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– and implications of climate change

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- och kopplingar till klimatförändringar

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Abstract

The impact of climate change on reptile populations is poorly studied, and this includes snakes, which are elusive by nature, making it problematic to preform long-term population studies. Here we have done both. With the help of over 60 years of mark-recapture data, 1942-2009 and 2021-2022, on a population of grass snakes (*Natrix natrix*), the goal was to assess the implications of climate change on the population dynamics.

The results found that adult survival was higher during the winter compared to the summer, especially for smaller individuals. Winter survival was positively influenced by increased winter precipitation, which is probably correlated with a greater snow cover. However, winter survival has decreased over time in line with climate change. The opposite was observed in summer survival, which has increased over time. Summer survival increased with the size of the snake, and along with this increasing winter and summer temperatures, associated with longer active periods, seem to have increased the body size of the snakes, especially the males. Males and females have increased in size with 5 and 9 cm, respectively, over a 60 years period.

Survival was also higher in males compared to a same sized female. Probably as a result of different predation pressure and/or higher survival cost of reproduction for the females. We also observed a decrease of the male ratio in the population over the years.

In line with a changed climate, the influence of season on survival, changes with increasing survival during the summers, and the opposite during the winter. But since the population seem to have been stable over time, the negative effects of increased winter mortality could have been balanced by the increased summer survival. As for now, there are no visible complications on the snake population due to climate change. But since the winters are expected to become more unstable which results in more extreme weathers, and as the survival is affected by factors associated with these changes, *N. natrix* could be threatened in a nearby future.

Keywords: body condition, hibernaculum, long-term data, mark-recapture, population size

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Abbreviations

To make it easier for the reader, you can make a list with common abbreviations in alphabetical order. Here you have a table you can use to make your list.
See example below:

AIC_c	Akaike's information criterion corrected
CJS	Cormack Jolly-Seber
GOF	Goodness of fit
LM	Linear model
LMM	Linear mixed model
OLS	Ordinary least squares
SMI	Scaled mass index
SMHI	Swedish Meteorological and Hydrological Institute
SVL	Snout vent length

1. Introduction

The reduction of global vertebrate populations is a fact; their numbers has declined on average 68% since 1970 (WWF 2020). One of these vertebrate groups are the reptiles, where approximately one in five species are in danger of extinction (Böhm et al. 2013). The most important threats to reptile populations are habitat loss and degradation (Ballinger & Congdon 1996; Gibbon et al. 2000; Todd et al. 2017; Huang & Peng 2019; Mayani-Parás et al. 2019), introduced invasive species (Gibbon et al. 2000; Fordham et al. 2006; Ballouard et al. 2021), environmental pollution (Guillette et al. 1994; Lamb et al. 1995; Gibbon et al. 2000), disease (Gibbon et al. 2000; Lorch et al. 2016; Franklinos et al. 2017), unsustainable harvest (Gibbon et al. 2000; Webb et al. 2002, 2021; Rasmussen et al. 2011), and climate change (Janzen 1994; Gibbon et al. 2000; Araújo et al. 2006; Webb et al. 2021). Even though there are several reports of decline in reptiles in general (Gibbon et al. 2000), one elusive group with little evidence of population decline is snakes. The reason for this shortage of information could be a general lack of long-term individual-based studies of snake populations (Reading et al. 2010). This lack is presumably to some extent a consequence of the snakes' biology and/or ecology, as there are highly venomous species, other are aggressive and nocturnal, and the secretive nature of many species leading to low recapture rates (Dorcas & Willson 2009). Furthermore, a general and unrealistic negative view from the public does not help either (Burghardt et al. 2009). However, there exists a consensus among herpetologists that snakes may be declining worldwide (Mullin & Seigel 2011), and reports of snake populations in decline are increasingly emerging (e.g, Baur & Jaggi 1999; Llorente 2009; Reading et al. 2010; Hagman et al. 2012; Reading & Jofré 2020).

As mentioned above, one of the most important reasons for population decline of reptiles, including snakes, is climate change (Janzen 1994; Gibbon et al. 2000; Araújo et al. 2006; Webb et al. 2021). Even so, the impact of climate change on reptile populations is poorly studied (Gibbon et al. 2000). In the boreal zone of the northern hemisphere, global warming is increasing twice as fast compared to the global average (Ruiz-Pérez & Vico 2020). With increasing temperatures, the annual duration of the thermal winter has decreased remarkably over the years in the Baltic countries and the Scandinavian peninsula (Ruosteenoja et al. 2020), which likely will make Swedish ectotherms particularly vulnerable. Linked to this increase in temperature, it has been predicted that the subnivium (the open space between the snow and the ground) duration will decrease, and so effecting negatively the survival of organisms depending on the subnivium when exposed to colder temperatures (Zhu et al. 2019). Snakes at higher latitudes are dependent on suitable hibernacula (refuge used during over-wintering), which are critical for winter survival (Prior & Weatherhead 1996). Therefore, the climatic impact on the subnivium could potentially be unfavourable for the survival of snakes in the boreal zone, as the isolating effect of the snow disperses subsequently leading to the ground frost reaching further down. However, less snow cover is not the only thing threatening snakes, climate change may increase the frequency and magnitude of extreme weather conditions (e.g. low winter temperatures and/or, high summer temperatures), as well as the unstable weather, which also have been shown to give negative effects on survival (Saint Girons 1981; Gregory 1982; Shine & Mason 2004; Altwegg 2005). These types of extreme weathers events are predicted to increase in Europe as an effect of climate change (Nikulin et al. 2009).

Snakes and other reptiles are strongly limited in their geographical distribution by ambient temperature. The mobility of adult and juvenile reptiles allows them to search and exploit external heat sources (e.g. sunny patches or thermal heat sources) within the environment to maintain an optimal body temperature (Huey 1982, 1991; Vitt et al. 1998; Huang & Peng 2019). Eggs on the other hand are not mobile. Thus, reptile species in the boreal zone are mostly ovoviviparous (giving live birth; Tinkle & Gibbons 1977; Shine 1985), which gives them an advantage in the cold climate; gravid females can regulate the temperature of the embryonic development by moving to suitable sites (Mathies & Andrews 1997; Shine 2006). This is the case for two of the three snake species native to Sweden: the common adder (*Vipera berus)* and the smooth snake (*Coronella austriaca*) (Speybroeck et al. 2016). However, the third species, the grass snake (*Natrix natrix*) stands out by being oviparous (laying eggs; Speybroeck et al. 2016). Given the geographical constraints of oviparity, *N. natrix* is the most northern oviparous reptile species in the world and occurs in colder climates than any other oviparous reptile (Gasc et al. 1997). Part of this success lies in *N. natrix* use of anthropogenic heat sources (e.g. manure heaps, compost piles, or mounds of sawdust) when depositing eggs (Madsen 1984; Löwenborg et al. 2012; Speybroeck et al. 2016). Furthermore, *N. natrix* is a wide spread species, found in most of central and northern Europe, and east to central Asia (Speybroeck et al. 2016). According to the IUCN red list (Aghasyan et al. 2021) *N. natrix* is considered as 'least concern', since current population trends are stable within its range. However, *N. natrix* is regionally or locally threatened in some parts of its range by decline of its prey, draining of wetlands, and other types of habitat loss (IUCN). In Switzerland it is categorized as 'endangered' (Monney & Meyer 2005), and it is considered to be 'near threatened' in Mongolia (Terbish et al. 2006). According to the Swedish law, it is required to have manure heaps surrounded by a one meter high concrete wall (due to overfertilization), which may have dire consequences for local *N. natrix* populations (Weatherhead & Madsen 2009). Hagman et al. (2012) also demonstrated a decline of specimens deposited in Swedish museum collections, implying that the Swedish population is in decline together with their anthropogenic nesting environments.

Another attribute, other than the abundance of individuals, is the general physical conditions of snakes in the population (e.g. size). Body size, which correlates positively with both fecundity and survival of snakes (Madsen 1987; Shine 1994; Luiselli et al. 2011; Hyslop et al. 2012), has over the past decades changed in a number of organisms (Gardner et al. 2011). Decline in body size has been observed reportedly in endotherm vertebrates, but ectotherm vertebrates are less represented in studies of this type (Gardner et al. 2011). However, there are reports of both increase and decrease in body size in ectotherm vertebrates, of which some are related to climate change (e.g. Chamaillé-Jammes et al. 2006; Tryjanowski et al. 2006; Caruso et al. 2014). A study from 2021 found that in a population of *N. natrix* in southern Poland, the snakes have declined in body size over a 40 year period, and suggests this could be the result of increased road mortality, human presence and decline of prey (Bury et al. 2021). Also, a change in sex ratio was observed, going from a higher ratio of females to 1:1 condition (Bury et al. 2021). Thus, sex also needs to be considered when evaluating survival of snakes. Males and females of *N. natrix* show different behaviours when emerging from hibernation (males emerging first; Phelps 1978), and in their movements during the active period (Madsen 1984). Also, sex biased mortality has been observed in other species of snakes (Lind et al. 2005; Sperry & Weatherhead 2009; Hyslop et al. 2012). This raises the question if *N. natrix* in Sweden displays the same pattern as observed in Poland (Bury et al. 2021).

The aim of the study was to evaluate the historical and current status and condition of a *N. natrix* population, and to evaluate if climate change had induced the population status and/or condition, based on long term data (1942-2009 and 2021-2022). More specifically, the main objectives of this research were:

(I) to evaluate the monthly apparent survival in relation to time, season, weather conditions and individual characteristics.

(II) to assess sex ratio, body condition and body size in the population over time, but also body condition and body size relation to weather conditions.

(III) to estimate the historical adult population size of *Natrix natrix*, and the historical and current population size a local hibernaculum.

2. Method

2.1. Data collection

This study is largely based on a unique data set collected by and “inherited from” the late Prof. Carl Edelstam of the Swedish Museum of Natural History. Between 1942 and 2009 he captured, marked, and recaptured *N. natrix* at several hibernacula sites and the surrounding area in what is known today as Nacka nature reserve, Stockholm. The study is also complemented with my own recent mark-recapture data 2021-2022.

2.1.1. Study site

Nacka nature reserve was founded in 2005 and is one of Sweden’s most visited out door areas (The City of Stockholm 2016). This nature reserve is enclosed within the urban areas of southern Stockholm, creating an exceptional situation with a semi-closed population. The reserve includes 754 hectares of coniferous forest, meadows and pastures, lakes and streams (of which water is 104 hectares). Most of Edelstam’s survey was performed in the area surrounding the lake Dammtorpssjön (today a Natura-2000 area), where three major hibernacula are located: Västvallen (SWEREF 99 TM, N 6576668, E 678929), Hammarbyröset (N 6575807, E 679072) and Hidet (N 6576204, E 679401).

Weather data

Historic weather data, including mean temperatures and total precipitation for winter and summer, were obtained from the weather station Stockholm-Observatoriekullen which is managed by the Swedish Meteorological and Hydrological Institute (SMHI). This weather station is located at Observatorielunden in central Stockholm (N 6582086, E 673729), which is approximately 8 km from the study site.

