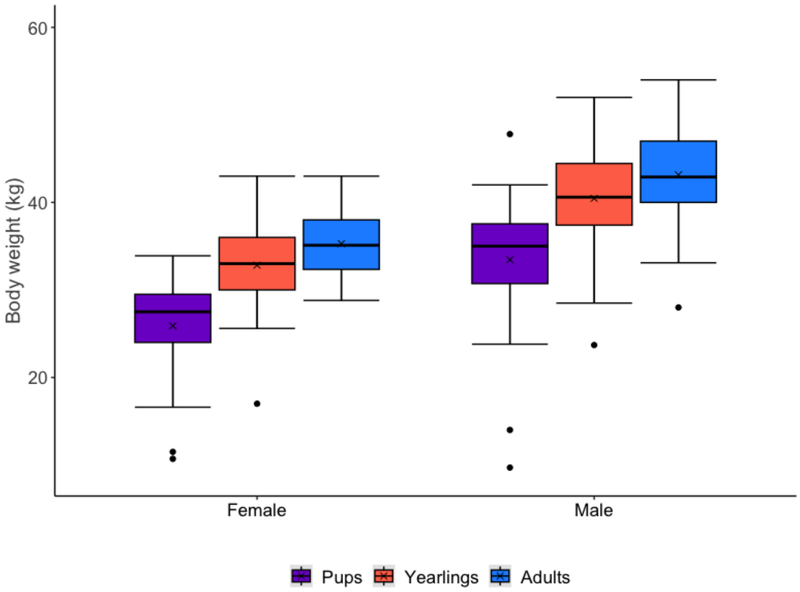

Figure 7. Body weight of necropsied individuals (median, mean (x), lower error-whisker (Q1 - 1.5 x IQR) and upper error-whisker (Q3 + 1.5 x IQR) and outliers) (n = 329) of the Scandinavian wolf population from 1999 to 2020, in relation to age groups; adults (n = 106), yearlings (n = 154) and pups (n = 69) as well as by sex, female (n = 143) and male (n = 186). Note that the Y-axis start at 9 kg.

Four models had a ΔAICc ≤ 2. The highest ranked model included season (Table 5), where the largest body weight was seen for wolves in quarter 1, and there was a difference between quarter 1 and 3 (Fig. 8). In the second highest ranked model only age and sex were included. In the third model inbreeding coefficient and season was included (Table 5). A 0.1 increase in inbreeding coefficient resulted in a decrease in body weight by 0.26 kg in the third highest ranked model (Appendix 7), however it was a weak effect (Table 6). In the fourth model only inbreeding coefficient was included, also here the effect was weak.

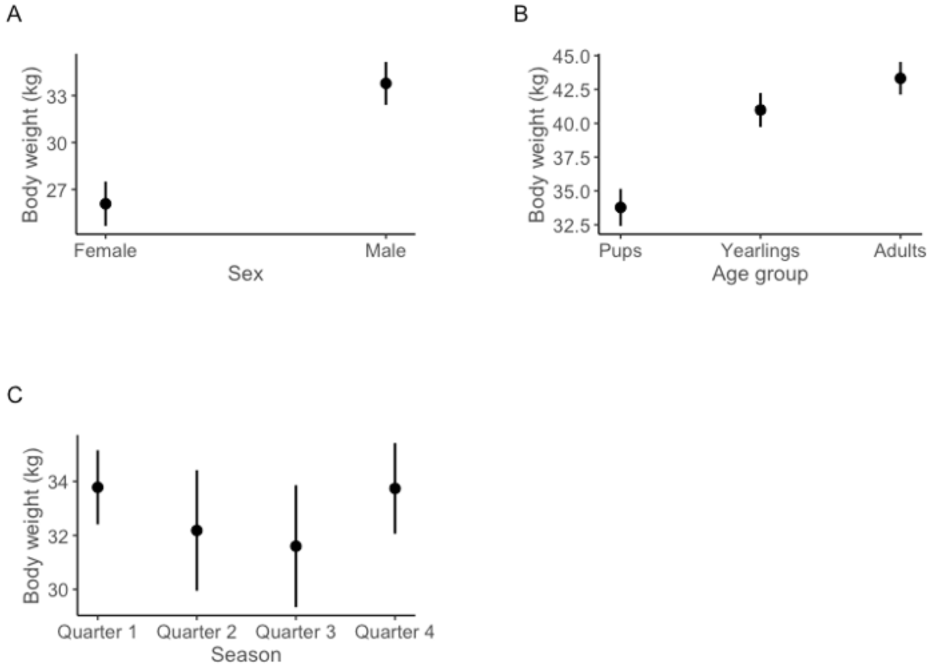

Figure 8. The result of the highest ranked model; the influence of A) sex, B) age and C) season on body weight for necropsied individuals of the Scandinavian wolf from 1999 to 2020 (n = 329). Note that the Y-axis do not start at zero and differ between the panels.

4.2.2 Body condition

For body condition (n = 311) (Appendix 8), males (n = 179) had a positive mean body condition while females (n = 132) had negative (Fig. 9). Both age groups adults (n = 107) and yearlings (n = 146) had positive mean body conditions while pups (n = 58) had negative.

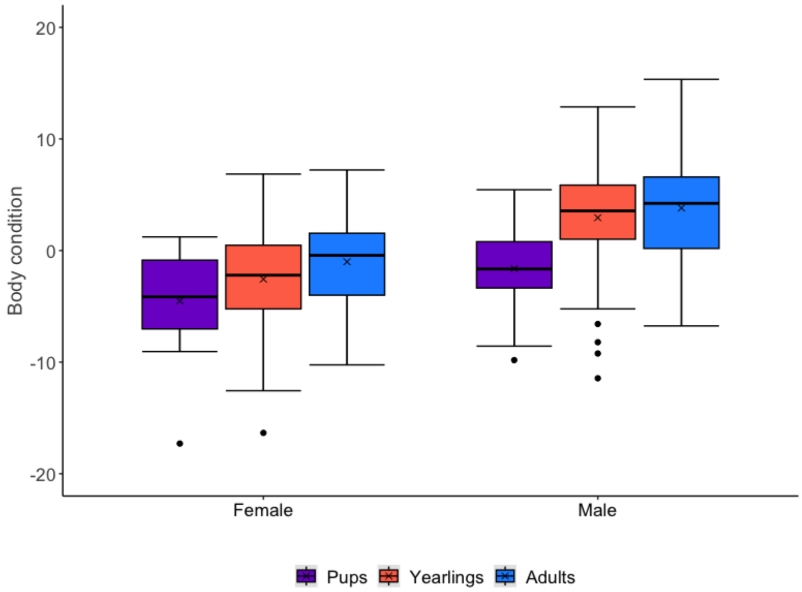

Figure 9. Body condition (residuals from a regression of body weight and body length) from necropsied individuals (median, mean (x), lower error-whisker (Q1 - 1.5 x IQR) and upper error-whisker (Q3 + 1.5 x IQR) and outliers) (n = 311) of the Scandinavian wolf population from 1999 to 2020, in relation to age groups; adults (n = 107), yearlings (n = 146) and pups (n = 58) as well as by sex, female (n = 132) and male (n = 179).

Three models had a ΔAICc ≤ 2, the highest ranked model only included age and sex (Table 5) (Fig. 10). In the second highest ranked model, wolf density was added (Appendix 9). There was a negative relationship between body condition and wolf density, however this effect was only weak (Table 6). Inbreeding was included in the third model, with a weak negative effect.

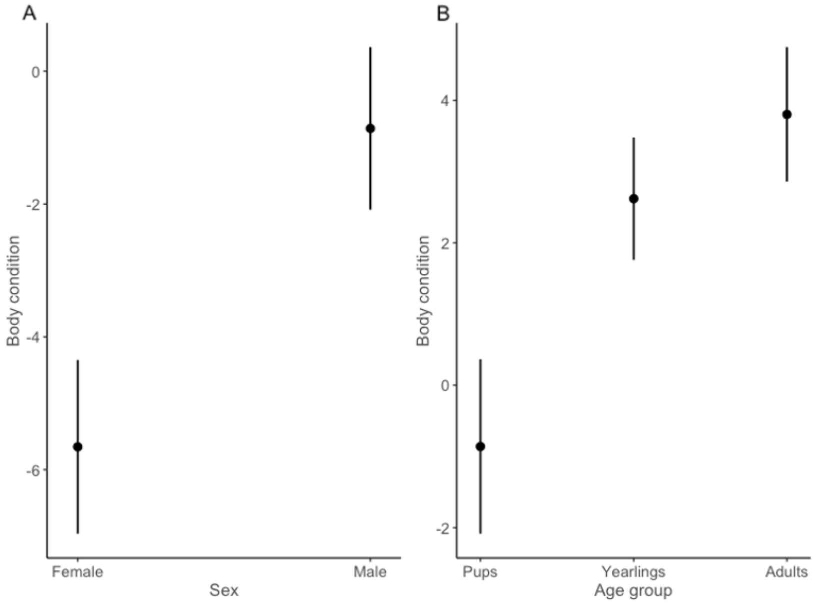

Figure 10. The result of the highest ranked model; the influence of A) sex and B) age on body condition (residuals from a regression of body weight and body length) in necropsied individuals of the Scandinavian wolf from 1999 to 2020 (n = 311). Note that the Y-axis differ between the panels.

