University of South Bohemia
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Svalbard reindeer and its interaction with extreme polar environment

Master thesis

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Annotation

Two distinct populations of Svalbard reindeer are compared based on their antler parameters. Relative antler size and number of tines are supposed to reflect well environmental conditions of the sedentary population within the growing season. Both studied populations are well spatially isolated due to high mountain ridges, glaciers and fjords. The population in Petuniabukta occupies sparsely vegetated region with harsh climatic conditions, whereas Skansbukta represents area with continuous tundra vegetation, milder climatic conditions and consequently also longer vegetation season. These environmental factors probably lead to significant differences in relative antler size and number of tines. Skansbukta population has larger relative antler size and higher number of tines than the population in Petuniabukta.

Keywords: Svalbard reindeer, antlers, population characteristics, environmental conditions

I declare that I am the author of this qualification thesis and that in writing it I have used the sources and literature displayed in the list of used sources only.

V Českých Budějovicích, 12. 4. 2022

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S pozdravem,
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Content

1. Introduction

1.1. Rangifer tarandus

Reindeer (*Rangifer tarandus*) is a typical representative of the large mammal found in the northern parts of the Holarctic realm. Its spatial distribution is highly heterogeneous. Reindeer can be found in different habitats: continental tundra (56%), mountain regions (19%), forests (14%), and the Arctic islands (11%) (Gunn, 2016). This species has been influenced by a repeated fluctuations of glacial and interglacial periods with more or less dramatic climatic changes, fluctuations of continental glaciers, and the associated biomes during the Pleistocene (Mattioli, 2011; Yannic et al., 2014; Lorenzen et. al., 2011). Currently, reindeer is found in the northern part of Asia and North America, Greenland, and northern Europe (Gunn, 2016; Tryland & Kutz, 2018). It was also introduced to Iceland by Norwegian whalers in 1771 (Thórisson, 1984; Mattioli, 2011) and even to the southern hemisphere, specifically to South Georgia in 1911-1912, and later again in 1925, and further also to the Kerguelen Islands in 1955 (Mattioli, 2011). The population in South Georgia had to be eradicated or transported to the Falklands Islands due to overpopulation, which threatened or even destroying the local ecosystems (Bell & Dieterich, 2010).

1.1.1. Reindeer and caribou

Rangifer tarandus belongs to Cervidae. It has different local names (reindeer and caribou) in different parts of its occurrence, although they are taxonomically considered the same species. Caribou comprises only wild populations in North America and Greenland (Tryland & Kutz, 2018). However, reindeer expression is used for wild and semi-domesticated species in Eurasia and semidomesticated populations in America. These two names certainly caused confusion in many classification and subdivision proposals (Tryland & Kutz, 2018).

1.1.2. Subspecies

Grubb (2005) provided a list of 15 valid subspecies (with a list of synonyms), of which two are already extinct. The subspecies are determined mainly on the basis of skeletal and skull characteristics, antler structure, and its behaviour (Gunn 2016). Tryland & Kutz (2018) stated that there are a large number of described subspecies without clearly defined subspecies characteristics. Such an ambiguous description clearly does not help to address the problem of subspecies determination. Therefore, the names of subspecies might often refer to local ecotype rather than subspecies under a standard 75% rule proposed by Mayr (1969).

The Eurasian tundra reindeer (*Rangifer tarandus tarandus*) is found in the tundra and mountainous areas of Eurasia. It is the most numerous wild subspecies in Eurasia, and this subspecies is the most semi-domesticated there (Cronin et al., 2006; Klein, 1980). It is less known that due to the inability to domesticate caribou, some individuals of this subspecies were introduced and domesticated in North America after 1890. However, by 1975 most or all of them had died out, probably due to poor care, overpopulation, and predation (Tryland & Kutz, 2018; Klein, 1980; Cronin et al., 2006; Long, 2003). The territory of European tundra reindeer overlaps with boreal forest reindeer (*R. t. fennicus*) in the south. This subspecies is located in the taiga in Finland and northwest Russia in the Karelia region (Rankama & Ukkonen, 2001; Mattioli, 2011).

The northernmost subspecies from Eurasia is the Svalbard reindeer (*Rangifer tarandus platyrhynchus*); it is a typical Arctic form (Mattioli, 2011; Tyler, 1987). Four other Old World subspecies are distributed in Asia, specifically in Russia, Mongolia, and northern China. However, these subspecies can also be considered by authorities as the subspecies of *R. t. fennicus* (Banfield, 1961; Mattioli, 2011).

The North American caribou consists of six subspecies including two already extinct. The large migratory tundra subspecies is the Grant´s caribou (*R. t. granti*), which is found from Alaska to Yukon. The barren-ground caribou (*R. t. groenlandicus*) and the woodland caribou (*R. t. caribou*) can be found in North Canada, from Yukon to Labrador and Newfoundland, and the Peary caribou (*R. t. pearyi*) occupies the high Arctic islands of northern Canada (Taylor et al., 2020; Mattioli, 2011).

Despite some genetic assessments (Yannic et al., 2014; Cronin et al., 2005; Taylor et al., 2020; Weldenegodguad et al., 2020; Horn et al., 2018; Cronin et al., 2006; Roed et al., 2020), the systematics of reindeer remains unclear (Gippoliti, 2020). This is due to the fact that there are and there were limited barriers between some proposed subspecies, regular genetic flow in this migratory species, and a limited overlap of genetically detected lineages and proposed taxa. However, some subspecies, such as the Svalbard reindeer, are also genetically well supported. Even within their subspecies, Svalbard reindeer is genetically differentiated into smaller populations with restricted gene flow (Côté et al., 2002).

1.1.3. Basic morphological adaptations

Reindeer is a medium-sized ruminant well adapted to life under arctic conditions (Tryland & Kutz, 2018). However, there are relatively large differences between the subspecies. On the one hand, Svalbard reindeer (*R. t. platyrhynchus*), as the smallest subspecies, is characterized by low body weight (53-70 kg for female and 65-90 kg for male - Pedersen 2018) and size (90-100 cm - Wollebaek, 1926) despite its large, rounded shape. Its short legs are also the result of adaptation to the harsh local climatic conditions of Svalbard. Svalbard reindeer was long believed to have no natural predators. However, this has recently denied by more frequent observations of reindeers being actively hunted by polar bears (Derocher et al., 2000; Kavan, 2018; Geist, 1998). On the other hand, the largest subspecies to be found in Canada is the migratory woodland caribou (*R. t. caribou*) (Kavanagh, 2005; Geist, 2006). The woodland caribou (*R. t. caribou*) with approximately 110-150 kg for females, and 160-210 kg for males has a shoulder height of 100-120 cm (Thomas & Gray, 2002).

The large hoof surface allows reindeer to make comfortable and fast movements in snow (Tryland & Kutz, 2018). Apart from the other members of the Cervidae family, reindeer has no bare skin. Its very dense fur with several layers is perfectly adapted to cold conditions. The winter coat is grey to white and is denser than the summer brown coat (Timisjarvi et al., 1984). Body fat content is highly variable during the annual cycle. Fat is quickly stored during the relatively short summer and early autumn and then used during the winter months when foraging abundance is limited. Females use body fat during gestation and lactation, whereas males also use body fat during rutting season. (Bardsen et al., 2011; Gerhart et al., 1996; Geist, 1998).

1.1.4. Antlers

Reindeer is the only deer species that grows antlers for both male and females. This is an interesting feature considering sexual selection and male-male competition that shape the evolution of antlers (Plard et al., 2011; Landete-Castillejos et al., 2019). Females have antlers for social reasons, but also to defend food sources during winter. Males have larger and heavier antlers than females.

Pedicles begin to grow very early, just 7-10 days of age, and the first set of antlers begins to grow in 4-6 weeks (Groves et al., 2011). Gómez et al. (2006) studied in Iberian red deer whether lactation (milk production and composition) has an effect on later male size and antler size. They found that a higher proportion of milk protein increased the probability of a higher antler weight and length. Body growth during the first year of life of a calf can positively influence later antler size. And they add that males with higher weaning weights caused earlier growth of heavier antlers, and these males had a larger base perimeter (Gómez et al., 2006).

Males and females begin to grow antlers during the period from April to July and shed their velvet antlers until far into August.

Antler size (both weight and length) and number of tines are honest signals of individual quality in reindeer and all deer species (Mateos et al., 2008). A strong relationship between energy allocation to antler growth and current environmental conditions is reported because antlers are cast and regrown each year from the pedicles and are costly to produce (e.g., Andersson, 1994; Landete-Castillejos et al., 2019). Vanpé et al. (2007) described a good correlation between antler size and body mass, for example, in the case of roe deer. The decrease in antler size related to harsh climatic conditions in deer was reported, e.g. by Pélabon & Van Breukelen (1998), Schmidt et al. (2001), or Mysterud et al. (2005). On this basis, the antler characteristics of the population are considered as a proxy of the population conditions, with certain limitations discussed later. A similar conclusion was also reported by Thomas and Barry (2005) for species, where antler mass was used as a proxy of the condition of each individual. Mateos et al. (2008) showed the U-shaped relationship between age and antler asymmetry in Iberian red deer. This effect leads to sexual selection in favour of larger and more symmetrical antlers during the prime age of males. Therefore, the selection of the most symmetrical antlers naturally excludes too young or too old individuals.

1.1.5. Life cycle

Reindeer is a polygynous species (Tryland & Kutz, 2018). Its reproduction is mainly driven by the light cycle during the polar day/night periods. This is also expressed in the level of melatonin hormone. Melatonin is suppressed during summer (polar day). On the contrary, during the dark winter period the melatonin level is still high. However, the highest level of melatonin is in the autumn, which is related to sexual activity and the rutting period (Eloranta et al., 1992; Lu et al., 2010).

The reindeer gestation period is 198 to 240 days and calves are born rather synchronously from May to June. The female usually has one calf with around 10% of the mother's weight. Shortly after birth, the calf is able to walk and follows its mother (Shipka et al., 2007; Ropstad et al., 2005; Geist, 1998; Rowell & Shipka, 2009). Tryland & Kutz (2018) estimated that the lactation period is approximately 3-4 months and the milk is extremely rich in protein and fat. At 1,5 to 3 years of age, calves reach their maturity. The reported life expectancy is 15-20 years. The main factors influencing group size, migration, and natural mortality are predation (the main predator is wolf (Bergerud, 1988; Seip, 1991; Boertje et al., 1996) and weather conditions (Boertje et al., 1996). The highest mortality occurs in the early stages of life. The peak of mortality occurs usually during autumn and winter (Tryland & Kutz, 2018; Geist, 1998).

1.1.6. Diet

There is not only one typical reindeer habitat (Geist, 1998). Habitat types range from the high Arctic tundra to the relatively rich coniferous forests of North America and the Eurasian taiga or alpine zones in Central Asia. Plant growth is affected by permafrost, air temperature, precipitation, soil nutrient content, and short growing season (Tryland & Kutz, 2018; Geist, 1998).