2.1.2. Mark-recapture 1942-2009

Each hibernacula and its surrounding area were surveyed each season (with some exceptions), most frequently in spring when snakes emerge from hibernacula, and in autumn when they congregate at hibernacula for the winter. Snakes were captured by hand and kept in cloth bags in the field. Each snake was marked by scale-clipping (Carlström & Edelstam 1946; Weary 1969; Brown & Parker 1976; Mullin & Seigel 2011), along with recording the natural markings (i.e. the ventral pattern of the grass snake is unique for each individual and can be used for individual identification; Carlström & Edelstam 1946). For each snake (with few exceptions) capture date, location, sex, snout vent length (SVL), tail length, total length, and weight were noted on each capture occasion. After data sampling, all snakes were returned to the same location where they had been captured.

2.1.3. Mark-recapture 2021–2022

Recent mark-recapture data were collected during two study periods: autumn 2021 and spring 2022. Both surveys were conducted at the hibernaculum Hidet (see 2.1.1), of approximately 340 m^2 over a sloping south-facing bank of the lake Dammtorpssjön with large rocks and trees (figure 1.). Surveys were performed during sunny or partly sunny days when snakes where most active, that is, 10:00 am – 05:00 pm, up to 5 – 6 hours (with one exception; see table A.1).

The mean volume of forest per hectares has increased with >30 % since year 2000 (quantified using kNN-Sverige, raster maps 25 × 25 m resolution based on satellite images and field data from the Swedish National Forest Inventory; Reese et al. 2003); using ArcMap 10.6 software; ArcGIS, ESRI, Redland, CA, USA). The overgrowth of many of the other hibernation areas was one of the reasons why the sites Västvallen and Hammarbyröset (see 2.1.1) were neglected in this sampling. This and limitations in fieldwork logistics.

Figure 1. The hibernaculum at Hidet during autumn 2021 (left) and spring 2022 (right).

Each snake was caught and measured with the same method as used by Edelstam (see 2.1.2, with the exception of scale clipping). A digital scale was used for body mass, while the animal was contained in a closed plastic box. To keep track of each individual snake, natural markings were photographed (figure 2.). As with the historical data, the ventral pigmentation of the snake was used to identify each individual (Carlström & Edelstam 1946). The first 15 ventral scales of each captured snake were photographed and compared with previous photos to find potential recaptures. SVL was measured by stretching the snake gently on the ground and noting the length from the tip of the snout to the cloaca. Tail length was measured in a similar manner but from the cloaca to the tip of the tail.

Figure 2. Natural ventral marking of a male grass snake (Natrix natrix), first caught in autumn 2021 (A) and then caught again spring 2022 (B).

Sampling procedures of the grass snakes for this study were approved by the Swedish Board of Agriculture and the Ethical Committee for Animal Experiments in Stockholm County (Dnr 11161-2021) and collection permits for the Nacka nature reserve were provided by the Administrative County Board of Stockholm (522-13116-2021).

2.2. Population dynamics and condition

2.2.1. Survival analyses

The historical mark-recapture data were implemented for survival analyses using the Cormack Jolly-Seber (CJS) model with mark-recapture data in the program MARK (Burnham 1987; White & Burnham 1999; Evan & Gary 2019). For the analyses, only adult individuals were selected from the data set based on SVL. Since there is a sexual dimorphism in reproductive body size, males were considered to be adult at SVL ≥ 43 cm, and females at SVL ≥ 55 cm (which corresponds to the total length of 55/63 cm of sexual mature individuals; Madsen 1983). Males and females were divided into two groups: sampled within the spring periods (April-May) or the autumn periods (Sep-Oct). All captures during one period (spring or autumn) for each year were pooled into one occasion. Summer observations were excluded, as *N. natrix* during this period are widespread (Reading & Jofré 2009) and thus, only a small proportion of individuals was sampled. Based on these premises, the most coherent time span for survival analysis ranged from autumn 1969 to spring 2002, with only two missed survey occasions (autumn 1980 and 1989).

The long-term mark-recapture history was constructed representing alternating sequence of autumn and spring samples, with every second occasions between the samples, including five pooled months from autumn to spring, and three pooled months from spring to autumn. The respective apparent survival intervals are therefore winter and summer. The data set corresponds to a snake being present "1", to a snake being absent "0", or "." for missing seasonal data. Finally, this resulted in a data set with 64 capture occasions (31 autumns and 33 springs). The CJS model (Lebreton et al. 1992) was used to estimate the apparent monthly survival (φ) and recapture rate (*p*). However, to perform the CJS model data must meet four assumptions (Pollock et al. 1990; Evan & Gary 2019); (1) every marked animal present in the population at time *i* has the same probability of recapture, (2) every marked animal in the population immediately after time *i* has the same probability of surviving to time $i+1$, (3) marks are not lost or missed, and (4) all samples are instantaneous, relative to the intervals, and the individuals are released immediately after the sample. Assumption 3 and 4 were presumed to be fulfilled.

Deviations from assumptions 1 and 2 were tested by calculating the variance inflation factor (ĉ) (Evan & Gary 2019). This was done on the highest dimensioned acceptable model, which is letting survival and recapture vary between time and sex; φ(~time+sex) *p*(~time+sex). The estimation of ĉ was calculated through a χ^2 goodness-of-fit (GOF) test (all "." were considered as

“0”) using the RELEASE program (within MARK; Burnham 1987; White & Burnham 1999).

Variance inflation factor – “c-hat” (ĉ):

$$\hat{c} \cong \frac{\chi^2}{df} = \frac{113.5584}{227}$$

Overdispersion was not detected. The estimated ĉ was 0.5, which indicated underdispersion (Evan & Gary 2019). However, it is considered to treat ĉ <1 as ĉ =1: thus, no quasilikelihood or variance inflation factor correction was necessary (Evan & Gary 2019).

Effect of climate

Seven parameters (table 1.) predicted to be related to monthly apparent survival and recapture were chosen to create a global model for the continued analysis. These seven parameters were selected based on previous information about *N. natrix* biology and the design of the study.

Table 1. Parameters used in p (recapture) or/and φ (apparent survival) to estimate the effects of weather, and the subscripts used for model notation in CJS analysis.

Notation	Meaning	Applies to
effort	Capture effort: the number of sampling occasions during one season	p
sex	Sex effect	φ, p
SVL	Individual covariate: the effect of the first measured SVL of an individual	φ, p
temp s	Mean temperature for the summer season	φ
temp w	Mean temperature for the winter season	φ
rain s	The total amount of precipitation (mm) during the summer season	φ
rain w	The total amount of precipitation (mm) during the winter season	φ

From the global model several nested models were constructed from the parameters related to recapture (table 1.), while the parameters related to survival were kept unchanged. These models were analysed trough CJS model. The model with the lowest Akaike’s information criterion corrected for small sample size (AIC_c) was picked (Burnham & Anderson 2002) and compared to adjacent models through a likelihood ratio test (Lebreton et al. 1992). After a satisfactory model of recapture was established, the same model was used to model monthly apparent survival. Similar to what was done when modelling recapture, nested models constructed from the parameters related to survival (table 1.) were compared to each other based on their $\mathrm{AIC_c}$, and the best adjacent models were tested with a likelihood ratio test (Lebreton et al. 1992). The summed Akaike's model weight ($\sum w_i$) for each parameter related to apparent survival was also calculated to estimate how likely it is for a parameter being part of the best model (Burnham & Anderson 2002).

Trends over time and season

To see if there were any implication of trends of the monthly apparent survival over the years and season, a secondary CJS model was constructed. For this model all weather parameters were excluded, and instead the effect of season and year was used, along with the interactions between sex and season, and year and season (table 2.).

Table 2. Parameters used in p (recapture) or/and φ (apparent survival) to estimate the trend effects over time and season, and the subscripts used for model notation in CJS analysis.

Notation	Meaning	Applies to
effort	Capture effort: the number of sampling occasions during one season	*p*
sex	Sex effect	φ, *p*
SVL	Individual covariate: the effect of the first measured SVL of an individual	φ, *p*
season	The effect of season (winter and summer)	φ
year	The effect of numbers of years from when the mark-recapture started	φ
sex:season	The interactive effect of sex and season	φ
year:season	The interactive effect of year and season	φ

The same recapture model as in the previous monthly apparent survival model related to the climate was used, '*Effect of climate*'. From the parameters of interest (table 2.) several nested models for the monthly apparent survival were constructed as above, and selected by the lowest $\mathrm{AIC_c}$. The best adjacent models were tested with a likelihood ratio test, and all parameters $\sum w_i$ were calculated.

However, to take into consideration when fitting a trend over the year in this type of model, the estimate is forced to fall in a line and with this statistical constraint enforces a biological hypothesis which is unlikely (Evan & Gary 2019). This means the results from '*Trends over time and season*' should be taken with a grain of salt.

2.2.2. Body measurements

Body condition

To avoid potential deceptive measurements of a female's weight in case of the her being gravid when captured only mature males (SVL ≥ 43) were included in the body condition analyses. Males captured in spring or autumn between 1945 and 2006 were used in the data set. Summer observations were excluded, for the same reason as above (see 2.2.1.). The body condition of each captured snake was calculated using the Scaled mass index (SMI; Peig & Green 2009). This body condition index performs better than traditional regression of body mass and size (Jakob et al. 1996; Green 2001; Hayes & Shonkwiler 2001).

Scaled mass index – (SMI):

$$\widehat{M_i} = M_i[\frac{L_0}{L_i}]^{b_{SMA}}$$

Where M_i is the observed weight and L_i the observed SVL of the individual. L_0 is the mean length of all induvial and b_{SMA} is the slope divided by Pearson's correlation coefficient from an ordinary least squares (OLS) regression of the logged weight and SVL data of the data set (Peig & Green 2009).

To compare the variations in SMI across seasons, a two-sample t-test was performed to compare first-time captured individuals between the spring and autumn seasons. The data were divided into spring or autumn observations. In addition, for each season a linear mixed model (LMM) was carried out with package lme4 (Bates et al. 2015) in R (R Core Development Team 2020), where SMI was related to year, and individual was set as a random effect. Further analyses were carried out to examine the seasonal effect of temperature and precipitation on SMI of spring and autumn data, respectively. Annual mean winter temperature and total winter precipitation were used for the spring data, while the annual mean summer temperature and total summer precipitation were used for the autumn data. This analysis was also carried out with a LMM, relating SMI to mean temperature and total precipitation (fixed effects). Year and individuals were used as random effects.

Body length analysis

As with body condition, the size, SVL, of the snakes was analysed across years. Here both adult males (SVL ≥ 43 cm) and females (SVL ≥ 55) captured in spring or autumn between 1945 and 2006 were used. However, due to sexual dimorphism, the two sexes were analysed separately (Madsen 1983). To find any potential trend in SVL over the years, a LMM was carried out on both sexes separately, where SVL was analysed against year, having individual as a random effect.

Similar to the body condition analysis, body length analysis was carried out on the seasonal effects on the SVL. For each sex and season, SVL was related to the corresponding mean temperature and total precipitation, using individual and year as a random effect.

Sex ratio analysis

The sex ratio was based on the proportion of adult males (SVL ≥ 43 cm) to females (SVL ≥ 55) for each decade, that is, 1940s-2000s. sex ratio for each year was also related to year in a linear model (LM).

2.2.3. Historical and recent population estimates

The population estimate of adults at Hidet, 2021-2022, was compared with the historical data. Due to the different nature of the data sets two approaches to estimate the populations size were selected based on the different model assumptions. This resulted in the use of both Open and Closed population models.