4.2.3 Structural size

PC1 stood for 55% of the total variance and there was a substantial drop in the variance explained by PC2 and PC3 (26% and 19%). All three variables in PC1 were equally important and positively associated with each other (Appendix 5). Hence, PC1 was used as a measurement for structural size.

For structural size (n = 216), males (n = 132) had a larger mean structural size than females (n = 84). Adults (n = 69) had a larger mean structural size than both yearlings (n = 121) and pups (n = 26) (Fig. 11).

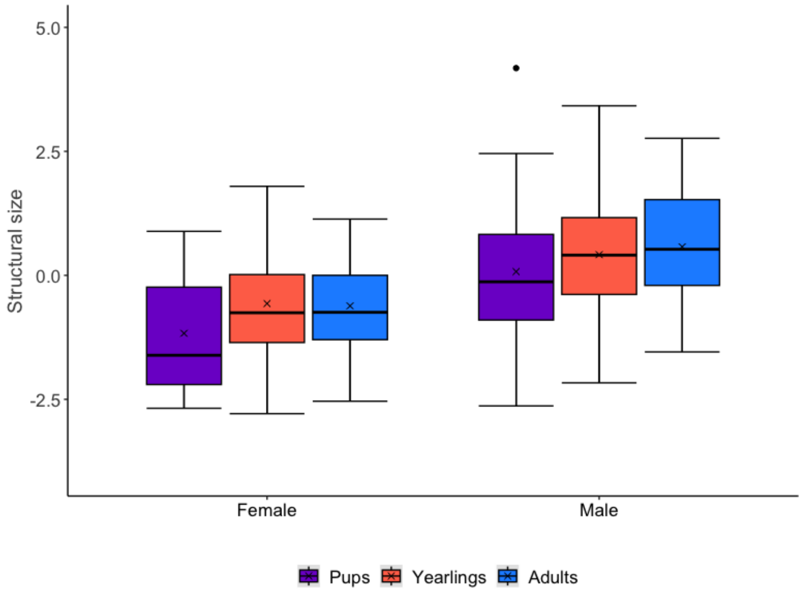

Figure 11. Structural size (PC1 from a PCA of body length, ear length and tail length) of necropsied individuals (median, mean (x), lower error-whisker (Q1 - 1.5 x IQR) and upper error-whisker (Q3 + 1.5 x IQR) and outliers) (n = 216) of the Scandinavian wolf population from 1999 to 2020, in relation to age groups; adults (n = 69), yearlings (n = 121) and pups (n = 26) as well as by sex, female (n = 84) and male (n = 132).

For structural size, only one model had a ΔAICc ≤ 2, it included inbreeding coefficient and wolf density (Table 5, Fig. 12). The differences in structural size between the age groups were only weak (Table 6). There was a negative relationship between inbreeding coefficient and structural size, as well as a positive relationship between wolf density and structural size. An increase in wolf density caused an increase in structural size. For a 0.1 increase in inbreeding coefficient there was a 0.25 decrease in structural size.

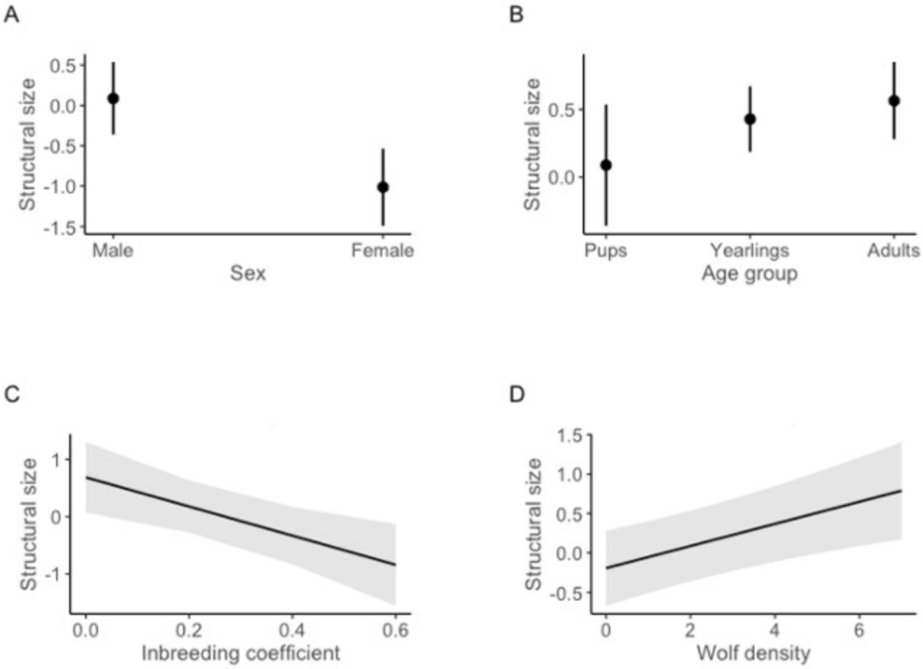

Figure 12. The result of the highest ranked model; the influence of A) sex, B) age, C) inbreeding and D) wolf density on structural size (PC1 from a PCA of body length, ear length and tail length) for necropsied individuals of the Scandinavian wolf from 1999 to 2020 (n = 216). Note that the y-axis differ between the panels.

Table 5. Necropsied individuals of the Scandinavian wolf population in 1999 - 2020. Generalized linear mixed models to assess the effect of age group, sex, inbreeding coefficient (F), wolf density (number of neighboring territories in natal territory, Wolf) food availability (based on moose harvest data in natal territory, Moose) and season, on three different body size measures of captured wolves in Scandinavia, 1998 – 2014,: body weight, body condition (body weight and body length residuals) and structural size (PC1 from a PCA of body length, ear length and tail length). For all models, degrees of freedom (df), AICc weight (AIC w.) and AICc relative to the highest ranked model (ΔAICc) are shown.

Response Variable	Model Rank	Intercept	Age group	Sex	F	Wolf	Moose	Season	df	AICc w.	ΔAICc
Body weight	1	X	X	X				X	6	0.27	0
	2	X	X	X					5	0.22	0.44
	3	X	X	X	X			X	7	0.13	1.54
	4	X	X	X	X				6	0.10	2.00
		X	X	X		X		X	7	0.10	2.02
		X	X	X		X			6	0.09	2.12
		X	X	X	X	X		X	8	0.05	3.56
		X	X	X	X	X			7	0	3.66
		X	X	X			X		6	0	34.28
		X	X	X			X	X	7	0	35.71
		X	X	X		X	X		7	0	36.25
		X	X	X	X		X		7	0	36.75
		X	X	X		X	X	X	8	0	38.11
		X	X	X	X		X	X	8	0	38.15
		X	X	X	X	X	X		8	0	38.73
		X	X	X	X	X	X	X	9	0	40.55
		X							2	0	221.27
Body condition	1	X	X	X					5	0.34	0
	2	X	X	X		X			6	0.25	0.58
	3	X	X	X	X				6	0.13	1.95
		X	X	X	X	X			7	0.09	2.57
		X	X	X				X	6	0.08	2.81
		X	X	X		X		X	7	0.05	3.75
		X	X	X	X			X	7	0.03	4.75
		X	X	X	X	X		X	8	0.02	5.71
		X	X	X			X		6	0	45.71
		X	X	X		X	X		7	0	47.35
		X	X	X	X		X		7	0	48.08
		X	X	X			X	X	7	0	48.19
		X	X	X	X	X	X		8	0	49.76
		X	X	X		X	X	X	8	0	50.18
		X	X	X	X		X	X	8	0	50.55

		X	X	X	X	X	X	X	9	0	52.56
		X							2	0	102.05
Structural size	1	X	X	X	X	X			7	0.91	0
		X	X	X	X	X		X	8	0.05	5.74
		X	X	X		X			6	0.02	7.40
		X	X	X	X				6	0.01	8.92
		X	X	X		X		X	7	0	13.44
		X	X	X	X			X	7	0	14.30
		X	X	X					5	0	16.60
		X	X	X				X	6	0	22.33
		X	X	X	X	X	X		8	0	27.00
		X	X	X		X	X		7	0	31.41
		X	X	X	X	X	X	X	9	0	31.91
		X	X	X	X		X		7	0	35.68
		X	X	X		X	X	X	8	0	35.82
		X	X	X			X		6	0	40.29
		X	X	X	X		X	X	8	0	42.00
		X	X	X			X	X	7	0	46.52
		X							2	0	53.89

Table 6. Necropsied individuals of the Scandinavian wolf population in 1999 - 2020. Conditional model parameter estimates (β), with standard error (SE) and a 95% confidential interval (CI) (explanatory variables shown in bold are not overlapping zero) for each explanatory variable in the models within ΔAICc ≤ 2 (Table 3) for all three response variables. The reference for sex is female, for age group the reference is adults and for season it is "Quarter 1".