In the past, it was thought that reindeer eat mainly lichens, but Webber et al. (2022) reported that they are not lichen specialists and, in fact, their diet is more variable. In the winter, lichens dominate their diet, but in summer vascular plants and graminoids dominate, and even mushrooms can be found in their diet during the late summer (Webber et al., 2022; Geist, 1998). Lichens make up 21% of their diet, shrubs 17,6%, forbs 17,1%, graminoids 15,6%, moss 13,2%, trees 4,1%, horsetail 3,9%, fungi 0,01%, and other items 6,3%. The diverse range of species in their diet depends on site conditions, biomass and biomass quality (Tryland & Kutz, 2018; Webber et al., 2022). Veiberg (2007) adds that reindeer in the Arctic wear out their teeth faster, due to abrasion by soil and stone particles chewed with a poor vegetation.

1.1.7. Migration

Reindeer is primarily a migratory or seasonally nomadic animal that affects vegetation in a large area. For example, the annual distance covered by Grant´s caribou (R. t. granti) between the summer and winter habitats is one of the largest overland migrations in the world, over 5 000 km (Fancy et al., 1989; Harris et al., 2009).

There are several reasons why reindeer migrate. Firstly, seasonal migration is related to snow cover and ice conditions. In the beginning of winter, when the snow cover is low, the reindeer is found in the lowlands around the waterways and lakes. As the thickness of the snow cover continuously increases in the lowland, reindeer move to higher altitudes, where the snow is blown away by strong winds. In summer, snow can provide protection from insects (Tryland & Kutz, 2018; Joly et al., 2021a).

Second, reindeer migration is guided by food availability and its quality; the third option is to migrate, which helps to avoid predators. In many cases, the motivation to migrate may simply be the combination of all the above-mentioned factors (Joly et al., 2021a; Joly et al., 2021b).

From late April to early June, females join together and move toward the north of the calving places to avoid predators and annoying insects (Jolly et al., 2021a; Tryland & Kutz, 2018; Joly et al., 2020b).

The exception to the migratory behaviour represents the Svalbard reindeer (*R. t. platyrhynchus*), which is nonmigratory and undertakes no important seasonal movements; one reason for this is likely to be the absence of predators and biting flies (Tyler & Øritsland, 1989). It was found that they used only small seasonal home ranges (Tyler & Øritsland, 1989). However, Svalbard reindeer usually leave to calve in places with a better availability of food resources (Garfelt-Paulsen et al., 2021).

Reindeer migration is highly disrupted by human activities, such as the construction of infrastructure within their territory. Such activities are often associated with high oil and gas production (Harris et al., 2009; Vistnes & Nellemann, 2007).

1.1.8. Impact of human and climate change

Since the Pleistocene, reindeer have been actively hunted (Harris et al., 2009; Tryland & Kutz, 2018; Niven et al., 2012). The continuous hunting of reindeer has been preserved throughout the Holocene in Norway, Greenland, Finland, and Russia. Nowadays, hunting is strictly controlled in Scandinavian countries and also officially in Russia (Tryland & Kutz, 2018). The man had started to domesticate reindeer since the very beginning of their hunting. Reindeer is used for their meat, milk, and fur is used for manufacturing of clothes, and for working especially with sleds. On the contrary, they are not restricted in movement and graze freely. This is the reason why they are considered to be semidomesticated and not fully domesticated animals. Reindeer is the only species of cervids which is domesticated and the last animal species to be domesticated (Baskin, 1974; Geist, 1998; Anderson et al., 2019). However, there are certain characteristics of wildness to this day. The semi-domestication leads to still ongoing migration. During migration, they are accompanied by nomadic herders (Tryland & Kutz, 2018).

Rapid climate change, together with increasing socioeconomic pressure in current reindeer habitats, may lead to smaller and more isolated populations that will be more vulnerable to extinction (Yannic, 2014; Vors & Boyce, 2009). Côté et al. (2012) emphasized that human activity continues to move northwards due to the warmer climate, which may also push the wild reindeer to areas with suboptimal conditions.

Another problem arising from the warming environment can be the increasing abundance of parasites and insects, and thus an increased risk of diseases and generally deteriorating health conditions (Kutz et al., 2014; Tryland, 2012).

A frequently discussed problem is the change of conditions within different seasons of the year. Although warm summers should have a higher plant yield, which should increase individual weight and fertility of individuals (Albon et al., 2017), warm winters, with more frequent rain-on snow events and subsequent ice layers within the snowpack can have devastating effects. Reindeer cannot reach the ground surface with vegetation as it is not capable of breaking through the massive icy layers of the snowpack. Such situations often lead to a prolonged period of starvation (Albon et al., 2017; Turunen et al., 2016). Despite these reported negative effects, Hansen et al. (2019) came up with an interesting modelling outcome suggesting that more frequent extreme events, such as rain-on-snow, may in a longer perspective lead to healthier and more resilient reindeer populations. The high frequency of extreme events can lead to stabilization of the population by regularly eliminating the weak and ill individuals.

1.2. Svalbard reindeer

Svalbard reindeer (*Rangifer tarandus platyrhynchus)* (Vrolik, 1829) is endemic to Svalbard, and it represents a typical Arctic form of the species. Due to the overall shorter and wider skull of Svalbard reindeer compared to other reindeer populations, Camerano was probably the first to recognize Svalbard reindeer as a very distinct subspecies (Gippoliti & Robovský, 2018). Its distinction is well supported by morphological and genetic evidence (Geist, 1998; Kvie et al., 2016; Weldenegodguad et al., 2020). Gravlund et al. (1998) illustrated that it probably evolved from some large-bodied Eurasian reindeer.

1.2.1. Biology and adaptations

Its total body length is similar to that of its closest relative in mainland Norway (Klein et al., 1987), but it has shorter legs compared to his body proportions (Geist, 1998; Klein et al., 1987). Klein et al. (1987) indicated that Svalbard reindeer, due to the absence of predators (wolves), and humans have lost its shyness. They assumed that the absence of such external pressure led to adaptation in terms of developing the short legs (Klein et al., 1987). The shortening of limbs is also a common trend in the island in deer, which are mainly found on islands with poor faunal diversity (Geer et al., 2010). The short-legged body form benefits from energy and nutrient conservation, as well as foraging efficiency (Klein et al., 1987).

The Svalbard reindeer is the smallest reindeer at all. The shoulder height is approximately 90-100 cm in males, some 20% smaller than the Norwegian subspecies (Wollebaek, 1926). The body mass of males is approximately 65 kg in spring and 90 kg in autumn, while the body mass is approximately 53 kg in spring and 70 kg in autumn (Pedersen, 2018). They accumulate fat during the summer grazing period, which is then used during the winter months with low forage abundance. Males lose 20-25% of their weight during the rutting period in October (Geist, 1998; Tryland & Kutz, 2018).

1.2.2. Population

The Svalbard reindeer was close to extinction due to hunting in the early 1900s. The population has increased thanks to strict protection after 1925 (Reimers, 1983), and the last estimation from the 1990s suggests that they form a population of around 10,000 individuals (Tyler, 1993). The local population in Adventdalen, for example, has grown from about 600 individuals in 1975 to around 1,000 in 2007 (Tyler et al., 2008). Svalbard reindeer often stay in a small group of three to five individuals, except during winter, when they can form large feeding groups. Males, which usually prefer the solitary way, join the herds during the rutting season. Rutting time begins at the end of September and ends at the end of October (Wollebaek, 1926; Pedersen, 2018).

1.2.3. Diet

The diet of Svalbard reindeer consists of all types of vegetation, mostly tundra vegetation dominated by different species of grass such as *Deschampsia* and *Poa*, mosses, and some vascular plants (Staaland, 1984). Lichens are the main forage plants during the winter season, when the accessibility of other plants is limited (Hansen et al., 2009). In addition to that, the diet is complemented by vascular plants, woody plants, herbs, and graminoids available under snow cover (Reimers, 2012).

1.3. Factors influencing the Svalbard reindeer population

The well-being of reindeer is the result of different environmental parameters that influence their ability to feed during the vegetation season. In general, the availability of food and the duration of such a period is an important factor that directly influences the well-being of each individual. Considering the specific local environmental conditions, in case of Svalbard reindeer, the basic parameters influencing feeding success are length of the summer vegetation season, total biomass production, and atmospheric conditions as a general factor influencing the above mentioned parameters. The overall population conditions are strongly influenced by winter conditions too, which significantly controls mortality. Snow depths of 50-70 cm form the approximate limit to cratering activity (Laperriere and Lent 1977), which goes well with

Svalbard snow depths being usually well within these thresholds for cratering (Hansen et al., 2010). The depth is therefore usually not an important factor, as the mean depth of snow in coastal areas of Svalbard is usually less than 50 cm. The ice layers within the snow cover are the main factor that influences the success of winter foraging and mortality level. This was documented to have a severe impact even on domesticated reindeer (see e.g. Sokolov et al., 2016). As stated by Hansen et al. (2010), more than 90% of low altitude environment in Svalbard could be covered by a thick ice coat on the ground (median thickness 9 cm). This often results in low numbers of calves surviving to the following summer (Tyler, 1987). Such extreme climatic event can result in the 80% reduction of the population during such winter (Chan et al., 2005). Winter conditions often represent a severe constraint even for domesticated reindeer populations (Vuojala-Magga et al., 2011) from mainland regions.

The starvation also occurs due to worn out teeth from grazing on sparse vegetation among stones and gravel or on icy surfaces (Pedersen, 2018), thus affecting mainly the older individuals. Except polar bears (*Ursus maritimus*) which occasionally hunt reindeer (Derocher et al., 2000) and Arctic foxes (*Vulpes lagopus*) (Eide et al., 2005) which kill a new-born calf (Prestrud, 1992), they have no predators, unlike reindeers which live in other regions (Reimers, 2012).

Density dependent food limitations is the second most important factor controlling population characteristics in regions with populations completely recovered from the hunting period. Soldberg et al. (2008) identified that fluctuations in the Svalbard reindeer population were due to both direct density-dependent food limitation and variation in winter climate associated with high precipitation and icing of the feeding range.

1.4. Environmental conditions in the study area

The Svalbard archipelago is covered by glaciers and ice caps on almost 60% of its area, making the terrain rather inaccessible. Together with heterogeneous shoreline and steep mountain ridges, it creates perfect conditions for existence of relatively isolated reindeer populations. The topography and other spatial limitations resulted in local populations being relatively isolated and sedentary (Tyler and Øritsland, 1989). Such conditions are typical for the area where the presented study was carried out.