Open population

Although Lincoln-Petersen models could provide population estimates there is in some cases not possible to assume that a population should be closed (Lincoln 1930; Pollock et al. 1990). Open population models allow the probability of births, deaths, immigration, and emigration. They have been used successfully to estimate population size over long-time scales of several vertebrate species (e.g. polar bear *Ursus maritimus,* humpback dolphin *Sousa chinensis,* jaguar *Panthera onca*; McDonald & Amstrup 2001; Guissamulo & Cockcroft 2004; Gutiérrez-González et al. 2012), along with snakes (e.g. black snake *Elaphe obsolete*; Weatherhead et al. 2002). One of the more popular open population models is the Jolly-Seber model, which requires at least three sampling occasions, separated by long intervals (Jolly 1965; Seber 1965; Pollock et al. 1990). The model follows the same assumptions as The CJS model (see. 2.2.1) (Pollock et al. 1990).

The historical estimate of adult snakes in Hidet populations was done for two periods, spring 1944 to spring 1950 and spring 1970 to spring 1974, where it was less than one period gap between two occasions or sample size of five or more. Historical estimates of adult snakes of the total Nacka population from spring 1944 to autumn 2004 was also calculated. The estimation was calculated in R (R Core Development Team 2020) with the package FSA (Ogle et al. 2021)

Jolly-Seber estimation:

$$\alpha = \frac{m_i}{n_i} \qquad M_i = \left(\frac{n_i z_i}{R}\right) + m_i \qquad \widetilde{N} = \frac{M_i}{\alpha}$$

Where n_i is the number of captured and marked animals on occasion i and m_i is the number of recaptures from earlier occasions. z_i is the number of marked individuals from earlier occasions that were ever caught after the capture, and R is the number of marked individuals on the current occasions that were ever caught again (on later occasions).

For the historical estimations for the three hibernacula 10 estimates were removed due to the confidence interval being predicted as infinity.

Closed population

One of the most traditional methods to estimate a population size is closed population models (Mullin & Seigel 2011). This approach has been used to estimate population sizes across numerous vertebrate populations (e.g. ornate tree lizard *Urosaurus ornatus*, natterjack toad *Bufo calamita*, wood duck *Aix sponsa*; Tinkle & Dunham 1983; Persson 2012; Shirkey & Gates 2020), including snakes (e.g. rough green snake *Opheodrys aestivus*, tiger snake *Notechis scutatus*, asp viper *Vipera aspis*; Plummer 1997; Bonnet et al. 2002; Lourdais et al. 2002), even *N. natrix* (Mertens 1995). Closed models use two or more samples collected over a short time period, and they are the simplest form of mark-recapture analysis (Pollock et al. 1990). One of these methods is the two-sample Lincoln-Petersen model (Lincoln 1930; Pollock et al. 1990). This method is based on a model with the following assumptions (Pollock et al. 1990); (1) that the population is closed, meaning no additions and deletions, (2) all animals are equally likely to be captured on each sampling occasion, and (3) marks are not lost or missed. Regarding premise 1, the population was considered as closed since the snake was in hibernation between the first occasion and the second. This is additionally supported by the CJS models, indicating a negligible winter mortality (see 3.2.1). Assumption (2) was treated as fulfilled, since approximately the same level of effort was done during the two seasons, and assumption (3) was considered as above (see 2.2.1.).

The population estimate of adults in Hidet, 2021-2022, was done with the two-sample Lincoln-Petersen method (Lincoln 1930; Pollock et al. 1990). Data from the autumn and spring sampling period were pooled, respectively, resulting in two sampling occasions for the years 2021 and 2022. The population estimate was then calculated with the bias-adjusted Lincoln-Petersen estimator (Pollock et al. 1990).

Bias-adjusted Lincoln-Petersen estimate:

$$\widetilde{N} = \frac{(n_1 + 1)(n_2 + 1)}{m_2} - 1$$

Where n_1 is the total number of individuals caught on the first occasion, and n_2 the total number of individuals caught on the second occasion. m_2 is all the individuals marked from the first occasion and then recaptured on the second occasion. This was followed by a calculation of variance and confidence interval.

Formula for variance:

$$Var(\widetilde{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 + m_2)(n_2 + m_2)}{(m_2 + 1)^2(m_2 + 2)}$$

Confidence interval:

$$CI_{95\%} = \widetilde{N} \pm 1.96\sqrt{Var(\widetilde{N})}$$

3. Results

3.1. Data collection

3.1.1. Historical data

From 1945 to 2009 a total of 802 adult snakes were captured (542 males and 260 females), and the total number of capture events was 1623, resulting in 50.6 % of the captures were recaptures.

3.1.2. 2021-2022 data

A total of 29 adult snakes were captured in autumn 2021, 22 of which were males, and seven females. In spring 2022 a total number of 29 adult snakes were captured, which 25 were males and four females. Three of the snakes captured spring 2022 were recaptures from autumn 2021, which resulted in that 49 individual snakes were captured 2021 and 2022.

3.2. Population dynamics and condition

3.2.1. Survival

For the mark-recapture analysis, snakes caught from 1969 to 2002, the total number of individual adult snakes captured were 537 (342 males and 195 females), and the total number of capture events were 1065, resulting in 49.6 % recaptures.

Recapture probability

The best fit for recapture (model 1; table 3.) was the full model including the effects of effort, sex, season, and size. All parameters had a positive influence on the recapture, and where season (spring; $\beta = 0.704 \pm 0.251$) had the strongest effect, followed by sex (males; $\beta = 0.689 \pm 0.461$), effort ($\beta = 0.11 \pm 0.03$) and SVL ($\beta = 0.036 \pm 0.018$), in that order.

The likelihood ratio test between the best model (model 1; table 3.) and the second best (model 2; table 3.) was significant (p-value < 0.0001), and therefore the full model should be used (model 1; table 3.).

Table 3. Results of the 5 best CJS models of recapture in a population of grass snakes (Natrix natrix), sorted from lowest to highest AICc, and where the bold is the best model.

	Model	AICc	ΔAICc	w_i	No. Par	Deviance
1	**p~ sex + effort + season + SVL**	3116.4	0.0	1.0	12	3092.1
2	p~ sex + effort + SVL	3148.9	32.5	0.0	11	3126.7
3	p~ sex + season + SVL	3156.6	40.2	0.0	11	3134.4
4	p~ season + effort + SVL	3159.9	43.6	0.0	11	3137.7
5	p~ season + SVL	3185.5	69.1	0.0	10	3165.3

Survival related to weather

The best fit for apparent monthly survival related to weather data (model 1; table 4.) included effects of sex, SVL and total winter precipitation. Males had a higher monthly apparent survival compared to a female of the same size (males; β = 1.496 ± 0.46) (figure 3.). The monthly apparent survival also increased with SVL (β = 0.075 ± 0.02), regardless of sex (figure 3.). The total winter precipitation (β = 0.032 ± 0.034) mostly had a positive influence on apparent survival (figure 4.).

Table 4. Results of the 10 best CJS models of monthly apparent survival with weather data in a population of grass snakes (Natrix natrix), sorted from lowest to highest AICc, and where the bold is the best model.

	Model	AICc	ΔAICc	w_i	No. Par	Deviance
1	**φ~ sex + SVL + rain w**	3072.6	0.0	0.393	9	3054.4
2	φ~ sex + SVL + rain w + rain s	3074.5	1.9	0.149	10	3054.3
3	φ~ sex + SVL + temp w + rain s	3075.2	2.6	0.108	10	3055.0
4	φ~ sex + SVL + rain s	3075.4	2.8	0.097	9	3057.2
5	φ~ sex + SVL + temp w + rain w + rain s	3075.4	2.8	0.095	11	3053.2
6	φ~ sex + SVL + temp s + rain w	3075.6	3.0	0.088	10	3055.4
7	φ~ sex + SVL	3076.0	3.5	0.07	8	3059.9
8	φ~ SVL + rain w	3107.9	35.4	0.0	8	3091.7
9	φ~ SVL + rain w + rain s	3109.9	37.3	0.0	9	3091.7
10	φ~ SVL + temp s + rain w	3111.2	38.6	0.0	9	3093.0

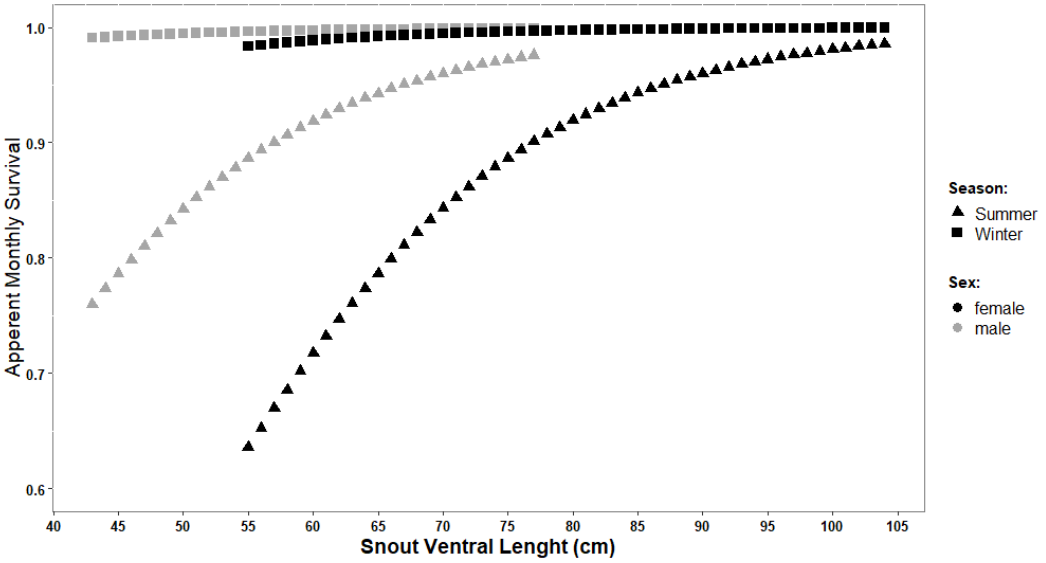

Figure 3. Apparent monthly survival in relation to snout vent length in a population of grass snakes (Natrix natrix) for summer (▲) and winter (■), and females (black) and males (grey), estimated from the Cormack Jolly-Seber model: φ~ sex + SVL + rain w. (For this figure, total winter precipitation was set to the average value of 109.45 mm).