Response variable	Model number	Explanatory variable	β	SE	95% CI
Body weight	1	**Intercept**	35.629	0.646	34.358 – 36.9
		Age group: yearlings	-2.34	0.67	-3.658 – -1.02
		Age group: pups	-9.543	0.807	-11.131 – -7.954
		Sex: male	7.695	0.582	6.55 – 8.84
		Season: Quarter 2	-1.598	1.063	-3.69 – 0.494
		Season: Quarter 3	-2.181	1.014	-4.175 – -0.187
		Season: Quarter 4	-0.042	0.679	-1.378 – 1.294
	2	**Intercept**	35.394	0.612	34.19 – 36.597
		Age group: yearlings	-2.598	0.658	-3.892 – -1.305
		Age group: pups	-9.577	0.805	-11.161 – -7.993
		Sex: male	7.691	0.58	6.551 – 8.831
	3	**Intercept**	36.262	1.066	34.166 – 38.359
		Age group: yearlings	-2.364	0.672	-3.686 – -1.043
		Age group: pups	-9.489	0.811	-11.085 – -7.893
		Sex: male	7.717	0.583	6.569 – 8.864
		Inbreeding coefficient	-2.582	3.452	-9.374 – 4.211
		Season: Quarter 2	-1.664	1.068	-3.765 – 0.437
		Season: Quarter 3	-2.164	1.014	-4.16 – -0.169
		Season: Quarter 4	0.062	0.68	-1.4 – 1.277
	4	**Intercept**	35.991	1.042	33.941 – 38.041
		Age group: yearlings	-2.629	0.66	-3.926 – -1.331
		Age group: pups	-9.527	0.809	-11.118 – -7.936
		Sex: male	7.707	0.58	6.565 – 8.849
		Inbreeding coefficient	-2.448	3.456	-9.248 – 4.352
Body condition	1	Intercept	-0.993	0.534	-2.044 – 0.059
		Age group: yearlings	-1.184	0.571	-2.307 – -0.06
		Age group: pups	-4.664	0.731	-6.102 – -3.225
		Sex: male	4.795	0.514	3.783 – 5.807
	2	Intercept	-0.667	0.598	-1.842 – 0.509
		Age group: yearlings	-1.155	0.571	-2.279 – -0.031
		Age group: pups	-4.483	0.745	-5.95 – -3.016
		Sex: male	4.805	0.514	3.794 – 5.817
		Wolf density	-0.16	0.131	-0.419 – 0.099
	3	Intercept	-0.737	0.888	-2.483 – 1.01
		Age group: yearlings	-1.196	0.573	-2.323 – -0.068

		Age group: pups	-4.636	0.736	-6.084 – -3.188
		Sex: male	4.798	0.515	3.784 – 5.812
		Inbreeding coefficient	-1.058	2.93	-6.824 – 4.708
Structural size	1	Intercept	-0.218	0.276	-0.762 – 0.327
		Age group: yearlings	-0.136	0.1704	-0.471 – 0.2
		Age group: pups	-0.476	0.258	-0.984 – 0.032
		Sex: male	1.099	0.157	0.789 – 1.409
		Inbreeding coefficient	-2.547	0.827	-4.177 – -0.916
		Wolf density	0.14	0.042	0.057 – 0.224

5. Discussion

It was hypothesized that the level of inbreeding would have an influence on all three body size measurements and this was confirmed for body weight and structural size, but with only weak to no effect on body condition. Both conditions in natal territory, wolf density and food availability, were hypothezised to influence body size. Food availability had weak to no effect while wolf density influenced all three body size measurements, however mostly with weak effects. Season also influenced body size as hypothesized, but only with weak effects for body condition and structural size. Age and sex influenced all three body size measurements.

5.1 Inbreeding

When inbreeding coefficient was included in a model it always had a negative effect on all three body size measures, this in accordance with the predictions. This is also shown in two other studies using both body weight and structural size as body size measures. Fredrickson & Hedrick (2002) found that body weight in Mexican wolves declined with a higher level of inbreeding and Brzeski et al., (2014) found that structural size also decreased with an increase in inbreeding in red wolves. The results in the present study shows that inbreeding does in fact influence body weight and structural size in the Scandinavian wolves. Further studies are however needed to better understand whether the effects of inbreeding are different between individuals, for example to explore if inbreeding influences the two sexes differently.

Only one of the highest ranked body condition models for necropsied individuals included inbreeding coefficient (Table 1), however only with weak effects. For captured individuals none of the highest ranked models included inbreeding coefficient. This means that when looking at body weight alone or a structural size alone, inbreeding coefficient negatively influenced these size measurements. However, when combining body weight with a size measure (body length) in a measurement of body condition, inbreeding coefficient had little to no effect. One reason for this could be that body condition is the only measurement, used in this study, showing the relationship between body weight and a size measure. It is likely that an individuals’ body condition might vary throughout its life due to external circumstances rather than to congenital inbreeding. Several studies have for example shown that external factors such as contamination of for instance mercury or plastic negatively affects body condition in different birds (Ackerman et al., 2019; Cousin et al., 2015), seasonal conditions and estrous cycles affects body condition in Asian elephants (*Elephas maximus*) (Yang et al., 2023) and changes in land use influenced body condition in the puma (*Puma concolor*) (Coon et al., 2019). It is also likely that the body condition of the Scandinavian wolf is more affected by such external factors rather than congenital factors such as inbreeding, and in that case more so than body weight or structural size. These studies did however use body condition scoring as a method for body condition, instead of the body weight and body length residuals used in this study, which makes it difficult to compare between studies. However, it is of interest to see whether future studies on body condition in different wolf populations show similar results as in this study. Future studies should also explore whether more inbred individuals are extra sensitive to other external factors than less inbred individuals.

5.2 Conditions in natal territory

For the conditions in natal territory, wolf density and food availability, the results showed some variation. Food availability did not seem to have any influence on body weight, body condition and structural size in this study. This since it was only included with weak effects, in one model within ΔAICc ≤ 2 across all models over the two data sets. One reason for this could possibly be the surplus of food available for this population (Zimmermann et al., 2015). Another reason could be that the measurement used for food availability (number of hunter harvested moose) might be a too crude index to mirror the natal territory condition for specific individuals. According to Ueno et al. (2014) the number of hunter harvested moose is a good measure of moose density, however this measure do not represent how much food a certain wolf individual gain per day. A more precise measure of food per day per wolf would perhaps have been needed for a more representative result. Wolf density, on the other hand, seemed to have more of an influence on the three measurements. A positive relationship of larger wolves with greater wolf density, as seen in all models where it was included (except one) was however not as predicted. It was instead predicted that a greater wolf density would cause a greater intra-specific competition and therefore lead to smaller wolves. These results could perhaps be explained by pack size, Sells et al. (2022) studied wolves and showed that in areas with higher densities of conspecific packs, pack sizes were larger. Several studies have shown the negative relationship between pack size and amount of food per individual in that pack (Thurber & Peterson, 1993; Schmidt & Mech, 1997; Sand et al., 2012). However, at the same time as the results from Schmidt & Mech (1997) supports the negative relationship between food acquired per wolf and wolf pack size, they also mention that young wolves acquire more food per wolf and day by staying with their parents. Young wolves are, according to Sells et al. (2022), more likely to stay in their pack for a longer amount of time if there are many close by packs. It is therefore possible that young wolves benefit from higher densities of conspecific packs since that makes them stay with their parents for longer. This could likely be a reason for the positive relationship between wolf density and the different body size measurements used in this study. To further investigate this it would be necessary to study whether wolf density affects young wolves and adults differently.

5.3 Season

Season only had weak effects on the three body size measurements for captured individuals. This could be due to only two season quarters being represented in that data set. The quarters were 1 and 4, which consists of the months October – March (with capture period between December – March), and conditions could therefore have been similar in both quarters. However, for necropsied individuals, where all four seasonal quarters were represented, a larger difference was seen in body size between quarter 1 and 3. These differences were seen in the analysis for body weight, wolves had a smaller body weight in quarter 3 than in quarter 1. This does agree with the prediction that wolves would be larger during winter months compared to summer months. One reason could be that, at temperate latitudes, carcasses from larger herbivores are often better preserved during the cold season and therefoe available longer time periods during the cold season (Selva et al., 2003). This could possibly provide more food for individuals during longer periods of time, especially since wolves are considered opportunistic predators (Janeiro-Otero et al., 2020). Another reason could be that northern ungulates, one of the wolves main preys (Wagner et al., 2012), often are in the worst condition during the time when the season changes from winter to spring (Pereira et al., 2014). This combined with the fact that an ungulates chances of escaping a wolf attack is hampered by snow cover (Wikenros et al., 2009; Pereira et al., 2014), could be a reason to why larger wolves were seen in winter months compared to summer months. In a study on wolves by Wikenros et al. (2009) they also found that the distances wolves chased their prey (moose and roe deer) were shorter in deeper snow conditions. Another difference between these two seasons is that wolves have small pups during spring and summer, which leads to them putting more energy and resources towards their pups during this time. This could therefore also be a reason for smaller body weights seen in summer compared to winter. It would be interesting to see whether the same results were found on captured individuals if future studies were able to include all four seasonal quarters instead of just two. Strong seasonal differences were only seen for body weight as a body size measure, it is reasonable that season did not strongly affect structural size since this is a structural body size measure which therefore should not fluctuate with season. However, why there were only weak seasonal differences seen for body condition, is not as self-explanatory. It could be possible that individuals with worse body conditions stay that way no matter the season, and the same for individuals with better body conditions. Whether this is the case or not could be of interest to further explore in future studies.