Two isolated populations of Svalbard reindeer were studied in Billefjorden, central Svalbard (Fig. 1). Observation and monitoring were carried out during the second half of August 2017. The first population is located in the northernmost part of the fjord, Petuniabukta, and its neighbourhood (78°41'21.1"N, 16°32'21.9"E). The second one is based just in the mouth of Billefjorden near Skansbukta, spreading along the coast about 4 km from Skansbukta to Rundodden (78°31'18.1"N, 16°00'23.2"E and 78°29'07.4"N, 15°56'43.3"E respectively). These two localities are only about 25 kilometres distant, but isolated by series of mountain ridges and ice caps, moving along the coast is not possible due to steep cliffs between the localities.

The first population in Petuniabukta is spread out in several different valleys around the bay, and it is limited by a discontinuous vegetation cover. The valleys are divided by rather steep mountain ridges and often glaciers as well. The average air temperature in Petuniabukta in 2013-2015 was -3.7 °C, the minimum temperature -28.3 °C (February 2015) and the maximum temperature 17 °C in July 2015 (Ambrožová and Láska, 2017). Other information related to climate characteristics can be found in Láska et al. (2012). The climate in Petuniabukta area is significantly colder (approximately 1 °C) with higher continentality leading to drier conditions during the vegetation season (Przybylak et al., 2014). The vegetation season itself is considerably shorter (approximately 2-3 weeks) as well especially due to later meltdown of snow cover. This is caused by permanent sea ice cover during winter blocking inflow of relatively warm Atlantic water to Petuniabukta, whereas Skansbukta is exposed to warm sea water during most of the winter (Nilsen et al., 2008) (Fig. 2). A longer season of vegetation with higher temperatures and precipitation leads to a higher amount of more nutritious vegetation in the Skansbukta region compared to Petuniabukta. Quite a lot of vegetation studies have been done in the Petuniabukta locality especially because of presence of research facilities based in Pyramiden town or Petuniabukta itself. Vegetation studies started already early before World War II (Walton, 1922; Acock, 1940) and continue until now (e.g. Prach et al., 2010; Prach et al., 2012 or Těšitel et al. 2014). However, there is lack of detailed information on Skansbukta vegetation. The comparison of vegetation characteristics on both localities is therefore based on data with low spatial resolution from the Svalbard vegetation map (Elvebakk, 2005) and work by Jónsdottir (2005). Although the two studies mentioned above are helpful, basic visual comparison can be made from the vegetation map available from the Norwegian Polar Institute Svalbardkartet online database as well (NPI, 2018).

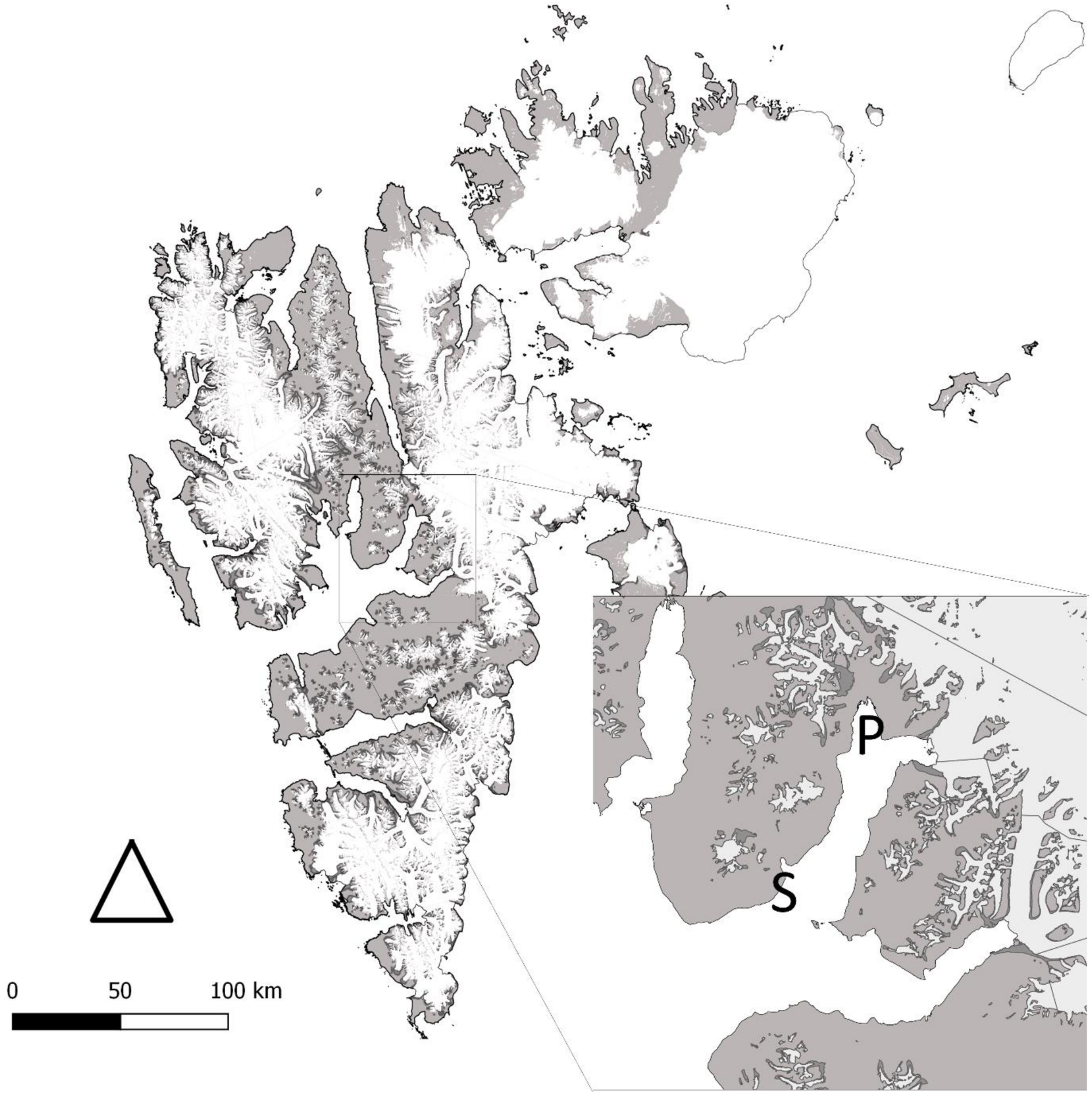

Fig. 1: Location of the study area in central Svalbard, P indicates Petuniabukta, and S stands for Skansbukta

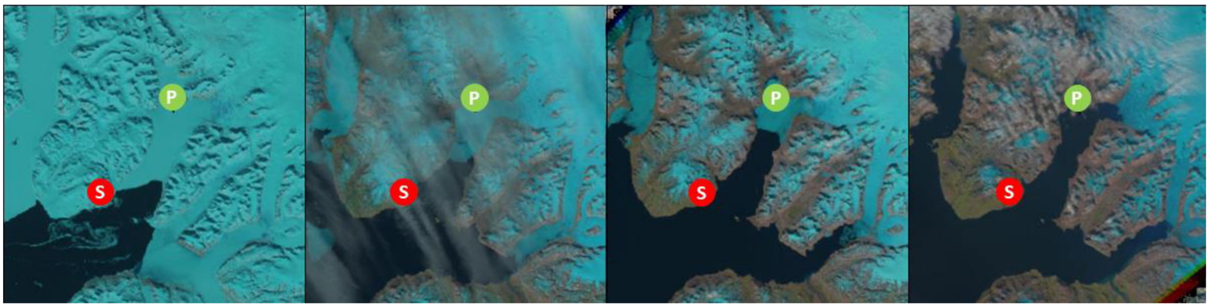

Fig. 2: Landsat_7 images illustrating sea ice breakup that affects onset of vegetation season and climate conditions in general, image from 12 May 2002, 13 June 2002, 22 June 2002 and

11 July 2002 (modified from USGS, 2018, available at:https://earthexplorer.usgs.gov/; accessed 13/08/2018). Petuniabukta area marked with green “P”, Skansbukta with red “S”

1.5. Body mass parameters

Animal body size parameters are often used in paleoecology (Damuth & MacFadden, 1990), but also for the study of animal ecology and evolution (Willish et al., 2013). Body mass is related to a number of biological characteristics, such as life history traits, diet, population density, home range size, population growth rate, and behavioural adaptation (Damuth & MacFadden, 1990). Peters (1983) recognized body mass as predictor for litter size, total litter mass, gestation time, age at weaning, time to maturity from birth (ungulates and carnivores), surface area, brain mass, lung volume, feeding speed, intestinal capacity, metabolic rate, pulse, walking speed, running speed, total sleep time, average life-span, population density (herbivores and carnivores in temperate regions), mean size of prey (carnivore), maximum size of prey (carnivore), home range (herbivores), and home range (carnivores). Damuth & MacFadden (1990) also added that body size may play an important role in studying evolution rate and mode and also in studying species adaptations.

1.5.1. Invasive methods

The traditional manual measurement of body parameters (and antlers in case of deer) was mostly done on hunted dead animals, or from captured animals (Allen, 1900; Rubio-Paramio et al., 2016; Willisch et al., 2013). However, the trapping procedure is quite difficult, expensive and also risky for the captured individual. It can significantly reduce the survival rate and affect reproduction and immune systems (Willisch et al., 2013; Cote et al., 1998).

1.5.2. Non-invasive methods

Therefore, there is a demand for non-invasive methods for measuring body parameters. These methods use telemetry, and calibrated photo cameras with known focal lengths have started to be used recently (Breuer et al., 2007; Della Roca, 2007).

Photographs with a scale rod are used for stationary or slow-moving animals that can be reached within a few meters (Ireland et al., 2006). For more mobile animals that we can reach only at a greater distance, Durban & Parsons (2006), Bergeron (2007) and Barrickman et al. (2015) used laser points and photographs.

Recently, 3D technology has been used a lot to estimate body size parameters. It is relatively very accurate, but it is also expensive and time-consuming and cannot be used in the field (Tsuboi et al., 2020; Rubio-Paramio et al., 2016). Therefore, the most widely used method is photogrammetry. It obtains 3D models from multiple photos at different angles (Rubio-Paramio et al., 2016). Photogrammetry is cheaper and it is easier to extract 3D models from photos (Falkingham, 2012). It is used mainly to estimate body size in a large number of species, most notably in marine mammals such as whales, dolphins, seals, and elephant seals, but also in gorillas, giant tortoises, etc. (Breuer et al., 2007; de Bruyn et al., 2009; Brager & Chong, 1999; Chiari et al., 2008; Beltram et al., 2018; Christiansen et al., 2019; Waite et al., 2007). It has even been applied on corals (Gutierrez-Heredia et al., 2016).

It has recently started to be used to measure horns and antlers. Its accuracy is the same as when using traditional manual measurement (Tsuboi et al., 2020; Rubio-Paramio et al., 2016; Willisch et al., 2013).