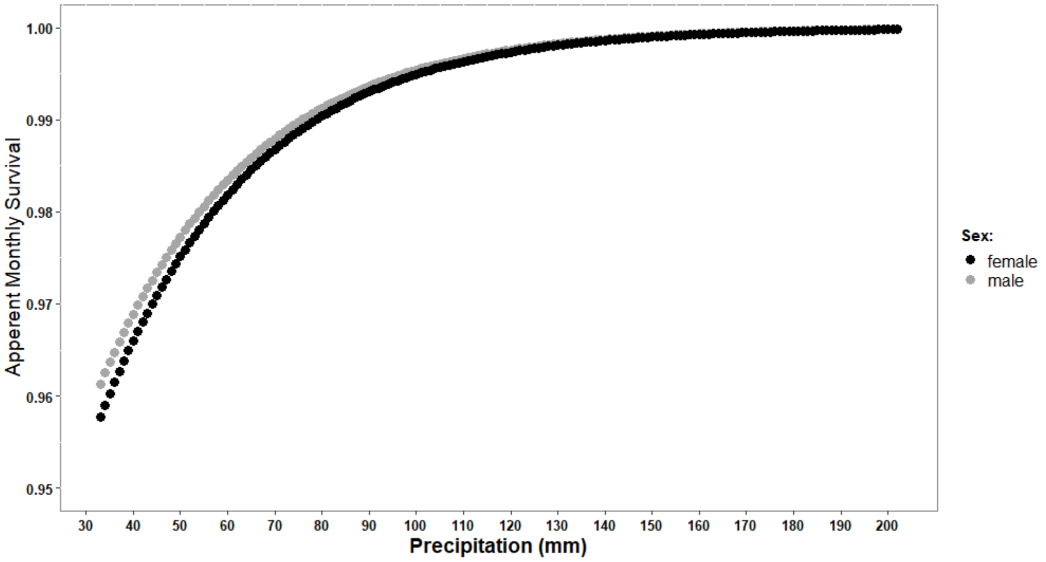

Figure 4. Apparent monthly survival in relation to total winter precipitation in a population of grass snakes (Natrix natrix) for both females (black) and males (grey), estimated from the Cormack Jolly-Seber model: φ~ sex + SVL + rain w. (For this figure, the average size of females, 73.51 ± 10.25 cm, and males, 54.92 ± 6.51 cm, was used).

The second-best model (model 2; table 4.), which also included total summer precipitation, was neglected because a likelihood ratio test between the two models turned out non-significant (p-value = 0.751), meaning the more parsimonious (model 1; table 4.) model explains the pattern equally well as the more complex model (model 2; table 4.).

The summed weight of all variables in the best model (model 1; table 4.) are all above 0.50 (table 5.), meaning they are very likely to be part of the best model (Burnham & Anderson 2002; Symonds & Moussalli 2011).

Table 5. Summed weight for all variables in model 1-7 in table 4. All variables in bold have a summed weight above 0.5 and are likely to be included in the most parsimonious model.

Variable	$\sum w_i$
sex	**1**
SVL	**1**
temp w	0.20
temp s	0.09
rain w	**0.72**
rain s	0.45

Survival over time and season

The best fit for apparent monthly survival over time and season (model 1; table 6.) was including the variables of, sex, size, season, year and year interacting with season. Males had a higher survival than females of the same size (males; β = 1.498 ± 0.445), and survival increased with SVL regardless of sex (β = 0.077 ± 0.019). Survival was higher during the winter season (winter; β = 3.766 ± 3.633). Summer survival increased over the years (β = 0.02 ± 0.027), but winter survival was decreasing over time (β = -0.117 ± 0.106) (figure 5.).

Table 6. Results of the 10 best CJS models of monthly apparent survival with trends over time, sex and season in a population of grass snakes (Natrix natrix), sorted from lowest to highest AICc, and where the bold is the best model.

	Model	AICc	ΔAICc	w_i	No. Par	Deviance
1	**φ~ sex + SVL + season + year + year:season**	3065.7	0.0	0.557	11	3043.4
2	φ~ sex + SVL + season + year + sex:season + year:season	3066.3	0.6	0.407	12	3042.0
3	φ~ sex + SVL + season + sex:season	3073.4	7.7	0.012	10	3053.2
4	φ~ sex + SVL + season	3073.4	7.7	0.012	9	3055.2
5	φ~ sex + SVL + year	3073.9	8.2	0.009	9	3055.7
6	φ~ sex + SVL	3076.0	10.4	0.003	8	3059.9

7	φ~ SVL + season + year + year:season	3101.0126	35.4	0.0	10	3080.8
8	φ~ SVL + season + year	3108.4435	42.8	0.0	9	3090.3
9	φ~ SVL + season	3109.9134	44.3	0.0	8	3093.8
10	φ~ SVL + year	3113.1933	47.5	0.0	8	3097.1

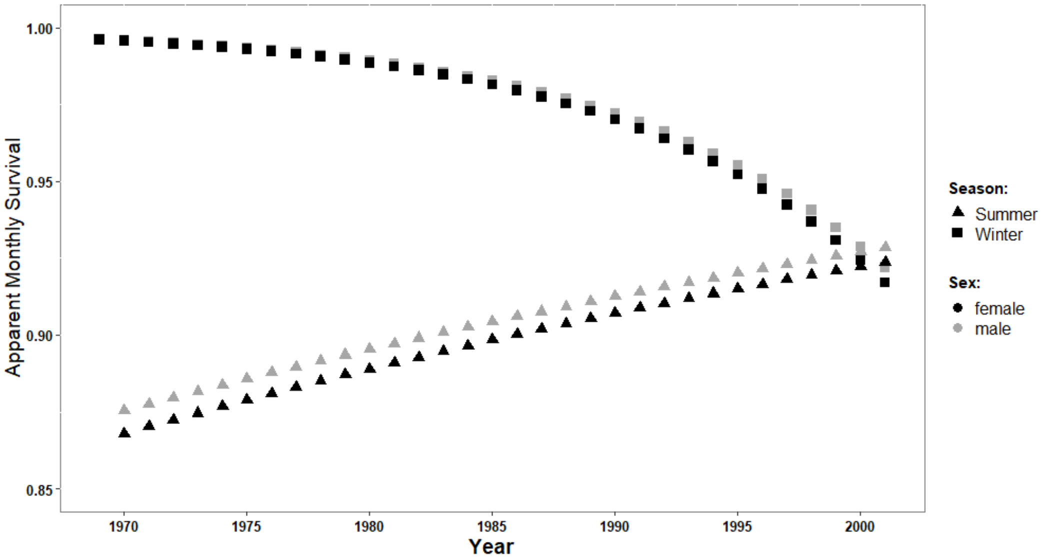

Figure 5. Apparent monthly survival over time in relation to season in a population of grass snakes (Natrix natrix) for summer (▲) and winter (■), and sex, females (black) and males (grey), estimated from the Cormack Jolly-Seber model: φ~ sex + SVL + season + year + year:season. (For this figure, the average size of females, 73.51 ± 10.25 cm, and males, 54.92 ± 6.51 cm, was used).

The second-best model (model 2; table 6.) was neglected because a likelihood ratio test between the two best models (model 1-2; table 6.) was non-significant (p-value = 0.234), meaning the more parsimonious (model 1; table 6.) model explains the pattern equally well as the more complex model (model 2; table 6.).

The summed weight of all variables in the best model (model 1; table 6.) are all above 0.50 (table 7.), meaning they are very likely part of the best model (Burnham & Anderson 2002; Symonds & Moussalli 2011).

Table 7. Summed weight of all variables in model 1-6 in table 6. All variables in bold have a summed weight above 0.5 and are likely to be included in the most parsimonious model.

Variable	$\sum w_i$
sex	**1**
SVL	**1**
season	**0.99**
year	**0.97**

sex:season	0.42
year:season	**0.96**

3.2.2. Body condition

Scaled Mass Index across seasons

In total, 466 first time captured adult males were used, from 1945-2006. The results of the t-test showed that it was a significant difference between the SMIs of the two seasons ($t = 4.6505$, $df = 293.33$, $p < 0.001$). The mean SMI of the snakes caught in autumn was approximately three units higher than in snakes caught in spring (figure 6).

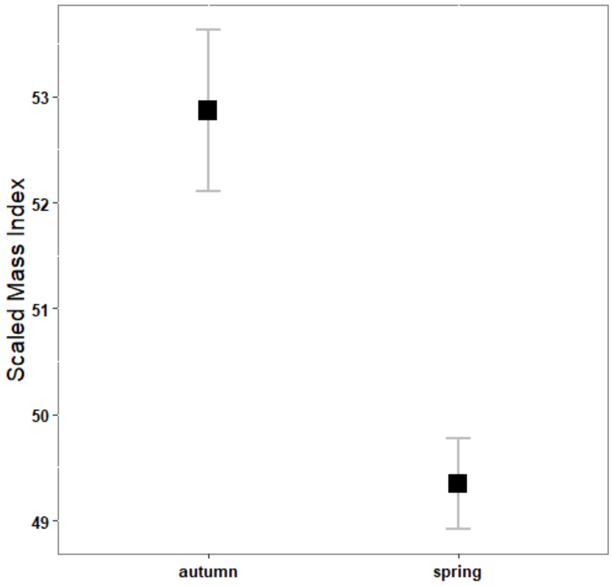

Figure 6. Mean Scaled Mass Index with a 95 % confidence interval for first caught males in spring and autumn in a population of grass snakes (Natrix natrix).

Scaled Mass Index over the years

The spring and autumn analysis included 750 and 285 observations from 1945-2006, respectively. Both LMMs showed that there was a significant increase of SMI over the years in both seasons (figure 7; table C.1).

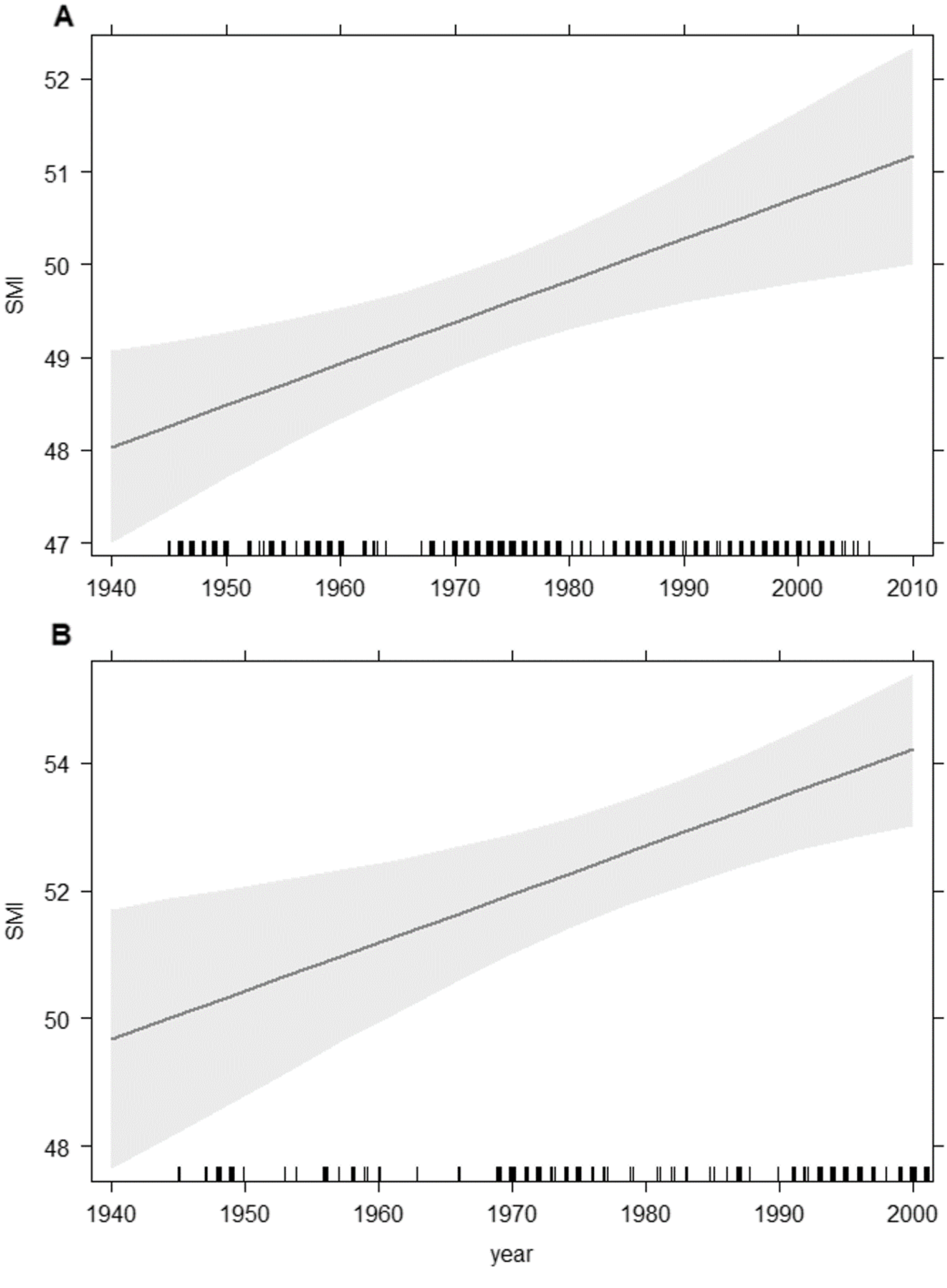

Figure 7. Predicted increase of SMI with a 95 % confidence interval in male grass snakes (Natrix natrix) over the years for each season, A) spring, and B) autumn, according to the linear mixed model.