5.4 Age and sex

It was predicted that both sex and age group would influence all three size measurements. This was also shown, where males were larger than females in all models. The variable age group did also have an influence on all three measurements in all models, older wolves had larger body sizes than younger, however the differences between adults and yearlings were weak in some models, since the 95 % CI overlapped zero. When looking at structural size for necropsied individuals the differences between adults and pups were also only weak. The reason to differences in body sizes between the two older age groups were weak in this study could possibly be due to some yearlings having already reached full-grown body size (Fredrickson & Hedrick, 2002). It could also possibly have been due to scenesence, meaning some of the older adults already having started to decline in body weight due to old age (Fredrickson & Hedrick, 2002).

5.5 Strengths and weaknesses

This study consisted of two different data sets, captured individuals and necropsied individuals, which makes for one of the strengths of the study. This since using only one of the data sets would have made its sources of errors more profound. Therefore, having both data sets made it beneficial. One of the strengths of the necropsied individuals was the size of the data set, having over 800 individuals as a starting point made it possible to be stricter when excluding the individuals that might have had their body sizes influenced by deceases or external factors post death without ending up with a too small data set. A weakness of the captured individuals is the possible difficulties of measuring some of the morphometrics (except body weight) out in the field. The measuring is a potential source of error in the overall study, this since the measurements have been taken by several different people throughout the years. An overall strength is in the method, where three different measurements (body weight, body condition and structural size) were included. By doing so the perspective was broadened and both body weights alone, body condition and structural sizes could be explored and compared. For both data sets one weakness is not knowing when the individuals ate last. Whether an individual just ate or if it had been a while since it ate would possibly influence their weight.

5.6 Summary

This study has provided insights to what factors influences body weight, body condition and structural size of the Scandinavian wolf population. It is the first study to show the possible negative influence of inbreeding on body weight and structural size in this population. The same influence of inbreeding was not seen for body condition, this could possibly be due to body condition varying due to external factors rather than to congenital factors such as inbreeding.

Food availability in natal territory did not seem to influence any of the three body size measurements. A greater wolf density in natal territory was however linked to larger wolves, which was contradictory to the prediction. This could possibly be explained by wolves staying longer with their parents at high wolf densities (Sells et al., 2022) and therefore gaining more food (Schmidt & Mech 1997). However, the effects were mostly weak and if this reasoning would be true then this relationship should be seen for young wolves but not for adults, which needs to be studied further to draw any conclusions.

When all seasons were included in the analysis it showed that wolves were larger during winter months than during summer months. All analyses also showed that males were larger than females, and older wolves were larger than younger. However, the differences between adults and yearlings were not always strong.

To gain knowledge in the effects and influences of these factors is useful when managing the Scandinavian wolf population. The link between inbreeding and body weight and structural size is important in a conservation perspective. The Scandinavian wolf population is growing (Åkesson et al., 2016; Liberg et al., 2005), however, the results from this study shows that, to make sure it is a healthy population, management should aim at reducing the inbreeding level.

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Popular science summary

Many large carnivour species are going localy extinct due to human influences such as deforestation and unstainable use of natural resources. Since large carnivores tend to need large living areas and large amounts of food it is often challenging to reintroduce them to areas where they have previously gone extinct. Following reintroduction or recolonization of such species they often end up as small populations separated by large distances. This is problemtic since small and isolated populations often suffer from lowered fitness and health. It is therefore important to know the factors affecting the health of these populations so that the conservation and management can be carried out in a way to prevent extinctions and enable persistence.

This study was carried out on the Scandinavian wolf population, which went extinct in the late 1960s and later managed to recolonize the Scandinavian peninsula. This population has since struggled with small population size and the health of the population is therefore important. The goal was to study the effects of age, sex, inbreeding, conditions in natal territory (wolf density, calculated by the number of nearby packs, as well as food (in this case moose) availability) and season on three body size measurements, body weight, body condition (relationship between body weight and body length) and structural size (body length, ear length and tail length combined). These measurements were used as a representative of fitness and health since it often is linked to traits affecting survival. The study was carried out on both alive individuals, which were captured and sedated (103 individuals but 159 data points since some individuals were captured more than once) between the years of 1998 – 2014, as well as necropsied individuals (338 individuals) between the years of 1999 - 2020. Age and sex were included in all models since they were already assumed to have an influence on body sizes. The other explanatory variables were included in all possible combinations (17 models in total). The models were run on both captured and necropsied individuals. The best models were then calculated using AIC.

Both age and sex influences all three body size measurements of the Scandinavian wolf population. Both adult wolves and yearlings were larger than pups and males were larger than females. The differences between adults and yearlings were however not always strong, which could be due to some yearlings already having reched their adult size or some adults having started to deacrease in size due to old age. Inbreeding also influenced body sizes in a negative way. A 0.1 increase in inbreeding coefficient (an inbreeding measurement) caused a 1 kg decline in body weight for captured individuals or a decline by 0.26 in the structural size measure for necropsied individuals. A similar influence of inbreeding was however not seen for body condition. This could possible be due to body condition being influenced by other factors, such as environmental circumstances instead of inbreeding. The conditions in natal territory showed positive relationships for wolf density, meaning that an increase in wolf density was linked to larger wolves. Food availability did however not seem to have an influence on any of the three body size measurements. This could likely be due to the Scandinavian wolf population having a surplus of food. Lastly, season only influenced body sizes when comparing between all seasons throughout the year, the individuals then showed larger body sizes in winter months (January – March) than in late summer (July – September). This is likely both a result of wolves having their pups during spring and summer, but also fact that the condition of their main prey (ungulates) are worse during winter, making their chances of escaping a wolf attack during winter and snow conditions lower.

These results provide knowledge in the factors influencing body weight, body condition and structural size, and therefore also fitness and health, of the individuals in the Scandinavian wolf population. This knowledge is important when managing this population in the future. For instance, it is clear that to maintain a healthy population, management aimed towards reducing inbreeding is required.

Acknowledgements

First and foremost, I would like to thank my supervisors, Camilla Wikenros, Håkan Sand and Emma Höök. A special thanks to my main supervisor, Camilla Wikenros, for excellent guidance and always being quick in answering any questions. I have had a very fun and instructive time working together with you, thanks Camilla!

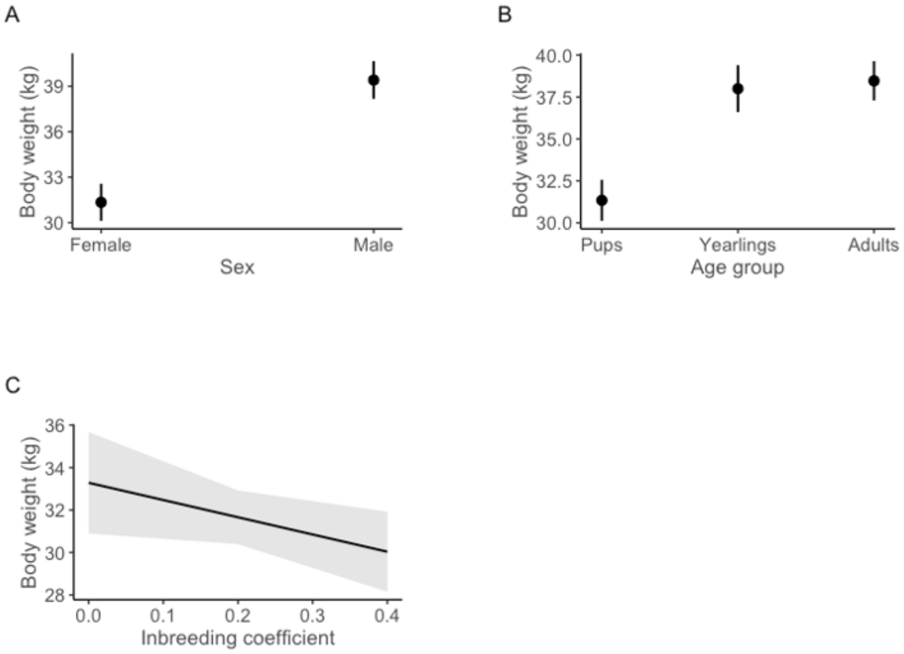
I would also like to thank my family and friends for supporting me and always being curious in what I do and cheering me on.