Although Tsuboi et al. (2020) indicated that 40 images taken from multiple angles at the shortest possible distance per sample are needed to maximize measurement accuracy, Willish et al. (2013) and Rubio-Paramio et al. (2016) reported that this method is accurate even in case the object of study is located far away from the camera and when using as little as only two photographs. Willish et al. (2013) reliably estimated the upper annuli of free-ranging Alpine ibex by using photographs taken at a distance of several hundreds of meters. They verified this by comparing the manually measured horn values with the horn measurements from the photographs. They found that the remote method had a sufficiently high measurement accuracy.

Rubio-Paramio et al. (2016) used two photos of Iberian deer antlers to create a 3D model. They compared these model results with measurements using a classical tape measure and an articulated arm coordinate measuring machine. They also achieved similar accuracy in their measurements.

2. Objectives

The study aims to inspect how the different environmental conditions can affect physical condition of the two relatively isolated populations of Svalbard reindeer. This is done using a simple distant method using the antler characteristics as a proxy for their physical condition. The population in Skansbukta experiencing more favourable environmental conditions is supposed to be in better physical condition, which should be reflected in its quantitative and qualitative antler characteristics.

3. Material and methods

3.1. Observation of reindeer

Reindeer observations were made directly in the field during the second half of August 2017. All individuals were photographed in their natural habitat with 300mm tele-objective. Observed individuals in the Petuniabukta area were scattered among several distinct locations in smaller groups, typically around 5 individuals (the largest group of 9). All individuals observed in Skansbukta were located in a relatively homogeneous region without significant spatial differences in its distribution. Despite some differences in the composition of the populations (sex) at the sites, the proportions are generally similar, i.e., it is a full-fledged slice of the population.

All individuals were photographed multiple times to ensure high quality pictures with the possibility of measuring the relative size of the antlers and counting the number of tines. However, a possible measurement error when using image analysis resulting from photos being taken from different angles is random and similar in both populations. This error was minimised by choosing the photos of each individual in upright position facing towards the photographer. All photographs were processed manually to obtain information on each individual. All individuals were then cross-checked to avoid multiple counting of the same individual when the individuals moved around Petuniabukta - one group moved between the two neighbouring valleys during August. Cross-checking of photographs was not necessary in the case of Skansbukta, where a single day survey was carried out and all individuals were met just once while passing through the locality. Each individual was measured for its relative shoulder height and antler length from a photo. The length was considered as a proxy of the size of the antler. The relative antler size was then calculated as the ratio of antler length to shoulder height. The number of tines was also counted. This was calculated as the average of the number of tines on both antlers.

3.2. Statistical evaluation

The statistical analysis of the parameters studied was performed in Statistica, version 13. The proportion of males, females and calves in Petuniabukta and Skansbukta was compared by Chi-square test. Although the Shapiro-Wilks test recognized some data as not being deviant from normality, the same nonparametric test variant (Mann–Whitney test) for all species was applied so as to minimise the risk of false positive results (type I error) due to small sample sizes. Subsequently, the same method was used to evaluate differences between the two study sites that differentiate between males/females subpopulations. Finally, a correlation of relative antler size and number of tines was made for each subset separately.

4. Results

4.1. Skansbukta and Petuniabukta populations

A total number of 157 individuals was observed and documented from which 65 individuals were found in Petuniabukta and 92 in Skansbukta. The distribution of males, females, and calves in Petuniabukta and Skansbukta is shown in Table I. A significant difference was found only in the proportion of calves between the two localities (Chi-squared test, p = 0,01) was performed to prove this difference.

The statistics presented further were performed for both populations excluding calves to avoid bias made by uneven distribution of calves in the two populations.

Tab. I: Gender distribution and antler parameters in each location specified as absolute and relative values, the relative values expressed as a percentage

Variables		Petuniabukta	Skansbukta
individuals	total number	65	92
	females	21	31
	females in %	**32**	**33,5**
	males	26	43
	males in %	**40**	**47**
	yearlings	18	18
	yearlings in %	**28**	**19,5**
antler size	total average	0,33	0,44
	females average	0,30	0,38
	males average	0,49	0,57
number of tines	total average	2,99	4,45
	females average	2,43	2,61
	males average	4,52	6,77

4.2. Comparison of males and females within the same locality

4.2.1. Petuniabukta

The antler size and number of tines in 21 females and 26 males in Petuniabukta. The difference between the sexes came out conclusively in both parameters. The difference in means between the two groups was statistically significant, (Mann–Whitney test, p = 0.001) for antler size and (Mann–Whitney test, p=0.006) for number of tines (Figs. 3 and 4). Considering the values of average antler size and average number of tines in both sexes (Table I), the relative size of the antler in females was 61% of the size in the males. An even greater disproportion was observed in terms of the number of tines (females attain only half - 54% - of tines in the males).

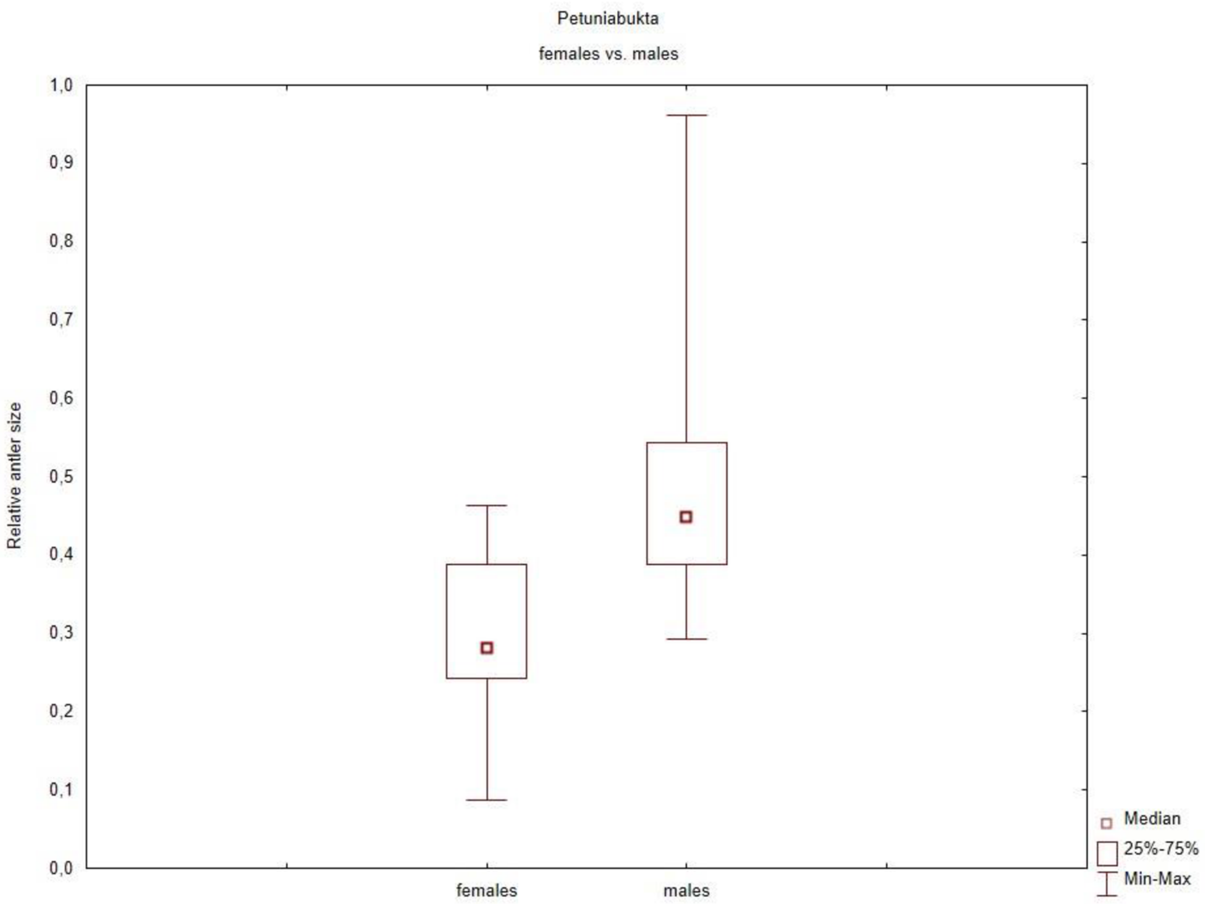

Fig. 3: Comparison of females and males based on antler size in Petuniabukta

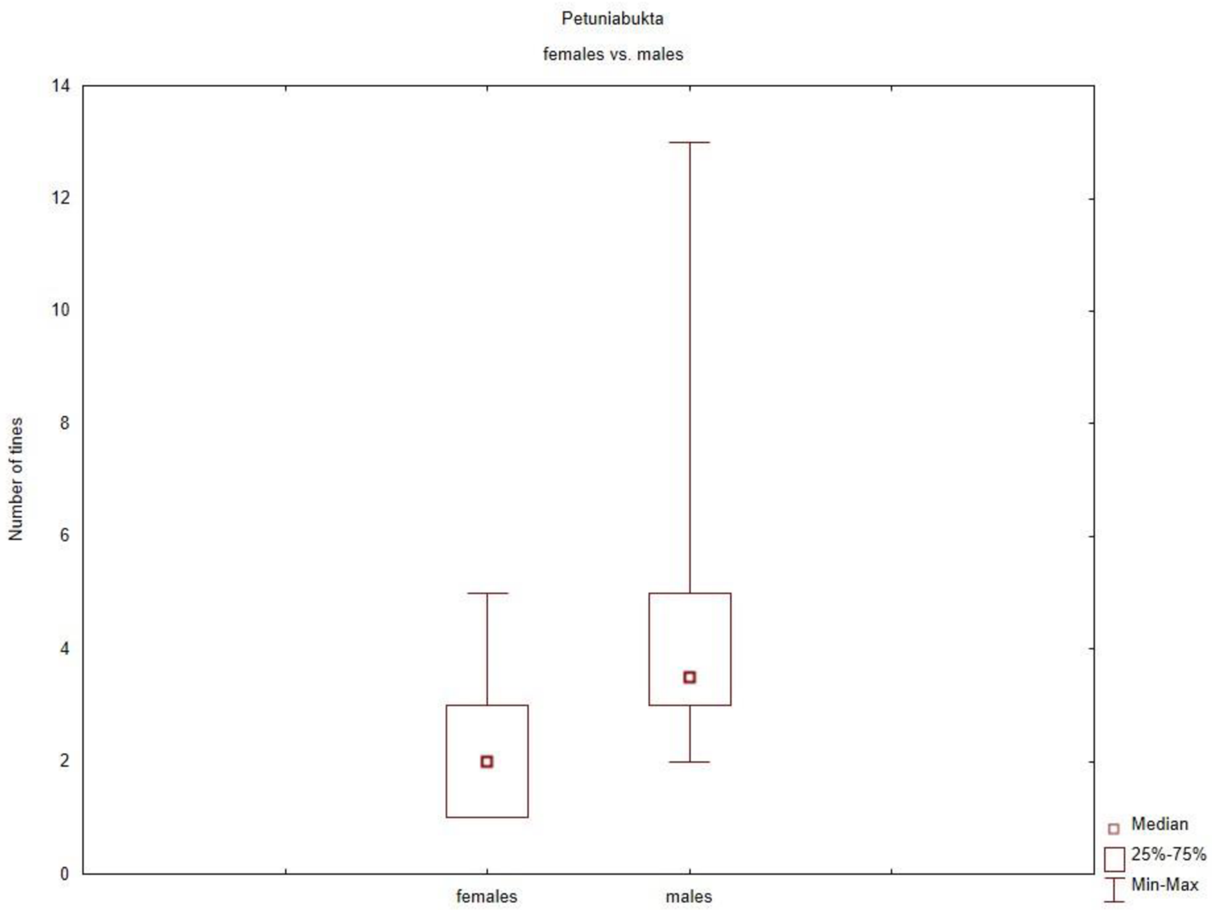

Fig. 4: Comparison of females and males according to the number of tines in Petuniabukta

4.2.2. Skansbukta

31 females and 43 males were observed in Skansbukta and included in the analysis. The difference in means between the sexes was again statistically significant in both parameters (Mann–Whitney test, p = 0,001) (Fig. 5 and 6). Considering the values of average antler size and average number of tines in both sexes (Table I), the comparison of the relative antler size in males and females showed approximately the same proportions as in Petuniabukta, with females having 67% of the male antler size. A greater difference was observed in terms of the average number of tines. In this case, the female values reached only 39% of the males average number of tines.