Scaled Mass Index and weather variables

Mean summer temperature had a positive effect on SMI during autumn (table 8.), meaning that males had a higher SMI during autumn if the mean summer temperature were higher. However, there were no evidence that mean winter temperature or total precipitation (regardless season) were related to SMI (table 8.).

Table 8. The Linear Mixed Model results for Scaled Mass Indices relation to the weather conditions for captured adult male grass snakes (Natrix natrix) in both spring and autumn. Significant results are bold.

Model	Variable(s)	Estimate	Std. Error	df	t-value	P-value
Spring.seasonal	Intercept	49.2	0.5	52.0	105.2	**<0.001**
	Mean temperature	-0.4	0.4	43.1	-1.0	0.34
	Total perception	0.1	0.4	44.1	0.2	0.83
	Mean temperature: total perception	0.2	0.4	45.7	0.6	0.57
Autum.seasonal	Intercept	53.0	0.7	39.2	76.0	**<0.001**
	Mean temperature	1.3	0.6	36.9	2.2	**0.04**
	Total perception	1.0	0.6	36.3	1.6	0.11
	Mean temperature: total perception	0.8	0.7	33.9	1.0	0.31

3.2.3. Body size

Snout Vent Length over the years

In total 1090 adult male and 537 adult female observations were used for the analysis of body size. Over the years, 1945-2006, both males and females increased their average SVL (table D.1) with 5 and 7 cm, respectively (figure 8.).

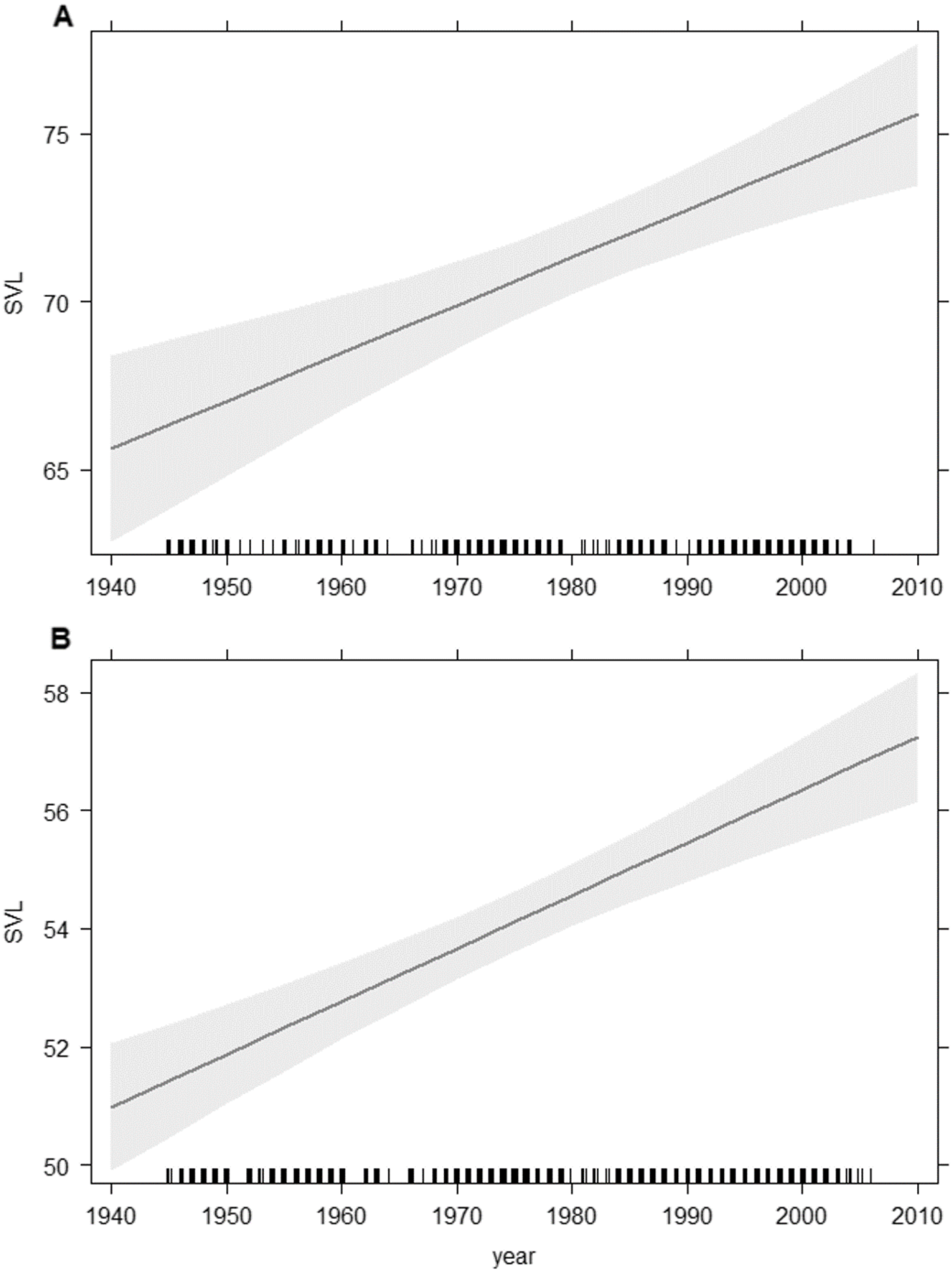

Figure 8. Predicted increase of SVL with a 95 % confidence interval in grass snakes (Natrix natrix) over the years for each sex, A) females, and B) males, according to the linear mixed model.

Snout Vent Length and weather variables

There were 316 observations of adult females in spring, and 158 in autumn. For adult males, 754 and 286 was observed in spring and autumn, respectively. SVL of males observed during spring had a significant positive correlation with mean winter temperature (table 9.). However, there were no evidence of precipitation or summer temperature being related to males SVL, and regarding females none of the weather variables were related to SVL (table 9.).

Table 9. The four Linear Mixed Model results for Snout Ventral Length and its relation to weather condition for each sex (adult female and male) and season (winter and summer) in a population of grass snakes (Natrix natrix).. Significant results are bold.

Model	Fixed effect	estimate	Std. Error	df	t-value	p-value
Spring Females	Intercept	69.7	1.0	46.6	67.2	**<0.001**
	Mean winter temperature	0.9	0.8	32.4	1.1	0.27
	Total winter precipitation	-0.4	0.9	30.8	-0.5	0.64
	Mean winter temperature: Total winter precipitation	0.2	0.8	29.6	0.2	0.83
Autumn Females	Intercept	70.6	1.0	146.7	73.2	**<0.001**
	Mean winter temperature	0.1	0.8	90.9	0.1	0.89
	Total winter precipitation	-0.03	0.8	109.2	-0.04	0.97
	Mean winter temperature: Total winter precipitation	-0.4	0.9	90.5	-0.4	0.67
Spring Males	Intercept	54.0300	0.4	85.1	142.4	**< 0.001**
	Mean winter temperature	1.0938	0.3	47.7	3.4	**<0.01**
	Total winter precipitation	-0.5461	0.3	46.9	-1.7	0.10
	Mean winter temperature: Total winter precipitation	0.0031	0.3	45.7	0.01	0.99

Autumn Males	Intercept	54.0	0.6	25.2	87.6	**<0.001**
	Mean winter temperature	0.01	0.6	23.2	0.02	0.98
	Total winter precipitation	-0.9	0.5	22.6	-1.6	0.12
	Mean winter temperature: Total winter precipitation	-0.4	0.6	20.9	-0.7	0.49

3.2.4. Sex ratio

The proportion of males versus females varied among decades; the highest count for both sexes was during the 1970s and the lowest during the 1960s (figure 9.). However, there was a significant negative trend over the years on male sex ratio according to the LM (estimate = -0.003; SE < 0.001; t-value = -2.921; p-value = 0.005), males decreasing from 74 % of the population during the 1940s to 54 % in the 2000s (figure 10.).

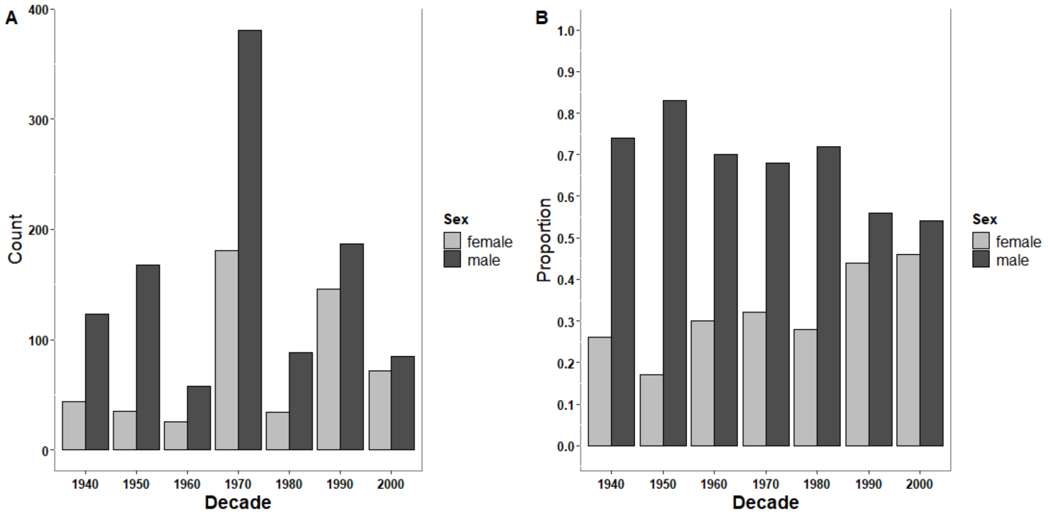

Figure 9. A) the count of males and females caught each decade from 1940th to 2000th. B) the proportion of males and females for each decade, 1940th to 2000th.