Appendix 1

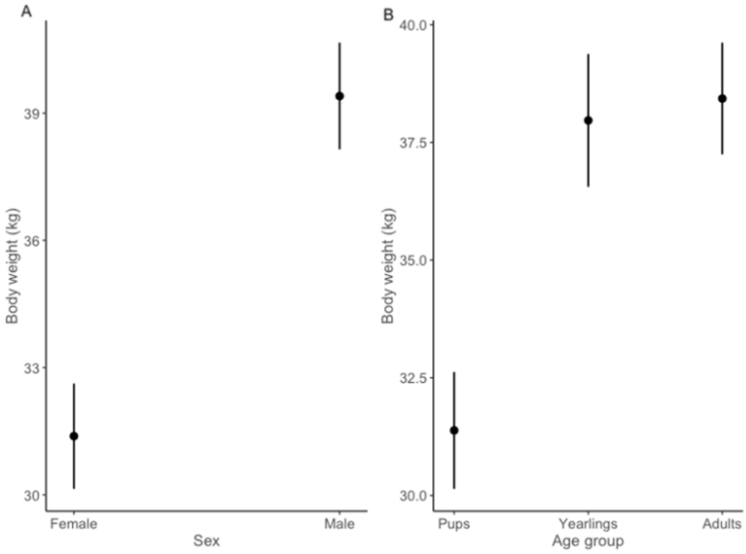
Appendix 1, Table 1. Results of a linear regressions of body size and age group adults, from all three body size measures; body weight, body condition and structural size, for both data sets; captured individuals and necropsied individuals, of Scandinavian wolves, 1998 – 2020. Showing parameter estimates (β), with standard error (SE) and p-value.

Data set	**Response variable**	**β**	**SE**	**p-value**
Captured individuals	Body weight	-0.305	0.236	0.203
	Body condition	-0.323	0.33	0.332
	Structural size	0.187	0.103	0.075
Necropsied individuals	Body weight	0.233	0.339	0.493
	Body condition	-0.155	0.286	0.589
	Structural size	0.003	0.091	0.975

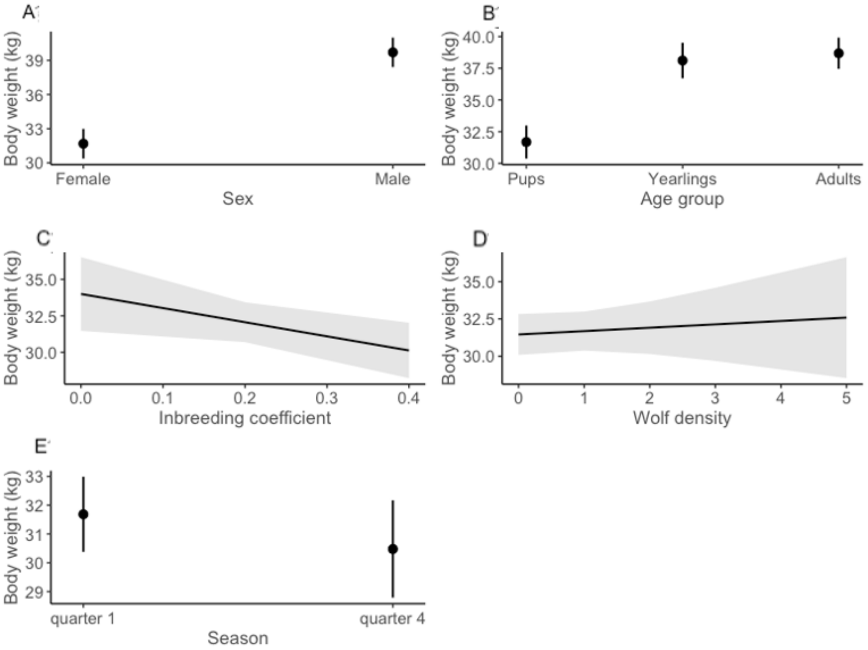
Appendix 2



Appendix 2, Figure 1. The result of the second highest ranked model; the effect of A) sex, B) age, C) inbreeding coefficient on body weight in captured individuals of the Scandinavian wolf in 1998 - 2014 (n = 159). Note that the Y-axis do not start at zero and are different between the sub-figures.

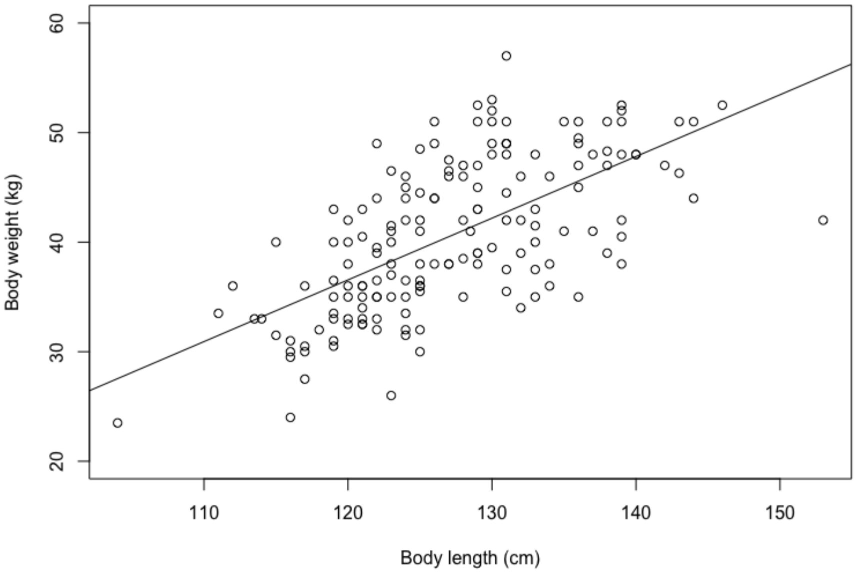


Appendix 2, Figure 2. The result of the third highest ranked model; the effect of A) sex and B) age on body weight in captured individuals of the Scandinavian wolf in 1998 - 2014 (n = 159). Note that the Y-axis do not start at zero and are different between the sub-figures.



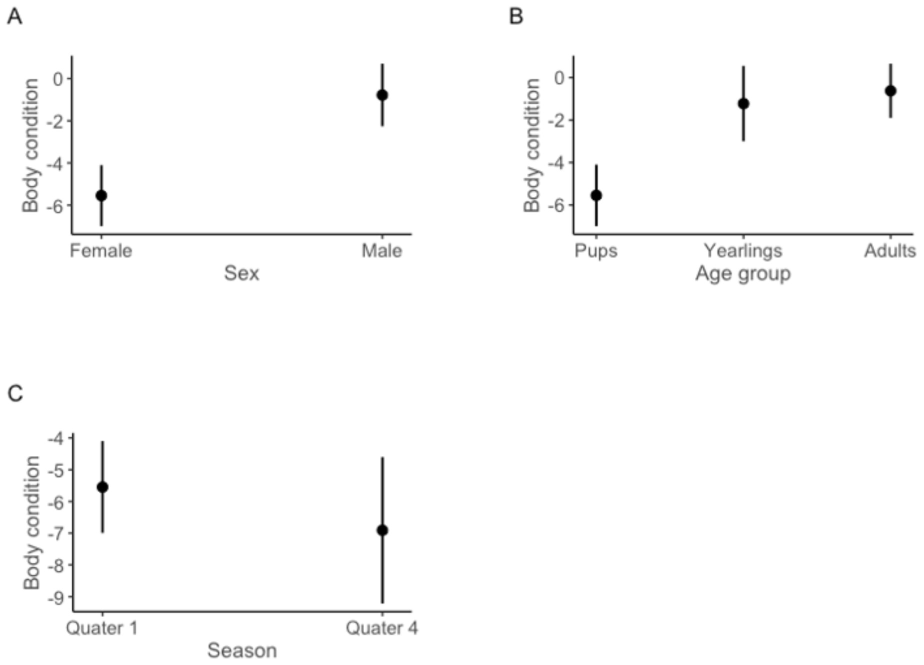
Appendix 2, Figure 3. The result of the fourth highest ranked model; the effect of A) sex, B) age, C) Inbreeding coefficient, D) Wolf density and E) Season on body weight in captured individuals of the Scandinavian wolf in 1998 - 2014 (n = 159). Note that the Y-axis do not start at zero and are different between the sub-figures.