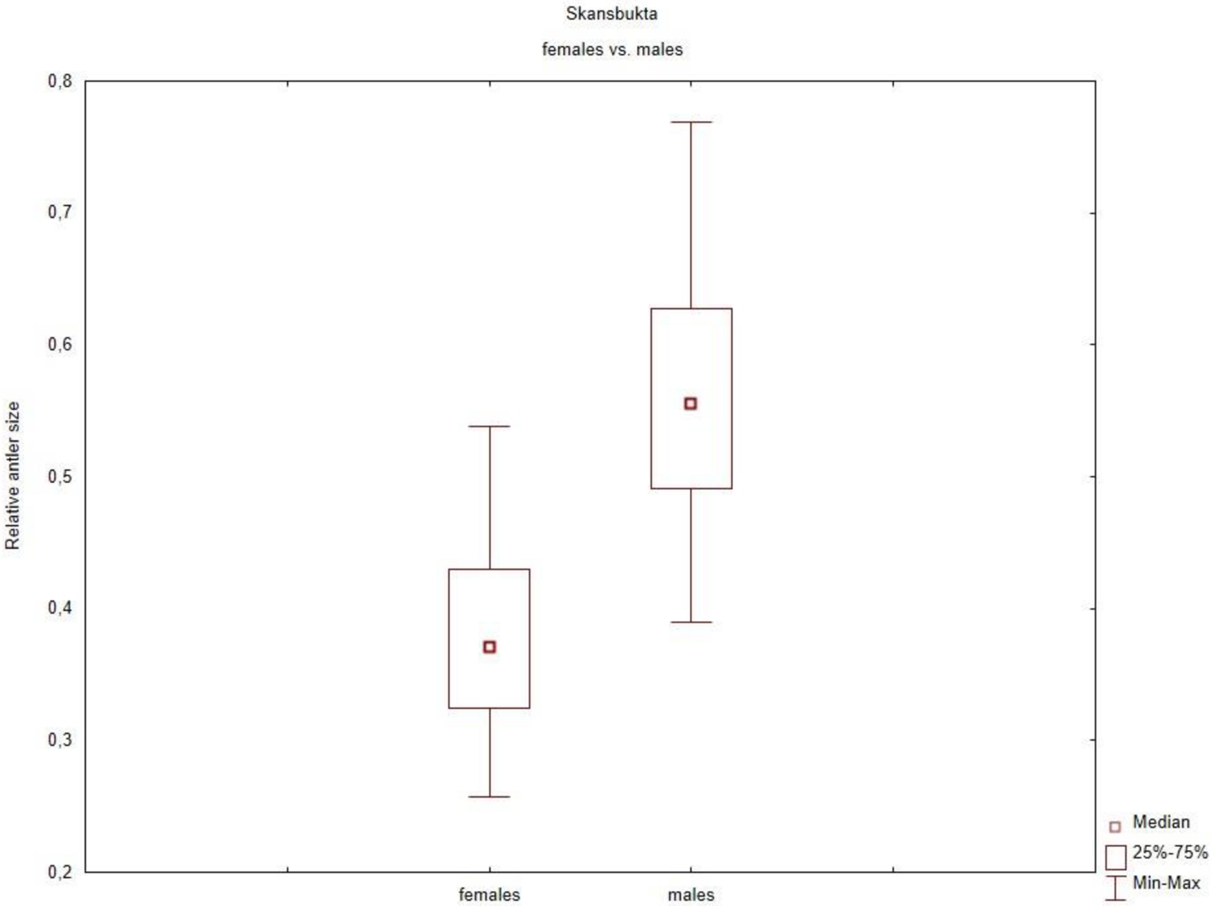

Fig. 5: Comparison of females and males based on antler size in Skansbukta

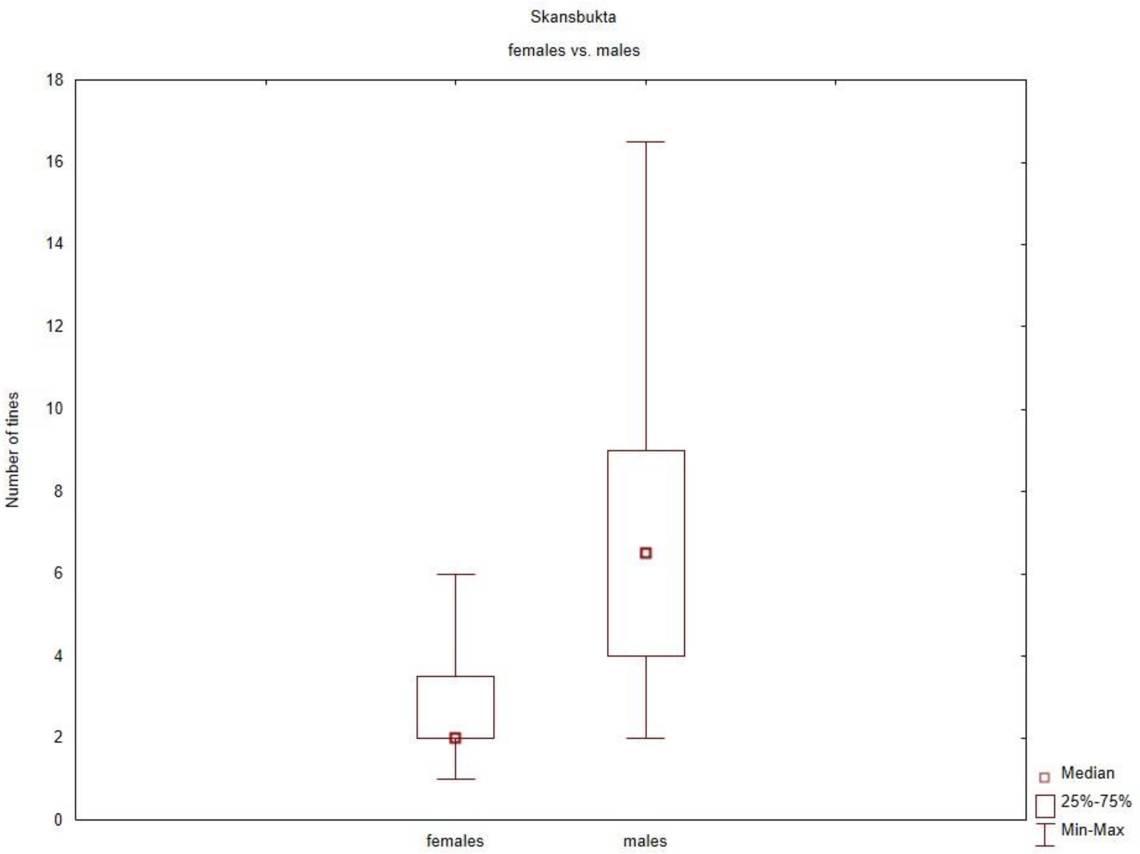

Fig. 6: Comparison of females and males based on the number of tines in Skansbukta

4.3. Comparison of the two localities

4.3.1. Females

Relative antler size and number of tines were compared between the two localities for both sexes separately. 21 Petuniabukta and 31 Skansbukta females were included in the analysis. A difference in the mean size of the relative antler size between females in Petuniabukta and Skansbukta was statistically significant (Mann–Whitney test, p=0,037) (Fig. 7). However, analysis of the number of tines did not show a statistically significant difference (Mann–Whitney test, p = 0.308) (Fig.8). The average relative size of the female antler size in Petuniabukta was approximately 79% of the the size of antlers in females of Skansbukta. The same comparison for the number of tines show that the Petuniabukta females had 93% of the Skansbukta female number of tines.