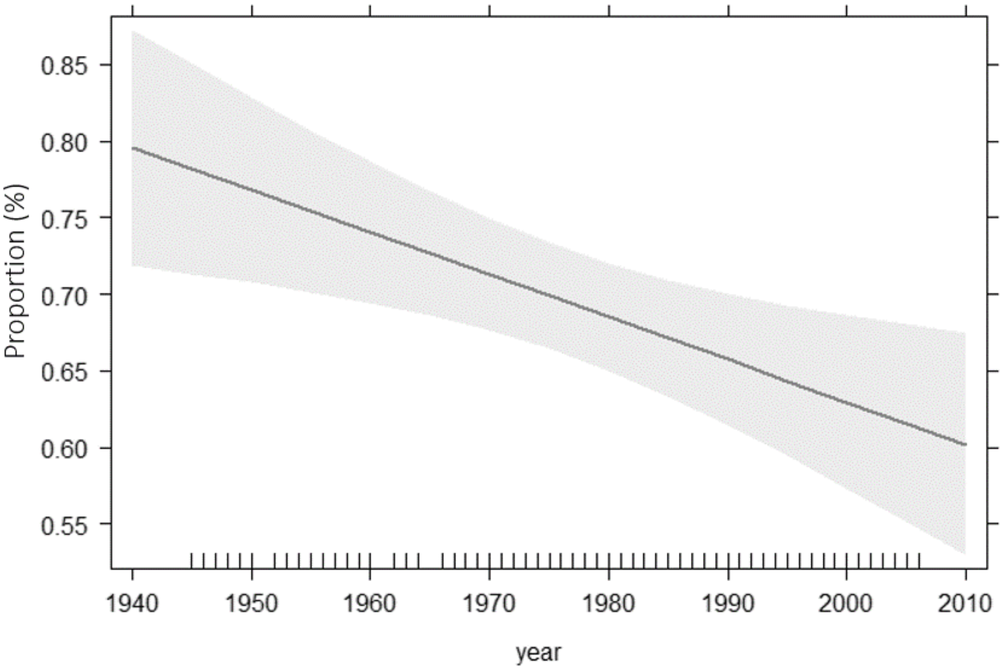

Figure 10. Predicted decline of male grass snake (Natrix natrix) sex ratio with a 95 % confidence interval over the years according to the linear model.

3.2.5. Population estimate

Hidet population

The population estimate of adult snakes in the hibernaculum at Hidet, 2021-2022, based on the Lincoln-Petersen model was 224 ± 171 (figure 11.). Estimates for the historical period based on the Jolly-Seber model fluctuate between 30.5 to 196 adults in the first period (spring 1945 to autumn 1949) and 21.9 to 58 in the second period (autumn 1970 to autumn 1973) (figure 11.; table E.1).

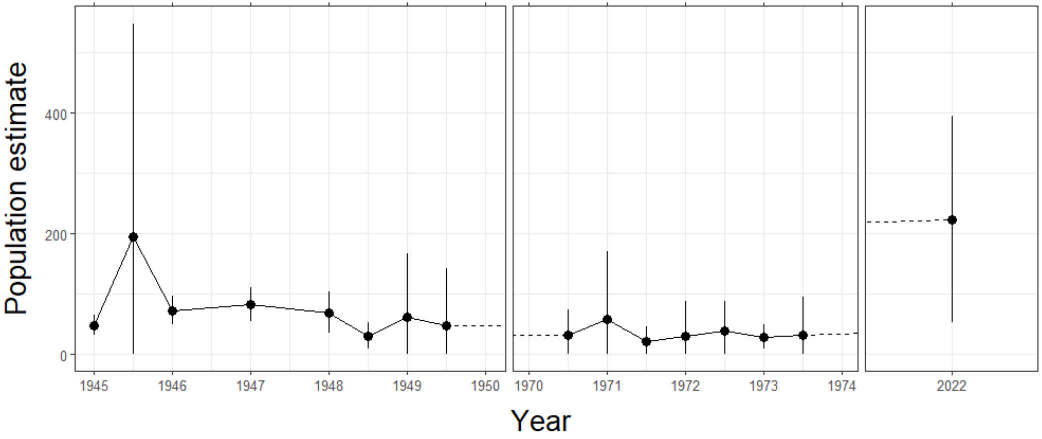

Figure 11. Population estimates and confidence interval 95 % of adult grass snakes (Natrix natrix) at the hibernaculum at Hidet during spring and autumn. The periods of spring 1945 to autumn 1949 and autumn 1970 to autumn 1973, was estimated through the Jolly-Seber model, and autumn 2021 to autumn 2022 was estimated through Lincoln-Petersen model

Nacka population

The historical estimate of adult snakes in the Nacka population was estimated with the Jolly-Seber model to fluctuate from five to 427 individuals (figure 12.; table E.2).

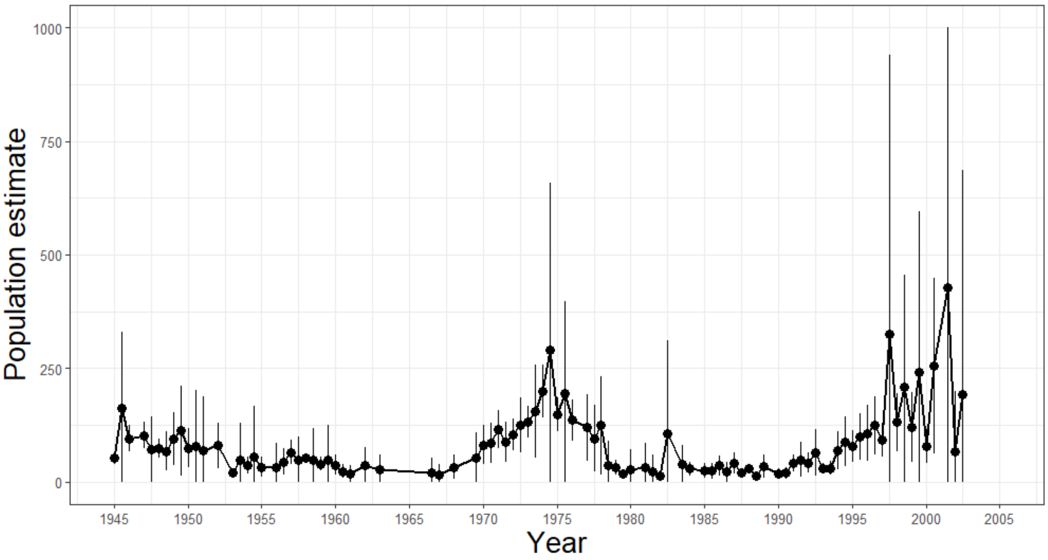

Figure 12. Population estimates of adult grass snakes (Natrix natrix) and confidence interval 95 % in the three hibernacula of Nacka nature reserve for the time period spring 1945 to autumn 2002. Based on the Jolly-Seber model. Some years was removed due to missing or insufficient data.

4. Discussion

The results of this study give important insights on the effect of climate change on a snake population in Sweden. The apparent survival estimates imply that adult survival was higher during the winter period compared to the summer, especially for smaller individuals. However, in line with a changed climate, the influence of season on survival changed with increasing survival during the summer season, and the opposite during the winter. A higher summer survival together with increased winter and summer temperatures associated with longer activity periods seem to have additionally increased the snakes' body size, especially in males. Survival was also higher for larger individuals, and males had higher survival compared to same-sized females. The results imply that since the 40s, the body length (SVL) of males and females have increased by approximately 5 and 7 cm, respectively.

Winter survival in relation to winter conditions

In analogy with several previous studies on hibernating snakes, the adult winter survival during the non-active period was higher compared to the summer survival (e.g. *V. berus*; Viitanen 1967, prairie rattlesnake *Crotalus viridis*; Parker & Brown 1974, *V. aspsi*; Altwegg 2005). However, it seems that there was a decline in *N. natrix* winter survival from 1969 to 2002, but the opposite for summer survival (see figure 5). These patterns probably happen as there also are increasing winter and summer temperatures in the same time period (Stockholms stad 2021). The quality of the hibernation habitat (and thus climatic aspects) is critical for the survival of snakes at higher latitudes (Prior & Weatherhead 1996), and if winter conditions are not favourable, survival could be dramatically reduced. Shine & Mason (2004) demonstrated that high mortality at the hibernacula of a garter snake, *Thamnophis sirtalis,* population, (another species of the Natricinae subfamily), was due to freezing, as an effect of thin snow cover. In my study, the adult winter survival of *N. natrix* increased with total winter precipitation. More precipitation during the colder months will likely result in a deeper snow cover, which in turn will improve the quality of the hibernacula, and lower the risk of freezing to death. Although total winter precipitation has not changed in the area during the time of study (Stockholms stad 2022), and is expected to get warmer (Ruiz-Pérez & Vico 2020), the duration of snow cover decreases (Zhu et al. 2019). Potentially this will lead to increased winter mortality. However, the quality of the hibernation habitat could be difficult to evaluate, only from the external. Other elements as the underground structure and the micro-climate of the hibernacula could also be important, but is often hard to assess (Prior & Weatherhead 1996).

As part of the global warming, the winter period is expected to be shorter and more unstable (Nikulin et al. 2009; Ruosteenoja et al. 2020), subsequently leading to shorter dormant periods for the snakes and unstable overwintering conditions. Moreno-Rueda et al. (2009) have already observed an increase of the active period for the Montpellier snake (*Malpolon monspessulanus*) over time in response to climate change, and Milton (2019) report *V. berus* being active the whole year in UK (where the population is also in decline; Gardner 2019). For another ectotherm and hibernating species, *Rana temporaria*, the adult survival and longevity are increasing with shorter active periods (Miaud et al. 1999), which could be the outcome of lower predation risk (Ryser 1996). So, as the activity period increases, *N. natrix* may be more exposed to predators over time (e.g. buzzard *Buteo buteo*, crows *Corvus cornix*, hedgehog *Erinaceus europaeus*). Additionally, as the winters become more unstable which results in more extreme weathers, the resilience of a hibernaculum could be reduced, implying that snakes may only be able to tolerate short periods of unsuitable weather conditions (Markle et al. 2020). Raising temperatures and floodings of the hibernaculum could drive the snakes to emerge too early (Todd et al. 2009), which might kill them if they get hit by a cold snap (Lueth 1941). Associating this with the result of this study, shorter dormant periods and unstable winters temperatures could subsequently lead to a decrease of *N. natrix* winter survival over time. However, based on the relatively stable population size estimates, it seems like these changes have not had an effect on the population, yet.

Summer survival in relation to body size

The apparent summer survival of adult *N. natrix* is increasing with size, which is in accordance with (Shine et al. 2001; Shine & Mason 2004; Luiselli et al. 2011; Hyslop et al. 2012), at least to a certain point (Rose et al. 2022), but see (Winne et al. 2010).

Larger *N. natrix* are likely to have fewer potential predators, and the opportunity to feed on larger preys can mean an energetic advantage (Schoener 1971; Madsen 1983). These traits may play a more important role for the survival during the active summer periods (even if larger prey also can be advantageous to development of energy reserves for the non-active period). As mentioned above, summer survival seems to have increased since the 70s. Along with this, the adult *N. natrix* population has also shown to increase in size and body condition since the 40s, in contrast to the Polish study (Bury et al. 2021). For the males in the present study, this increase is probably related to warmer summers and winters. *N. natrix* digestion is highly regulated by the temperature, where the process of degradation could take up to 6 days when the temperature is 15 ºC, or even less so, 2.5 day, when the temperature is 25 ºC or higher (Skoczylas 1970a; b). As the active periods gets warmer and longer, *N. natrix* could get more time to forage, similar to what has been observed in *M. monspessulanus* (Moreno-Rueda et al. 2009). This is additionally supported by a temporal increase in body condition in the studied *N. natrix* population. In another case, Chamaillé-Jammes et al. (2006) demonstrated that both fecundity and survival of a European common lizard *Zootoca vivipara* population in south-east France have increased due to warmer summer temperatures. This *Z. vivipara* population has therefore been advantaged by the shift in temperature (Chamaillé-Jammes et al. 2006).