Appendix 3

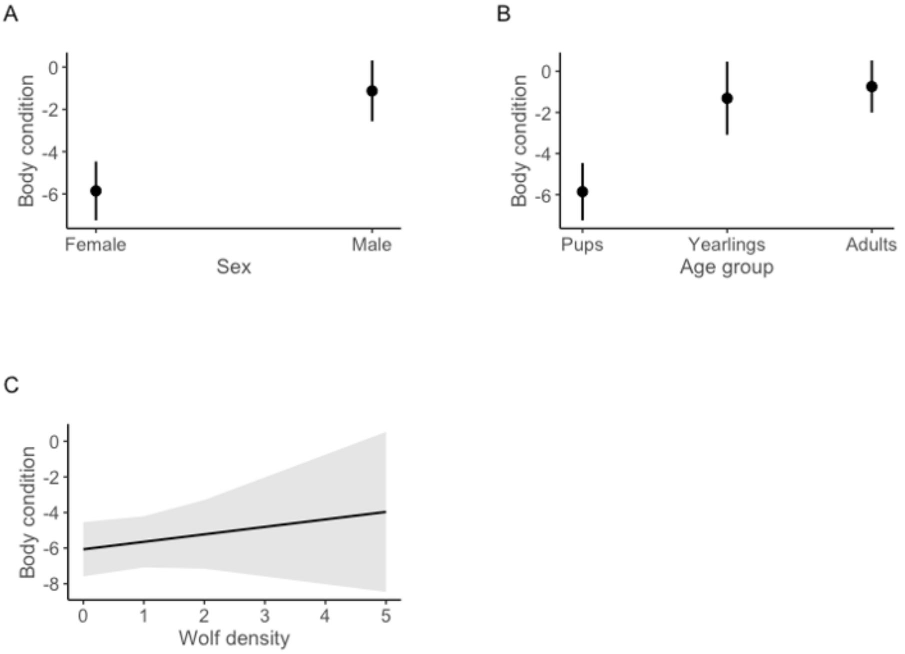


Appendix 3, Figure 1. A linear regression of body weight and body length of captured individuals of Scandinavian wolves, 1998 – 2014. Used to extract the residuals for the body condition measure. Note that the y-axis is starting at 20.

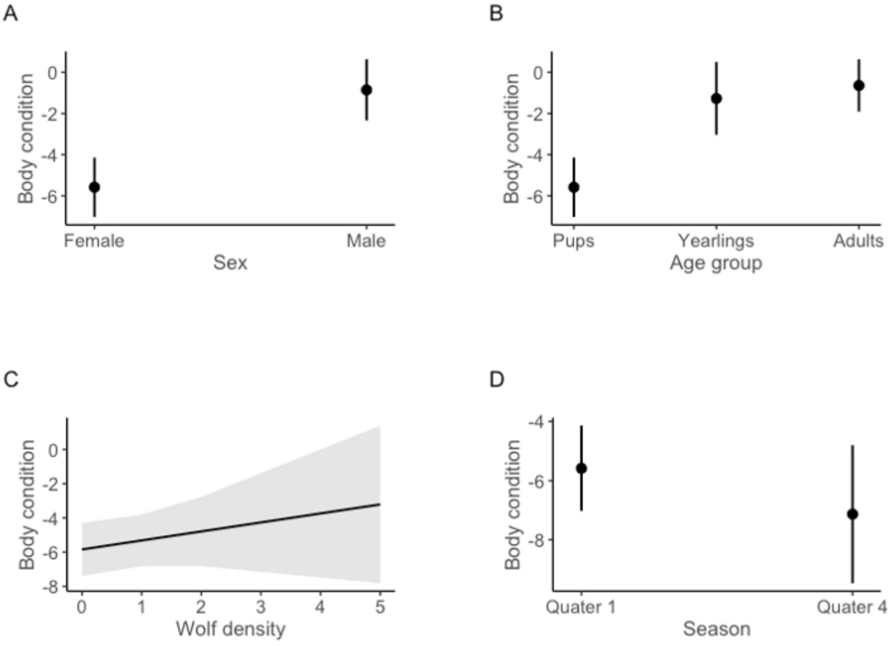
Appendix 4



Appendix 4, Figure 1. The result of the second highest ranked model; the effect of A) sex, B) age and C) season on body condition (residuals from a regression of body weight and body length) in captured individuals of the Scandinavian wolf in 1998 - 2014 (n = 140). Note that the Y-axis are different between the sub-figures.



Appendix 4, Figure 2. The result of the third highest ranked model; the effect of A) sex, B) age and C) wolf density on body condition (residuals from a regression of body weight and body length) in captured individuals of the Scandinavian wolf in 1998 - 2014 (n = 140). Note that the Y-axis are different between the sub-figures.



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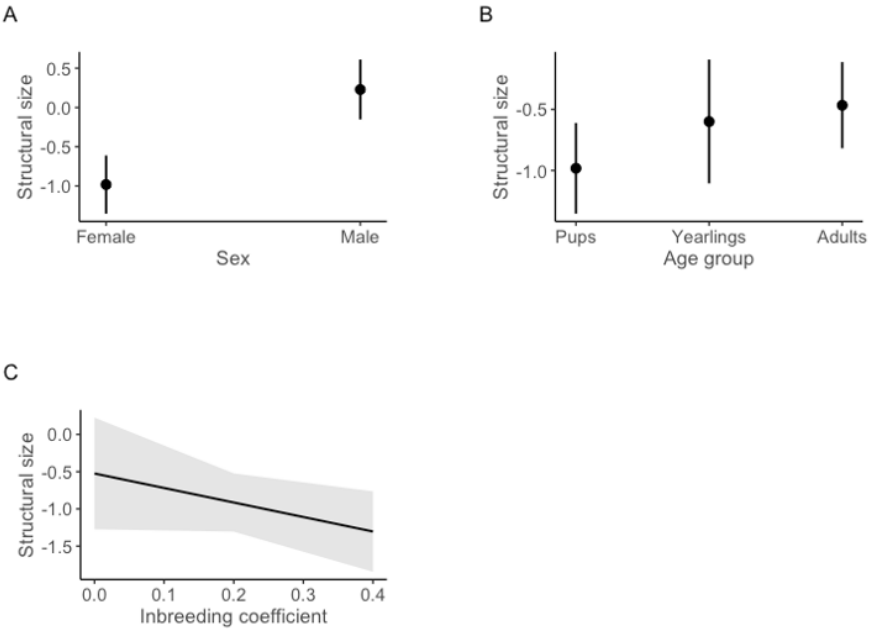
Appendix 5

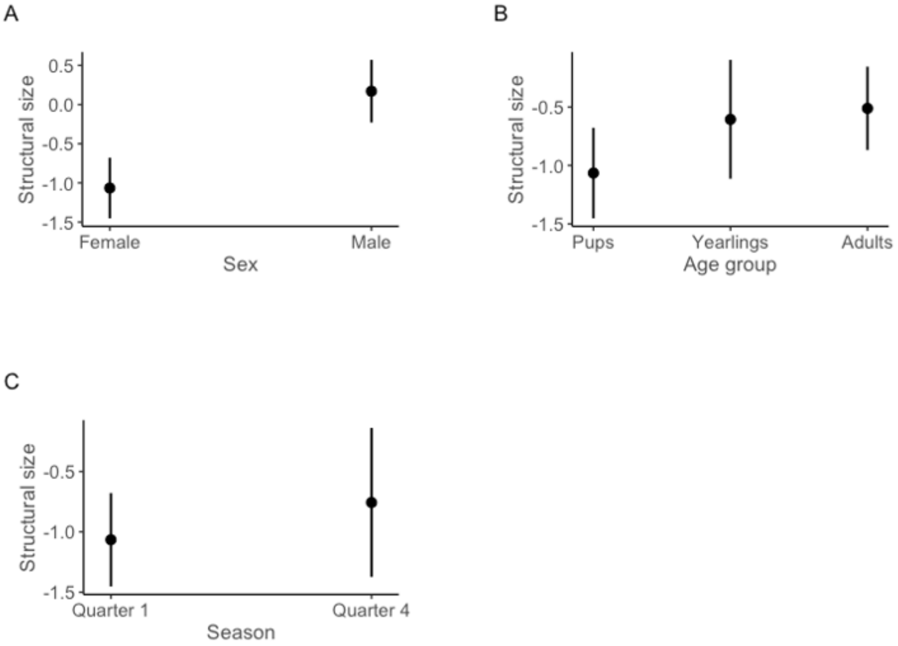
Appendix 5, Table 1. Results of principle components analyses for both data sets; captured individuals and necropsied individuals, created from three size measures; body length, body condition and structural size, used for the structural size measure for Scandinavian wolves, 1998 – 2020. The different loading values for the three measures and the variance represented by each PC are shown.