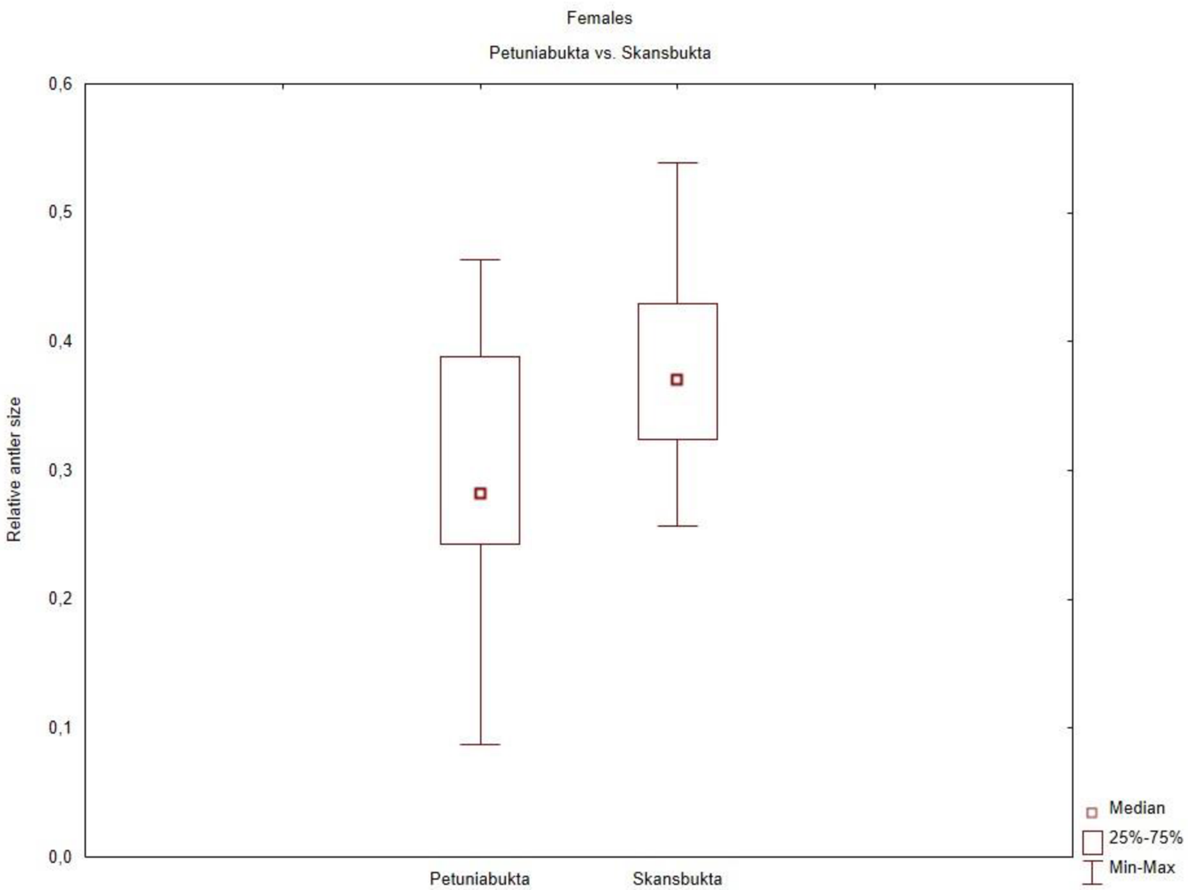

Fig. 7: Comparison of females from Petuniabukta and females from Skansbukta based on antler size

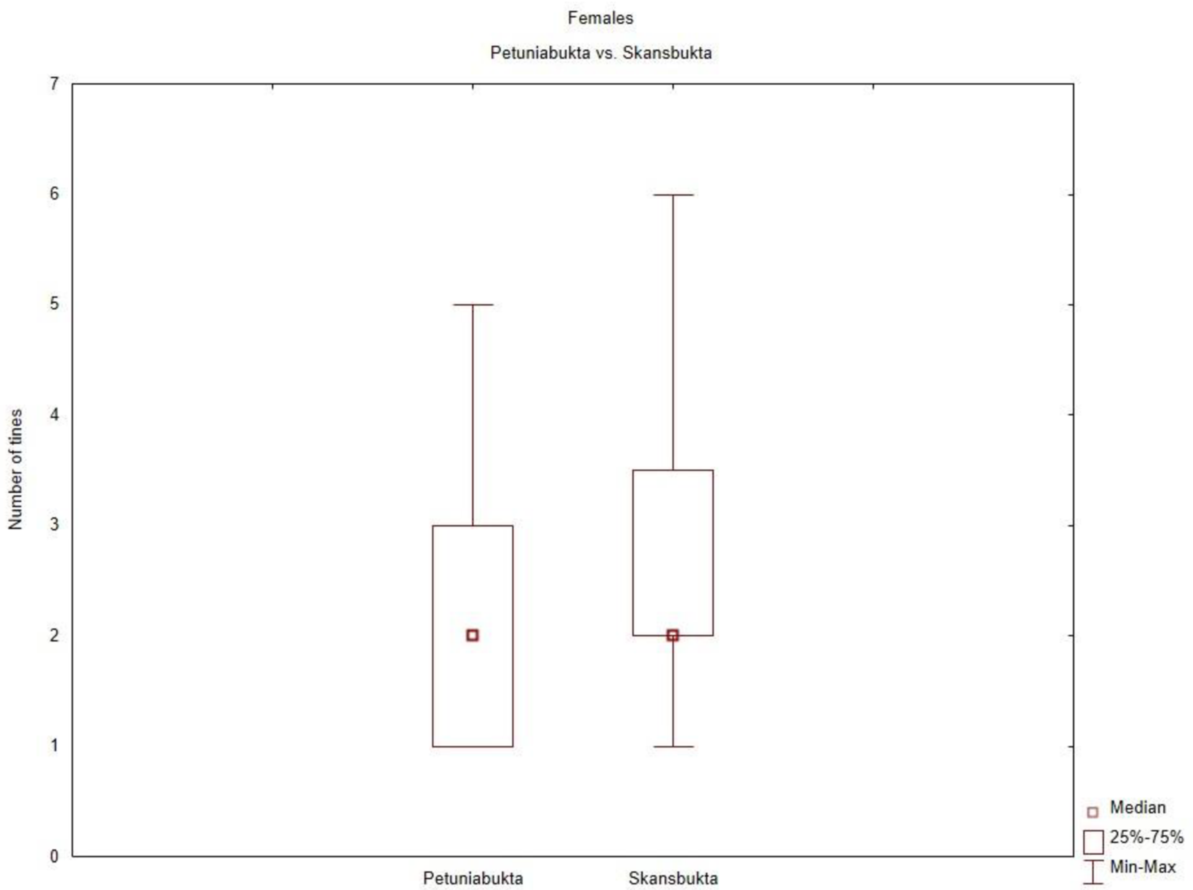

Fig. 8: Comparison of females from Petuniabukta and females from Skansbukta based on the number of tines

4.3.2. Males

26 Petuniabukta and 43 Skansbukta males from were participated in the statistical analysis of both parameters (relative antler size, number of tines). The difference in means between the two groups was statistically significant (Mann–Whitney test, $p = 0.006$ for antler size and $p=0.004$ for number of tines) (Figs. 9 and 10). The average relative antler size in male Petuniabukta was 86% of the Skansbukta male population, whereas the difference in the case of number of tines was even more pronounced (67%).

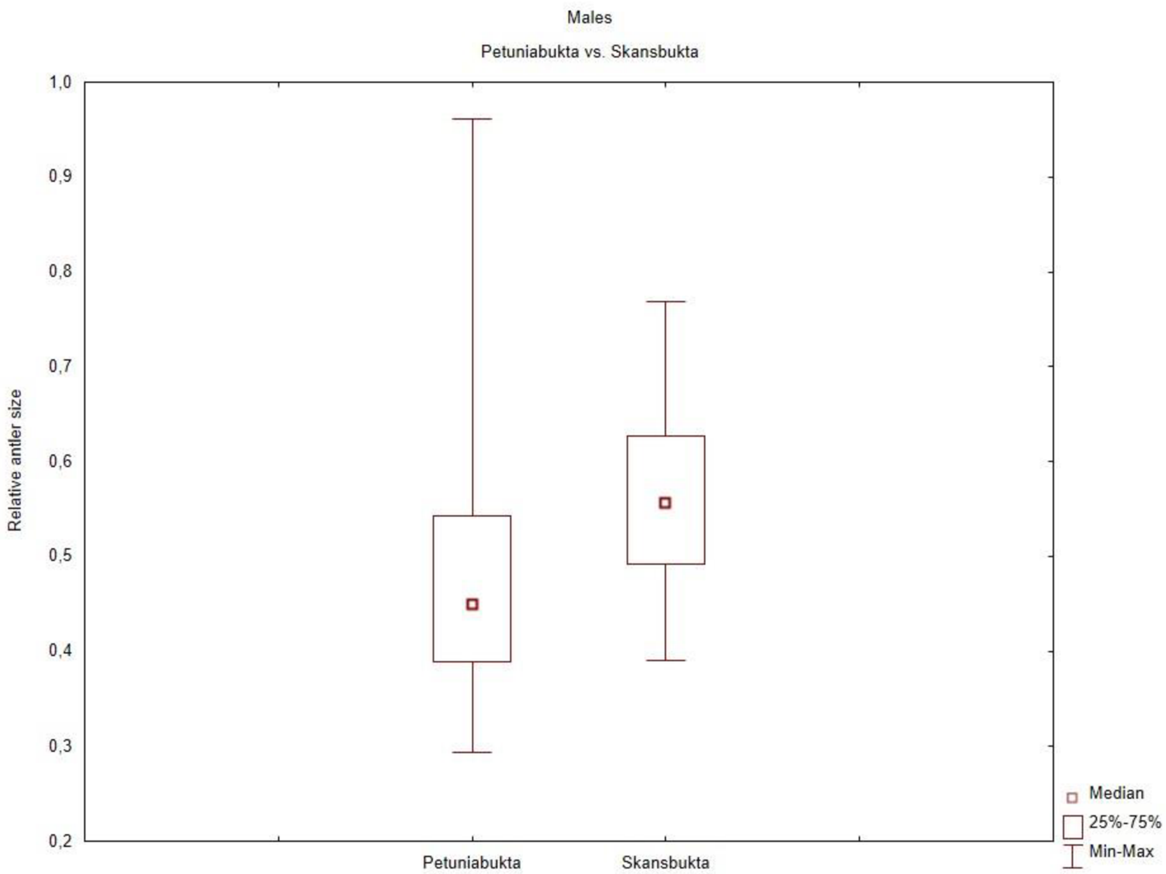

Fig.9: Comparison of males from Petuniabukta and males from Skansbukta based on antler size

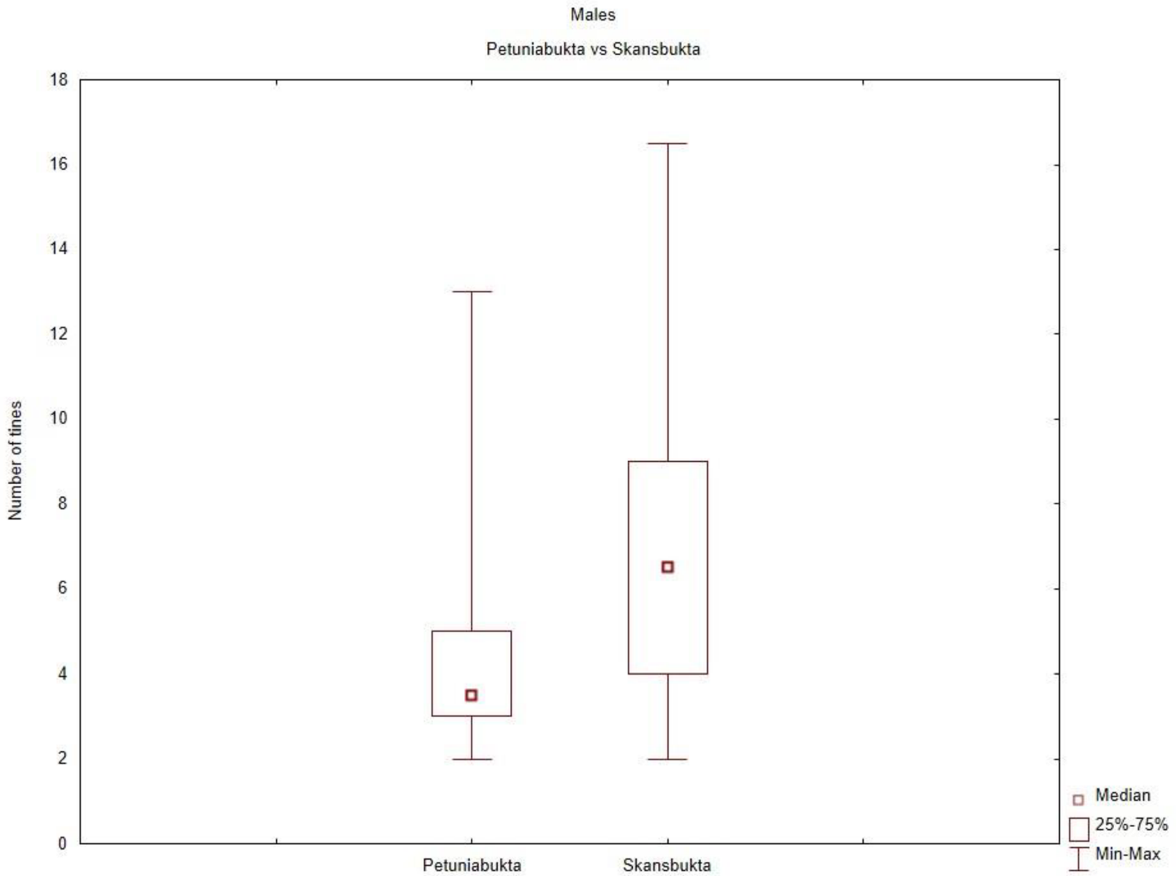

Fig. 10: Comparison of males from Petuniabukta and males from Skansbukta based on the number of tines