The benefits from the longer and warmer active-period may have balanced the disadvantages that also come with climate change on the dormant period during the time of this study. But since the decline of winter survival has been larger and the winters are expected to change faster in the future (Nikulin et al. 2009; Zhu et al. 2019; Ruosteenoja et al. 2020), the balance between winter and summer survival could reach a tipping point, where winter mortality will overcome summer survival (figure 5). This would subsequently lead the *N. natrix* population to decline. However, that is not the case yet. Over the time span of this study the *N. natrix* adult population seems not to have declined, but rather fluctuated, which is common for vertebrate populations (Elton & Nicholson 1942; Perrins 1965; Wolff 1996; Ranta et al. 1997; Kendall et al. 1999; Lind et al. 2005). Population size has had two peaks (1970s and 1990s) with approximately a 20 to 25 years interval. Considering the recent estimate of 224 adult snakes and the interval between the last historical peak and now, this might suggest that the population is currently in another peak. However, this is highly speculative.

Differences between sexes

Even if most studies on snakes generally obtain a higher mortality in males (e.g Bonnet et al. 1999; Shine et al. 2001; Lind et al. 2005), the opposite with a lower female survival has also been observed in a number of studies (e.g Shine & Mason 2004; Sperry & Weatherhead 2009; Fornasiero et al. 2016). The higher survival of *N. natrix* males may suggest that there is a different predation pressure on males and females (Shine et al. 2001; Sperry & Weatherhead 2009), and/or that there is a higher survival cost of reproduction for females then males (Madsen & Shine 1994).

As male and females differ in both size and behaviour (Phelps 1978; Madsen 1983, 1984), the processes behind the sex biased mortality could be rather complex (Shine et al. 2001). Different movement patterns of males and females with the interaction of size could result in specific predation pressures. Shine et al. (2001) observed that female *Thamnophis sirtalis* were taken by crows more often than would be expected from their larger body size. The reason for this could have been that the larger females, newly emerged from the hibernaculum, are colder and less alert, moving slower compared to the males (Shine et al. 2000). A similar behaviour was observed during the recent field observations, where large females were experienced as being more sluggish than males.

Higher mortality among females could essentially be related to seasonal movements and basking behaviours related to being oviparous (Bonnet et al. 1999; Sperry & Weatherhead 2009). For instance, the female biased mortality in the oviparous *Elaphe obsoleta* was associated with their extensive movements after spring and increased basking during the summer until autumn (Sperry & Weatherhead 2009). The movements of female *N. natrix* are most extensive prior to and one week after oviposition (Madsen 1984). Movements exceeding one km to find a good oviposition spot have been observed in females on a site not far from my study site (Stockholm; Elmberg et al. 2019). Being oviparous, females in the *Natrix* genus may put themself at risk when migrating for a suitable oviposition site (Bonnet et al. 1999), resulting in a higher female mortality.

What is striking with the relationship between sex and survival is that males have higher survival than same sized females. However, if the survival between the averages size of each sex would to be compared (males 54.92 cm; females 73.51 cm), then the survival is approximately the same. Reproductive females pay a higher prize in relation to their body size, having lower survival rate than reproductive males (Madsen & Shine 1994). *N. natrix* females have a higher growth rate than males and reach maturity at an age of four to five years instead of three years (Madsen 1983). The results of a relatively high survival rate in females that are sexually mature at four to five years of age are supported by a general survival in reptiles at that age (Shine & Charnov 1992).

Sex ratio

The sex ratio of the Nacka population has shifted over time. This is contrary to what they observed in Poland (Bury et al. 2021), where the ratio of *N. natrix* males was decreasing in the population. Since males have a higher survival than females, it seems very unlikely that this shift increased male mortality. However, as females have become bigger, and even more so than the males, predation risk should have been reduced (Shine et al. 2001; Hyslop et al. 2012), enabling higher female survival.

Nevertheless, the shift in sex ratio could also be the result of females emerging earlier in the spring. Normally, males emerge earlier than females (Phelps 1978) which could be the reason for the higher recapture probability in males. Accordingly, as the winter periods have become shorter over the years (Ruosteenoja et al. 2020), this could have led to more females getting caught over time. Additionally, an another possibility is that the warmer climate has allowed a sexual maturity from a younger age of the females in comparison to when it was colder (Fornasiero et al. 2016).

Conclusion

With the historical impact of climate change the population was stable and the snakes' well-being was good. As for now, there are no evident complications with the snakes and climate change. However, even though there are indications of climate change having positive effects on the increasing apparent summer survival (diff 0.05), the opposite trend was shown for apparent winter survival (diff 0.10). As winter precipitation increased so did winter survival, which is probably associated with snow cover (and should be considered in future studies). So even though the effect of the increased body size in the population may have increased summer survival and balanced the effect of increased winter mortality, future winters are expected to change more radically than summers due to climate change. Today the population seems to be stable but survival is affected with factors associated with climate change and the future of *N. natrix* will probably be affected by future winters. These effects cannot be seen in the population estimates, but will probably emerge in the future.

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Appendix A

Table A.1 General information on the recent field work (autumn 2021 – spring 2022).

Date	**Start – End**	**Weather**	**Fieldworkers**	**Nr. Snakes**
2021-09-18	14:01 – 16:00	Cloudy	Ludvig Palmheden, Simon Kärvemo, Nils Edelstam, Daniele Marini	1
2021-09-20	10:15 – 16:00	Cloudy	Ludvig Palmheden	2
2021-09-22	10:15 – 15:15	Cloudy, with some sun	Ludvig Palmheden	2
2021-09-26	10:30 – 15:55	Sunny	Ludvig Palmheden, Emma Engvall	13
2021-09-27	10:30 – 16:25	Sunny	Ludvig Palmheden	11
2021-10-01	10:00 – 15:30	Cloudy, with some sun and very windy	Ludvig Palmheden	5
2021-10-08	10:30 – 15:30	Sunny, with clouds	Ludvig Palmheden	5
2022-04-22	09:55 – 14:30	Sunny	Ludvig Palmheden, Simon Kärvemo	18
2022-04-22	10:10 – 15:36	Sunny	Ludvig Palmheden, Elina Thorsson	12
2022-04-26	10:06 – 15:47	Sunny with clouds	Ludvig Palmheden, Emma Engvall, Signe Hägglund	8

Appendix B

Table B.1. Program MARKs estimate of recapture rate for grass snakes (Natrix natrix), males and females with a SVL of 62.71 cm over the years from the model: p~ sex + effort + season + SVL

Period	Male		Female	
	Recapture	Confident interval 95 %	Recapture	Confident interval 95 %
1970 Spring	0.2355	± 0.0427	0.1555	± 0.0715
1970 Autumn	0.1090	± 0.0242	0.0681	± 0.0358
1971 Spring	0.3621	± 0.0426	0.2534	± 0.0946
1971 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1972 Spring	0.2355	± 0.0427	0.1555	± 0.0715
1972 Autumn	0.1692	± 0.0367	0.1085	± 0.0547
1973 Spring	0.3621	± 0.0426	0.2534	± 0.0946
1973 Autumn	0.1304	± 0.0273	0.0823	± 0.0420
1974 Spring	0.5869	± 0.0835	0.4592	± 0.1375
1974 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1975 Spring	0.4104	± 0.0499	0.2938	± 0.1044
1975 Autumn	0.1090	± 0.0242	0.0681	± 0.0358
1976 Spring	0.3165	± 0.0394	0.2168	± 0.0858
1976 Autumn	0.1090	± 0.0242	0.0681	± 0.0358
1977 Spring	0.2741	± 0.0399	0.1842	± 0.0781
1977 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1978 Spring	0.3165	± 0.0394	0.2168	± 0.0858
1978 Autumn	0.0907	± 0.0228	0.0563	± 0.0309
1979 Spring	0.2543	± 0.0411	0.1693	± 0.0747
1979 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1980 Spring	0.1849	± 0.0476	0.1194	± 0.0631
1980 Autumn	0.0826	± 0.0225	0.0511	± 0.0288
1981 Spring	0.2008	± 0.0460	0.1306	± 0.0658
1981 Autumn	0.0907	± 0.0228	0.0563	± 0.0309
1982 Spring	0.1849	± 0.0476	0.1194	± 0.0631
1982 Autumn	0.1090	± 0.0242	0.0681	± 0.0358
1983 Spring	0.1849	± 0.0476	0.1194	± 0.0631

1983 Autumn	0.0995	± 0.0234	0.0619	± 0.0332
1984 Spring	0.3165	± 0.0394	0.2168	± 0.0858
1984 Autumn	0.0907	± 0.0228	0.0563	± 0.0309
1985 Spring	0.2543	± 0.0411	0.1693	± 0.0747
1985 Autumn	0.1090	± 0.0242	0.0681	± 0.0358
1986 Spring	0.2176	± 0.0444	0.1426	± 0.0685
1986 Autumn	0.0907	± 0.0228	0.0563	± 0.0309
1987 Spring	0.3165	± 0.0394	0.2168	± 0.0858
1987 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1988 Spring	0.2948	± 0.0393	0.2000	± 0.0818
1988 Autumn	0.0907	± 0.0228	0.0563	± 0.0309
1989 Spring	0.2355	± 0.0427	0.1555	± 0.0715
1989 Autumn	0.0826	± 0.0225	0.0511	± 0.0288
1990 Spring	0.2008	± 0.0460	0.1306	± 0.0658
1990 Autumn	0.0907	± 0.0228	0.0563	± 0.0309
1991 Spring	0.2948	± 0.0393	0.2000	± 0.0818
1991 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1992 Spring	0.2948	± 0.0393	0.2000	± 0.0818
1992 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1993 Spring	0.2543	± 0.0411	0.1693	± 0.0747
1993 Autumn	0.1193	± 0.0255	0.0749	± 0.0387
1994 Spring	0.2543	± 0.0411	0.1693	± 0.0747
1994 Autumn	0.1304	± 0.0273	0.0823	± 0.0420
1995 Spring	0.3165	± 0.0394	0.2168	± 0.0858
1995 Autumn	0.1553	± 0.0328	0.0990	± 0.0500
1996 Spring	0.3389	± 0.0405	0.2346	± 0.0901
1996 Autumn	0.1998	± 0.0468	0.1299	± 0.0659
1997 Spring	0.3860	± 0.0458	0.2731	± 0.0994
1997 Autumn	0.1090	± 0.0242	0.0681	± 0.0358
1998 Spring	0.3389	± 0.0405	0.2346	± 0.0901
1998 Autumn	0.0907	± 0.0228	0.0563	± 0.0309
1999 Spring	0.2355	± 0.0427	0.1555	± 0.0715
1999 Autumn	0.0995	± 0.0234	0.0619	± 0.0332
2000 Spring	0.3389	± 0.0405	0.2346	± 0.0901
2000 Autumn	0.1692	± 0.0367	0.1085	± 0.0547
2001 Spring	0.2355	± 0.0427	0.1555	± 0.0715
2001 Autumn	0.1304	± 0.0273	0.0823	± 0.0420
2002 Spring	0.2741	± 0.0399	0.1842	± 0.0781