Data set	**Measurement**	**PC1**	**PC2**	**PC3**
Captured individuals	Body length	0.598	-0.046	0.8
	Ear length	0.564	0.733	-0.38
	Tail length	0.569	-0.679	-0.464
	Proportion of variance	0.553	0.236	0.211
Necropsied individuals	Body length	0.565	-0.635	0.526
	Ear length	0.531	0.768	0.357
	Tail length	0.631	-0.078	-0.772
	Proportion of variance	0.552	0.26	0.188

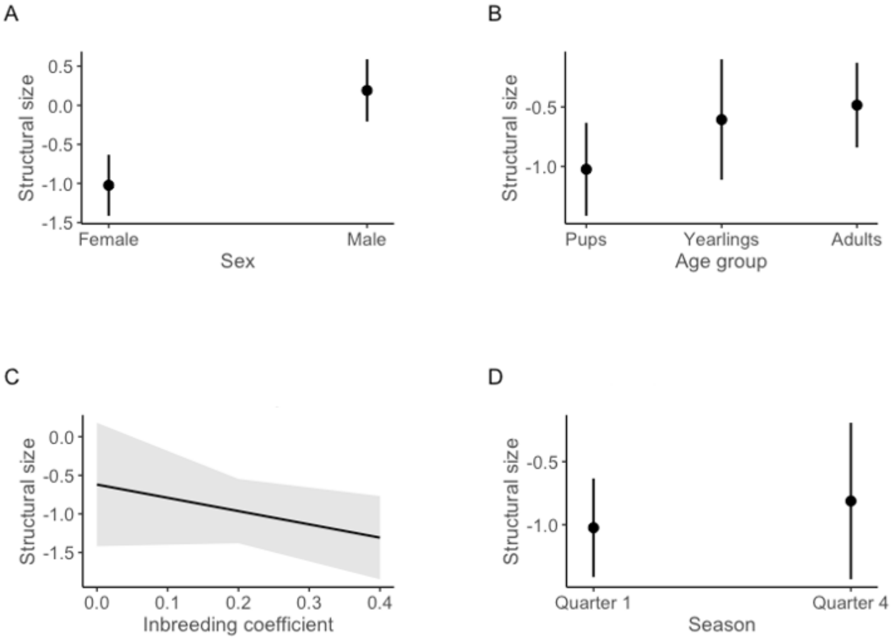
Appendix 6



Appendix 6, Figure 1. The result of the second highest ranked model; the effect of A) sex and B) age group and C) inbreeding coefficient on structural size (PC1 from a PCA of body length, ear length and tail length) in captured individuals of the Scandinavian wolf in 1998 – 2014 (n = 130). Note that the Y-axis are different between the sub-figures.



Appendix 6, Figure 2. The result of the third highest ranked model; the effect of A) sex and B) age group and C) season on structural size (PC1 from a PCA of body length, ear length and tail length) in captured individuals of the Scandinavian wolf in 1998 – 2014 (n = 130). Note that the Y-axis are different between the sub-figures.



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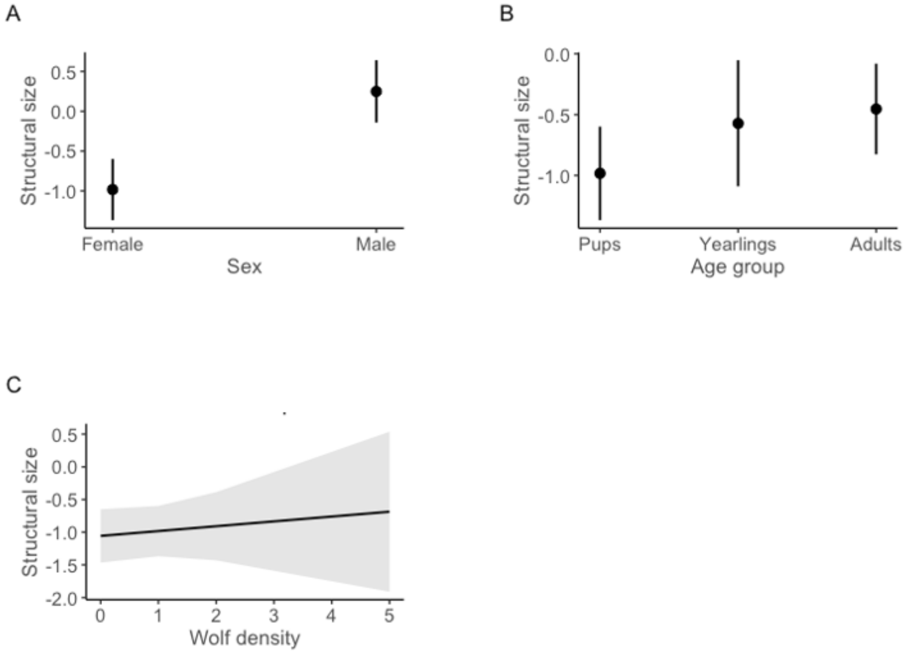
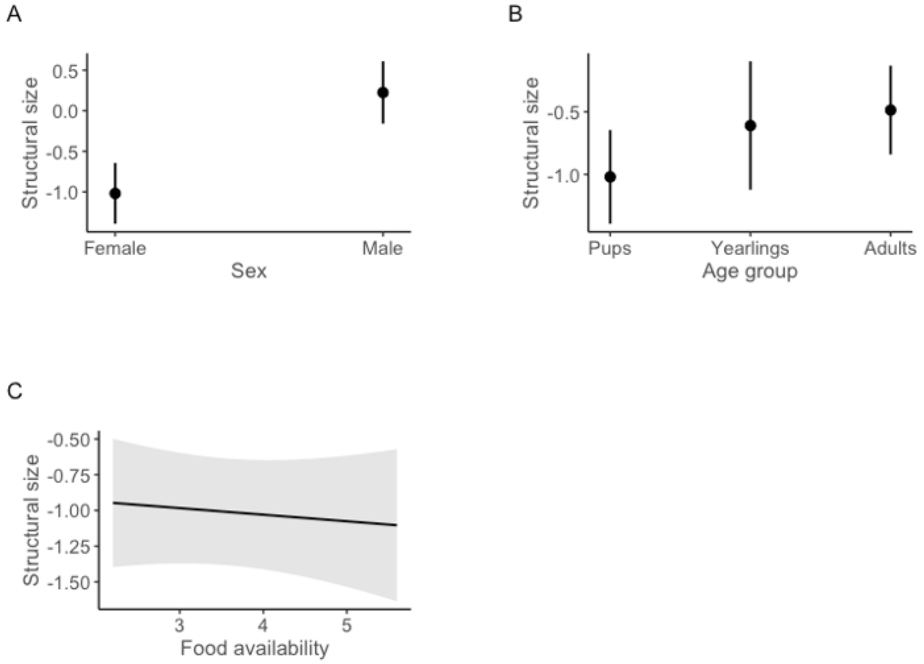
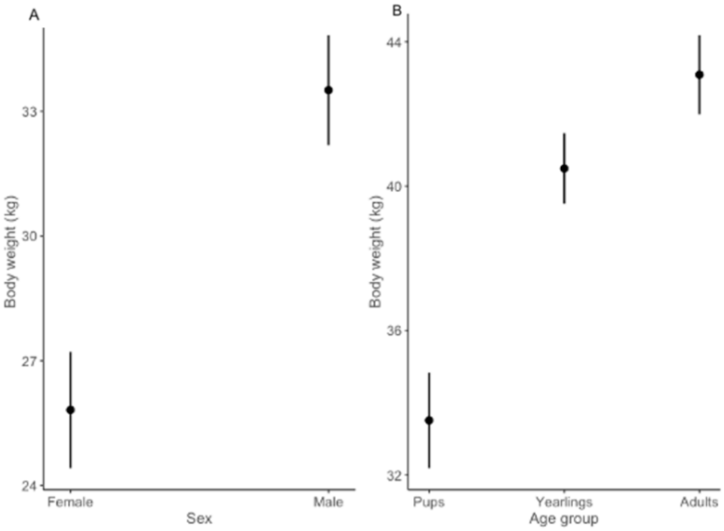


Appendix 6, Figure 4. The result of the fifth highest ranked model; the effect of A) sex and B) age group and C) wolf density on structural size (PC1 from a PCA of body length, ear length and tail length) in captured individuals of the Scandinavian wolf in 1998 – 2014 (n = 130). Note that the Y-axis are different between the sub-figures.

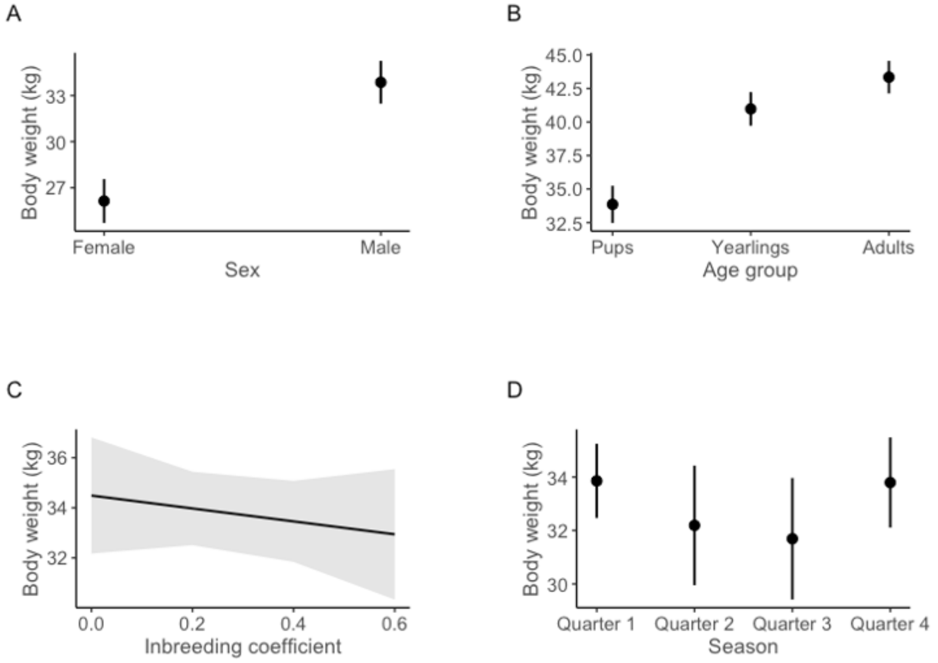


Appendix 6, Figure 5. The result of the sixth highest ranked model; the effect of A) sex and B) age group and C) food availability on structural size (PC1 from a PCA of body length, ear length and tail length) in captured individuals of the Scandinavian wolf in 1998 – 2014 (n = 130). Note that the Y-axis are different between the sub-figures.