4.4. Correlation

The two parameters studied, relative antler size and number of tines, are not independent as is demonstrated by the correlation coefficient. The correlation coefficient ranges from 0.59 to 0.95 and is generally higher in the case of males, probably due to a greater spread of values in the case of the number of tines. The correlation coefficient for the females was 0.67 (Petuniabukta) and 0.59 (Skansbukta), while 0.95 (Petuniabukta) and 0.72 (Skansbukta) in case of males. The shape of the curves (see Appendix: Figs. A1-A4) suggest that it is probably more energy demanding to build a larger antler (in terms of size) than to build a higher number of tines.

5. Discussion

5.1. Sex dimorphism in reindeer and antlers

The dimorphism in mammals is usually expressed in body size/mass. Males are generally larger than females (Glucksmann, 1974). Geist & Bayer (1988) argued that sexual mass dimorphism in ungulates increases with larger body size in males. But, of course, this varies between species and subspecies (Geist & Bayer, 1988). Tryland & Kutz (2018) reported that the strongest sexual dimorphism among ungulates is observed in reindeer. Geist & Bayer (1988), concurred, when recognized the fallow deer and this species with the markest sexual dimorphism in body mass in Cervidae (with a weight male/female dimorphism 2.25 and 2.0, respectively). However, sexual dimorphism in reindeer varies according to specific populations/subspecies due to the large diversity in its morphology. Geist & Bayer (1988) noted a dimorphism of 2.2-2.8 for Norwegian reindeer, while Canadian tundra caribou reach only 1.2-1.6.

The lower level of sexual dimorphism in reindeer is caused by a trend of females towards male traits in open landscapes. This can explain the antlers in reindeer females as part of a trend towards male traits (Geist & Bayer, 1988).

One of the visible signs that differentiates sexes in reindeer is the thickening of the neck muscles and the larger and thicker mane on the neck in males (Tryland & Kutz, 2018; Geist & Bayer, 1988).

Another visible feature represents the antlers. The antlers are usually one of the visible signs of the difference between the sexes in deer due to their absence in females (Goss, 1983; Lincoln, 1992). However, this is not the case in reindeer, because females also have antlers. Differences between male and female antlers are, for instance, in weight, size, and number of tines (Melnycky et al., 2013; Hoymork & Reimers, 1999). This was also confirmed in the present study that compared males and females in the two different localities. Males had a larger relative antler size, as well as a larger number of tines in comparison to females from the same localities.

The weight and size of the antlers also depend on the age and weight of the individual (Geist & Bayer, 1988; Melnycky et al., 2013). Antlers can also be used to distinguish young males from adult females, which are otherwise visually very similar in other body parameters (Geist & Bayer, 1988; Hoymork & Reimers, 1999). Thus, these results may reflect not only differences between males and females, but also differences in weight and age, as well as differences in locations (see below).

5.2. Comparison of locations

Significant differences were found between the two populations studied. The reindeer population in Svalbard, in general, is growing (Pedersen, 2018) and is primarily controlled by winter conditions leading to starvation (Reimers, 2012). The density should not be a limiting factor, as the total number of reindeer is still lower compared to the pre-hunt period (Reimers, 1983). Alendal et al. (1979) reported differences in Svalbard reindeer populations probably due to dissimilarities in food quality and feeding conditions caused by climate. We can distinguish two basic climatic factors influencing the population conditions. The length of the vegetation period and, consequently, biomass production affect the availability of diet and the ability to gain enough body mass to survive the winter. At the same time, unfavourable snow cover properties (in terms of snow depth or presence of icy layers) during winter may alter the ability of reindeer to feed. The frequency of 'rain on snow events" is growing in recent years which negatively influence the populations of reindeers. It was shown that the Petuniabukta population that occupies a harsher environment (as deduced from Nilsen et al., 2008, Przybylak et al., 2014 for climate and from Elvebakk, 2005; Jónsdottir, 2005 for vegetation) has on average significantly lower number of tines and a smaller relative antler size than the population in Skansbukta. The size of the antler also dependents on age. Therefore, these results reflect both population condition and population age structure. However, the two populations as a whole should follow the rather narrow correlation of antler size and environmental conditions as expected by Andersson (1994). The influence of age and environmental conditions cannot be distinguished without having precise age data on each observed individual requiring physical examination. The comparison of both populations probably suggests a lack of well-developed group of older individuals in Petuniabukta (Fig. 13) with relative antler size between 0.6-0.9 and number of tines between 7-10. This might be associated to general lower abundance of forage during summer season, shorter vegetation season or possible harsh winter conditions (see, e.g., Pélabon and Van Breukelen, 1998; Schmidt et al., 2001, Mysterud et al., 2005) affecting this group of older individuals with starvation and possible higher mortality. Even without distinguishing males and females, differences between populations at different locations were confirmed (Kavan & Anděrová, 2019).

Based on antler size and number of tines, correlations were made for males and females from both locations. The graphs show that it is probably more energetically demanding to produce a larger antler than to produce a larger number of tines. This suggests that antler size is probably a better parameter to show the intensity of the investment.

5.3. Conclusions and perspectives

The simple distant non-invasive method for assessing population well-being was introduced and tested. The method is rather robust and can be used during regular annual reindeer monitoring carried out, for example, in Adventdalen (as reported by Pedersen, 2018). It was shown that the two populations compared in the study differ significantly. This can probably be attributed to the dominant effect of different environmental conditions. Recent rapid climate change driven changes in the Arctic (Comiso and Hall, 2014) can have long-term implication on local reindeer populations. These can also be assessed with help of this method. Such an approach of assessing the antler characteristics can bring a new qualitative information to the long-term trends observed presently only in terms of population size. The characteristics of reindeer antlers can serve as a useful proxy for assessing environmental conditions at specific sites and comparison of local atmospheric conditions on an interannual scale as well.

However, it would be necessary to validate the findings by comparing distantly measured antler parameters with more detailed data on the individuals (body weight and size) in respect to sex and age to implement and fully approve the methodology. At this stage, the interpretation of the results is based on the assumption that environmental and atmospheric conditions are the main factors influencing the antler parameters. Density dependent food limitations are considered to have minor effect in the region where the population probably did not fully recover to its pre-hunting level, but this effect should be analysed in detail in further studies as well.

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7. Appendix

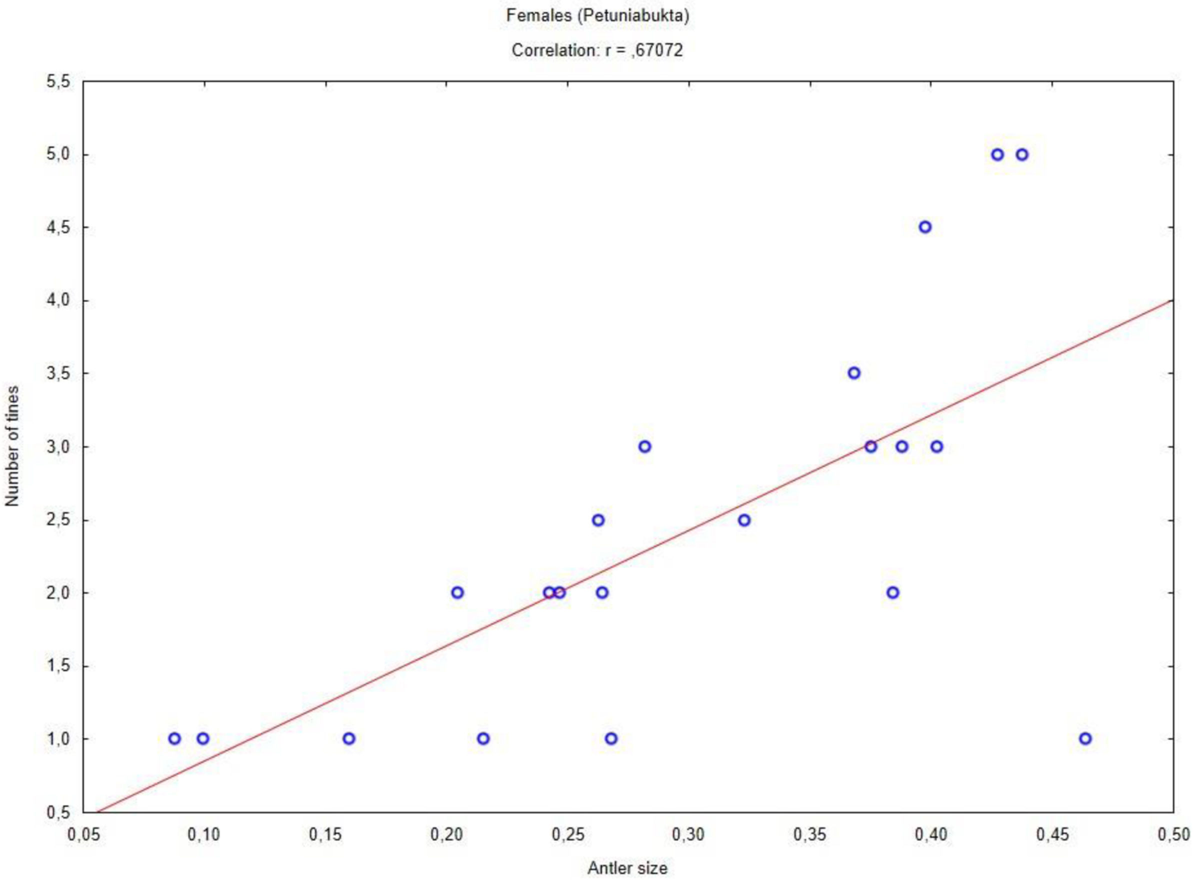

Fig. A1: Relationship between the number of tines and the relative size of the antler with correlation coefficient - females in Petuniabukta

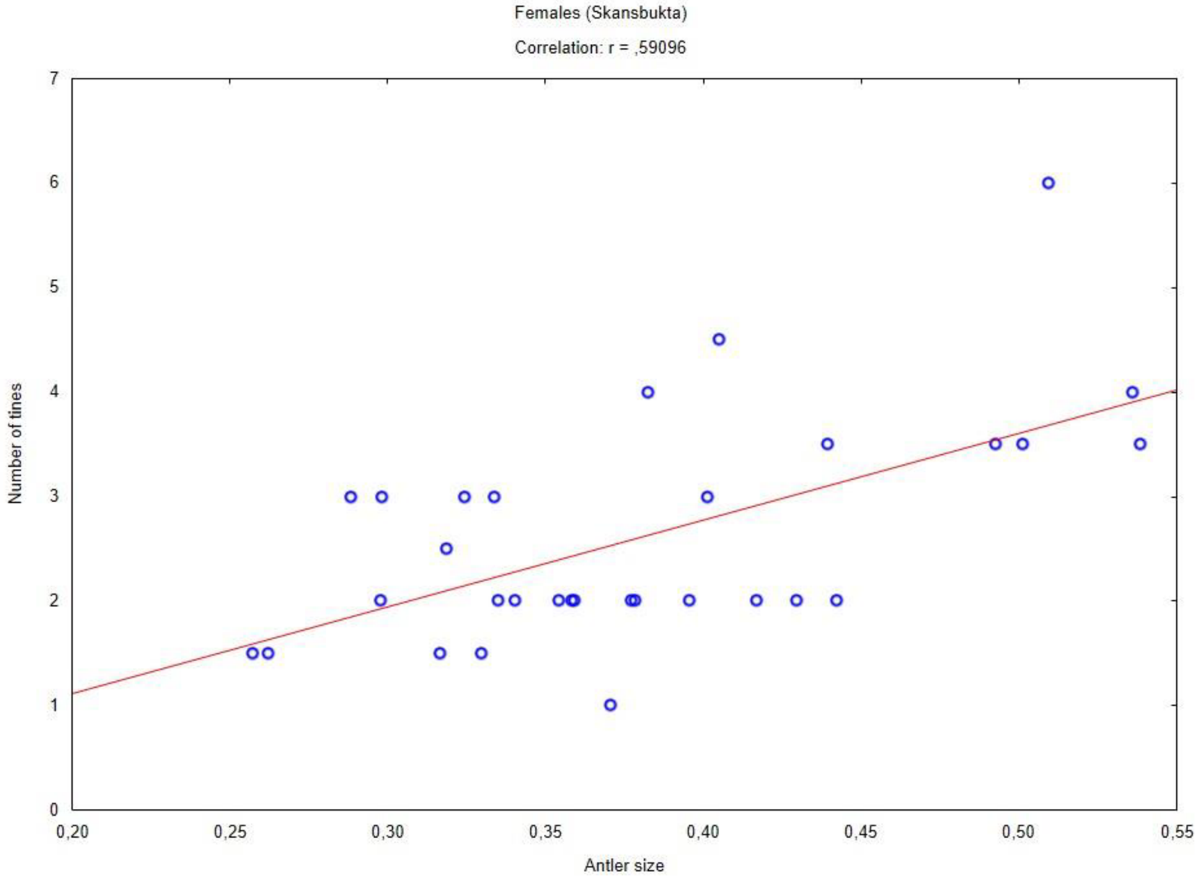

Fig. A2: Relationship between the number of tines and the relative size of the antler with correlation coefficient - females in Skansbukta

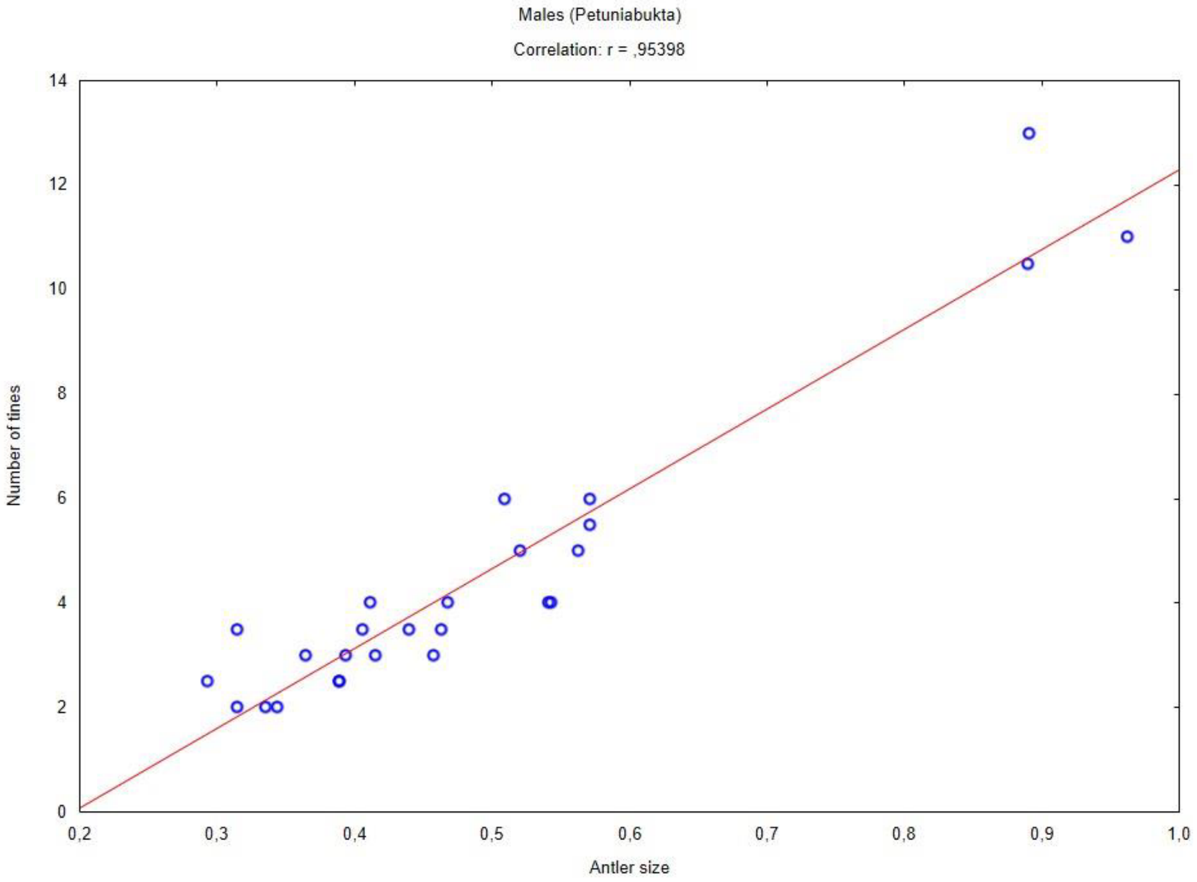

Fig. A3: Relationship between number of tines and relative antler size with correlation coefficient - males in Petuniabukta

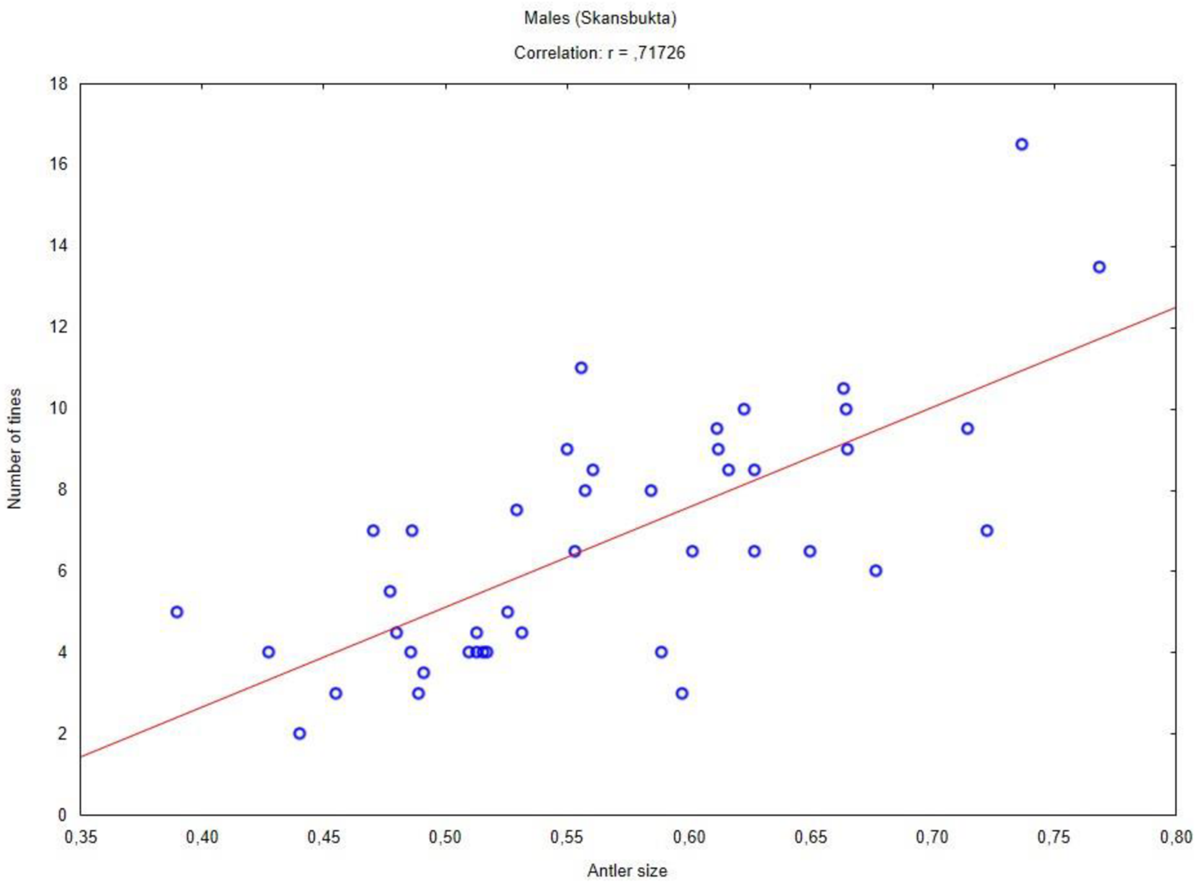

Fig. A4: Relationship between number of tines and relative antler size with correlation coefficient – males in Skansbukta