Appendix 7



Appendix 7, Figure 1. The result of the second highest ranked model; the effect of A) sex and B) age on body weight for necropsied individuals of the Scandinavian wolf in 1999 – 2020 (n = 329). Note that the Y-axis do not start at zero are different between the sub-figures.



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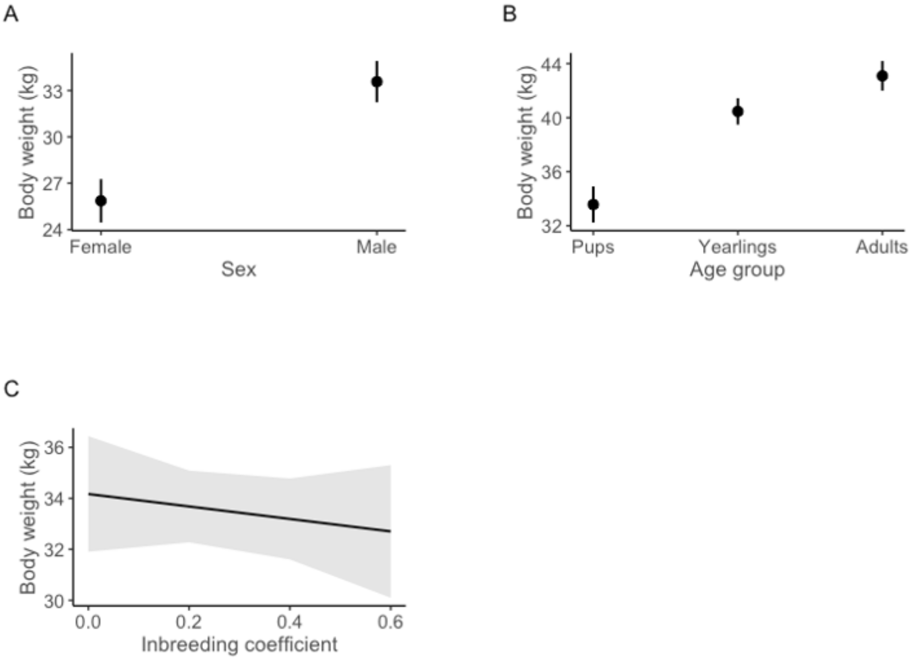

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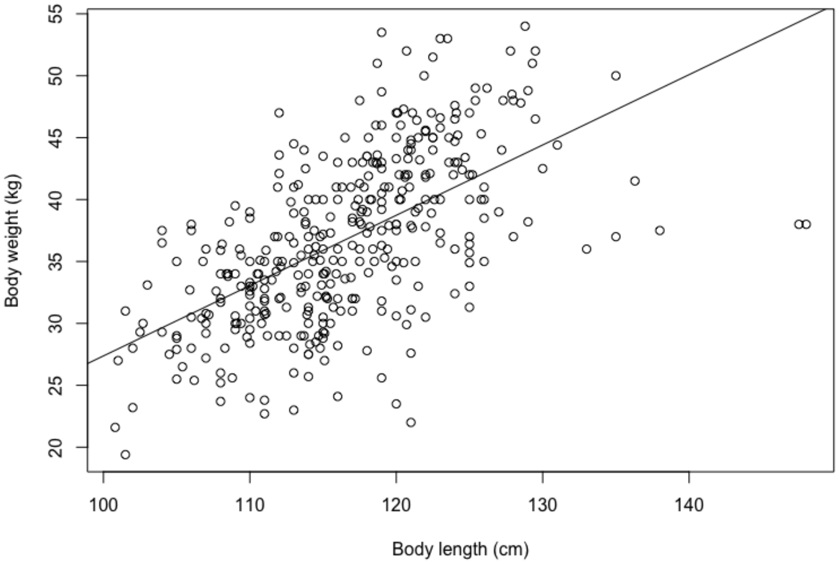
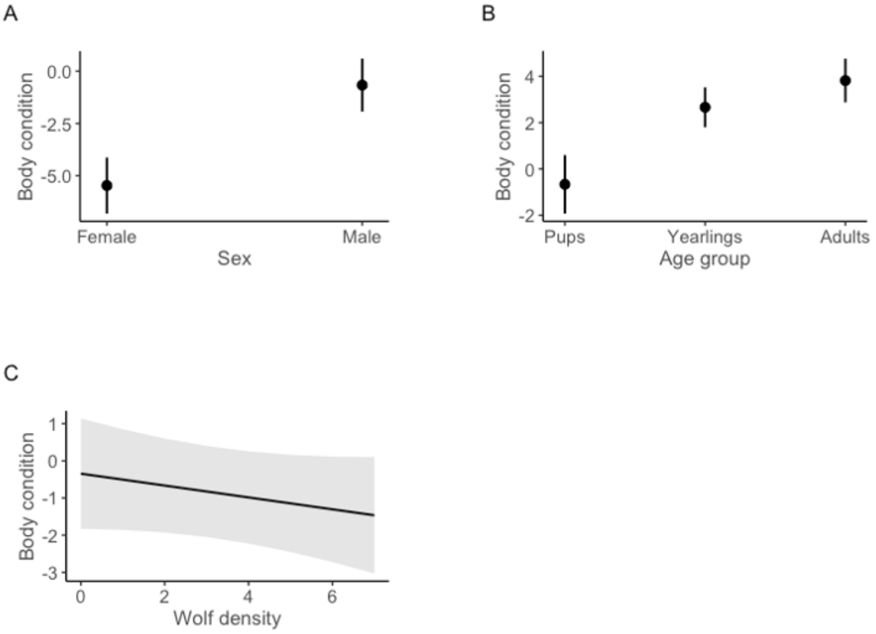
Appendix 8

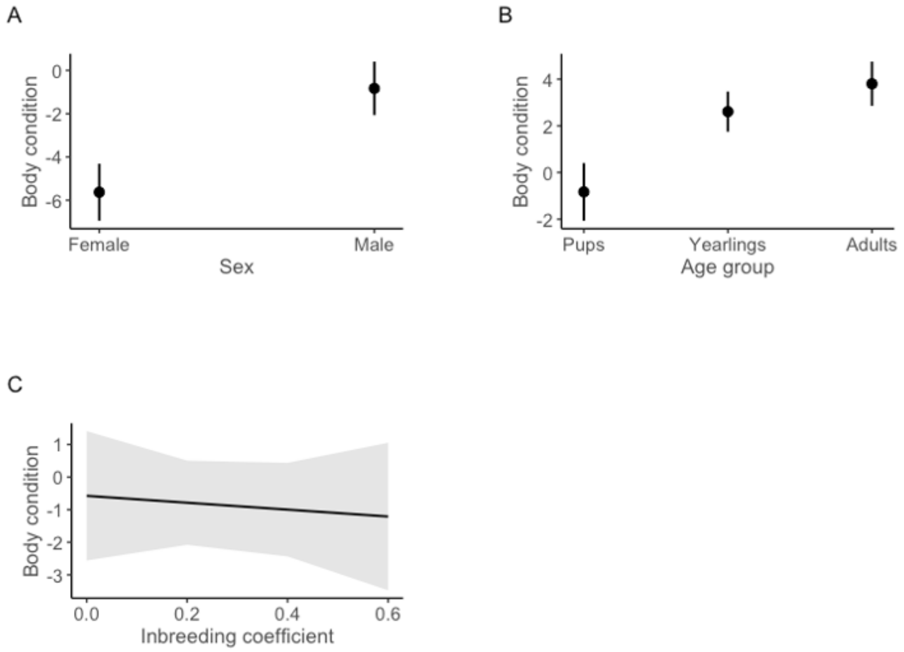


Appendix 8, Figure 1. A linear regression of body weight and body length of necropsied individuals of Scandinavian wolves, 1999 – 2020. Used to extract residuals for the body condition measure. Note that the y-axis is starting at 20.

Appendix 9



Appendix 9, Figure 1. The result of the second highest ranked model; the effect of A) sex, B) age and C) wolf density on body condition (residuals from a regression of body weight and body length) in necropsied individuals of the Scandinavian wolf in 1999 – 2020 (n = 311). Note that the Y-axis are different between the sub-figures.



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