Table B.2. Program MARK's estimate of apparent monthly survival rate for grass snakes (Natrix natrix). males and females with a SVL of 62.71 cm over the years and weather condition from the model: φ~ sex + SVL + rain w

Period	Male		Female	
	Apparent survival	Confident interval 95 %	Apparent survival	Confident interval 95 %
1969 Winter	0.9981	± 0.0018	0.9917	± 0.0081
1970 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1970 Winter	0.9918	± 0.0071	0.9643	± 0.0311
1971 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1971 Winter	0.9947	± 0.0048	0.9770	± 0.0212
1972 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1972 Winter	0.9959	± 0.0038	0.9821	± 0.0168
1973 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1973 Winter	0.9940	± 0.0054	0.9739	± 0.0237
1974 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1974 Winter	0.9985	± 0.0014	0.9936	± 0.0063
1975 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1975 Winter	0.9976	± 0.0023	0.9892	± 0.0104
1976 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1976 Winter	0.9962	± 0.0036	0.9832	± 0.0158
1977 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1977 Winter	0.9999	± 0.0001	0.9995	± 0.0005
1978 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1978 Winter	0.9954	± 0.0043	0.9797	± 0.0189
1979 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1979 Winter	0.9965	± 0.0033	0.9847	± 0.0145
1980 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1980 Winter	0.9890	± 0.0090	0.9528	± 0.0389
1981 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1981 Winter	0.9981	± 0.0019	0.9914	± 0.0084
1982 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1982 Winter	0.9991	± 0.0009	0.9961	± 0.0038
1983 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1983 Winter	0.9971	± 0.0027	0.9874	± 0.0121
1984 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1984 Winter	0.9994	± 0.0006	0.9972	± 0.0028
1985 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1985 Winter	0.9986	± 0.0014	0.9938	± 0.0061
1986 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1986 Winter	0.9989	± 0.0011	0.9950	± 0.0049

1987 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1987 Winter	0.9988	± 0.0012	0.9945	± 0.0054
1988 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1988 Winter	0.9988	± 0.0012	0.9945	± 0.0054
1989 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1989 Winter	0.9944	± 0.0051	0.9755	± 0.0224
1990 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1990 Winter	0.9996	± 0.0004	0.9982	± 0.0018
1991 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1991 Winter	0.9979	± 0.0020	0.9908	± 0.0089
1992 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1992 Winter	0.9957	± 0.0040	0.9809	± 0.0178
1993 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1993 Winter	0.9944	± 0.0051	0.9755	± 0.0224
1994 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1994 Winter	0.9985	± 0.0015	0.9931	± 0.0067
1995 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1995 Winter	0.9995	± 0.0005	0.9976	± 0.0024
1996 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1996 Winter	0.9757	± 0.0142	0.9001	± 0.0598
1997 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1997 Winter	0.9952	± 0.0044	0.9790	± 0.0194
1998 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1998 Winter	0.9990	± 0.0009	0.9958	± 0.0042
1999 Summer	0.9327	± 0.0160	0.7564	± 0.0698
1999 Winter	0.9990	± 0.0010	0.9955	± 0.0045
2000 Summer	0.9327	± 0.0160	0.7564	± 0.0698
2000 Winter	0.9994	± 0.0005	0.9975	± 0.0024
2001 Summer	0.9327	± 0.0160	0.7564	± 0.0698
2001 Winter	0.9980	± 0.0019	0.9911	± 0.0086

Table B.3. Program MARK's estimate of apparent monthly survival rate for males and females with a SVL of 62.71 cm over the years and seasons from the model: φ~ sex + SVL + season + year + year:season

Period	Male		Female	
	Apparent survival	Confident interval 95 %	Apparent survival	Confident interval 95 %
1969 Autumn	0.9980	± 0.0020	0.9910	± 0.0087
1970 Spring	0.9288	± 0.0200	0.7448	± 0.0787

1970 Autumn	0.9978	± 0.0021	0.9901	± 0.0095
1971 Spring	0.9301	± 0.0194	0.7485	± 0.0770
1971 Autumn	0.9975	± 0.0024	0.9891	± 0.0105
1972 Spring	0.9314	± 0.0188	0.7522	± 0.0755
1972 Autumn	0.9973	± 0.0026	0.9879	± 0.0115
1973 Spring	0.9326	± 0.0184	0.7559	± 0.0743
1973 Autumn	0.9970	± 0.0028	0.9867	± 0.0126
1974 Spring	0.9339	± 0.0181	0.7595	± 0.0733
1974 Autumn	0.9967	± 0.0031	0.9854	± 0.0137
1975 Spring	0.9351	± 0.0178	0.7631	± 0.0725
1975 Autumn	0.9964	± 0.0034	0.9839	± 0.0150
1976 Spring	0.9363	± 0.0177	0.7666	± 0.0719
1976 Autumn	0.9960	± 0.0037	0.9823	± 0.0164
1977 Spring	0.9374	± 0.0177	0.7702	± 0.0715
1977 Autumn	0.9956	± 0.0040	0.9805	± 0.0179
1978 Spring	0.9386	± 0.0177	0.7736	± 0.0714
1978 Autumn	0.9951	± 0.0044	0.9785	± 0.0195
1979 Spring	0.9397	± 0.0178	0.7771	± 0.0713
1979 Autumn	0.9946	± 0.0048	0.9764	± 0.0212
1980 Spring	0.9408	± 0.0179	0.7805	± 0.0715
1980 Autumn	0.9941	± 0.0052	0.9740	± 0.0230
1981 Spring	0.9419	± 0.0181	0.7838	± 0.0717
1981 Autumn	0.9935	± 0.0057	0.9714	± 0.0250
1982 Spring	0.9430	± 0.0183	0.7872	± 0.0721
1982 Autumn	0.9928	± 0.0062	0.9686	± 0.0270
1983 Spring	0.9440	± 0.0185	0.7905	± 0.0726
1983 Autumn	0.9921	± 0.0067	0.9655	± 0.0292
1984 Spring	0.9451	± 0.0188	0.7937	± 0.0732
1984 Autumn	0.9913	± 0.0072	0.9621	± 0.0314
1985 Spring	0.9461	± 0.0190	0.7969	± 0.0738
1985 Autumn	0.9904	± 0.0077	0.9583	± 0.0337
1986 Spring	0.9471	± 0.0193	0.8001	± 0.0745
1986 Autumn	0.9894	± 0.0083	0.9543	± 0.0361
1987 Spring	0.9481	± 0.0195	0.8032	± 0.0752
1987 Autumn	0.9883	± 0.0089	0.9498	± 0.0385
1988 Spring	0.9490	± 0.0198	0.8063	± 0.0759
1988 Autumn	0.9871	± 0.0094	0.9449	± 0.0409
1989 Spring	0.9500	± 0.0200	0.8094	± 0.0766
1989 Autumn	0.9858	± 0.0100	0.9396	± 0.0432
1990 Spring	0.9509	± 0.0203	0.8124	± 0.0773
1990 Autumn	0.9844	± 0.0106	0.9338	± 0.0455

1991 Spring	0.9518	± 0.0205	0.8154	± 0.0780
1991 Autumn	0.9828	± 0.0111	0.9275	± 0.0476
1992 Spring	0.9527	± 0.0207	0.8184	± 0.0787
1992 Autumn	0.9811	± 0.0116	0.9207	± 0.0496
1993 Spring	0.9536	± 0.0209	0.8213	± 0.0794
1993 Autumn	0.9792	± 0.0121	0.9133	± 0.0514
1994 Spring	0.9545	± 0.0210	0.8242	± 0.0800
1994 Autumn	0.9771	± 0.0126	0.9052	± 0.0530
1995 Spring	0.9553	± 0.0212	0.8270	± 0.0806
1995 Autumn	0.9748	± 0.0130	0.8965	± 0.0545
1996 Spring	0.9562	± 0.0213	0.8298	± 0.0811
1996 Autumn	0.9723	± 0.0135	0.8871	± 0.0561
1997 Spring	0.9570	± 0.0214	0.8326	± 0.0816
1997 Autumn	0.9696	± 0.0141	0.8769	± 0.0579
1998 Spring	0.9578	± 0.0215	0.8353	± 0.0821
1998 Autumn	0.9665	± 0.0150	0.8659	± 0.0604
1999 Spring	0.9586	± 0.0216	0.8380	± 0.0825
1999 Autumn	0.9632	± 0.0162	0.8542	± 0.0640
2000 Spring	0.9594	± 0.0217	0.8407	± 0.0829
2000 Autumn	0.9596	± 0.0179	0.8416	± 0.0690
2001 Spring	0.9601	± 0.0217	0.8433	± 0.0832
2001 Autumn	0.9556	± 0.0203	0.8281	± 0.0758

Appendix C

Table C.1. The Linear Mixed Model results for Scaled Mass Indices for spring captured adult male grass snakes (Natrix natrix). autumn captured. and all captures. Significant results are bold.

Model	Variable(s)	Estimate	Std. Error	df	t-value	P-value
Spring.SMI	Intercept	-24.1	30.2	436.4	-0.8	0.43
	Year	0.04	0.02	436.7	2.4	**<0.05**
Autumn.SMI	Intercept	-93.3	46.7	228.9	-2.0	**<0.05**
	Year	0.07	0.02	228.9	3.1	**<0.01**
SMI.YEAR	Intercept	-88.6	27.2	511.8	-3.3	**<0.01**
	Year	0.1	0.01	512.2	5.1	**<0.001**

Appendix D

Table D.1. The Linear Mixed Model results for Snout Ventral Length of adult female and male grass snakes (Natrix natrix) over the years. Significant results are bold.

Model	Fixed effect	estimate	Std. Error	df	t-value	p-value
Females	Intercept	-209.9	62.5	306.2	-3.4	**<0.001**
	Year	0.1	0.03	306.2	4.5	**<0.001**
Males	Intercept	-122.6	27.7	592.5	-4.4	**<0.001**
	Year	0.09	0.01	592.8	6.4	**<0.001**

Appendix E

Table E.1. Population size with 95 % confidence interval of adult grass snakes (Natrix natrix) at Hidet from spring 1945 to autumn 1949. spring 1970 to autumn 1973. and spring 2022 estimated from the either Jolly-Seber or Lincoln-Petersen model.

Period	Estimate	Confident interval 95 %	Model
1945 Spring	48.5	± 16.2	Jolly-Seber
1945 Autumn	196	± 351.9	Jolly-Seber
1946 Spring	73	± 23.5	Jolly-Seber
1947 Spring	83.3	± 28.3	Jolly-Seber
1948 Spring	69.7	± 34	Jolly-Seber
1948 Autumn	30.5	± 21.9	Jolly-Seber
1949 Spring	61.8	± 106.2	Jolly-Seber
1949 Autumn	47.2	± 95.1	Jolly-Seber
1970 Autumn	33	± 40.8	Jolly-Seber
1971 Spring	58	± 112.9	Jolly-Seber
1971 Autumn	21.9	± 24.3	Jolly-Seber
1972 Spring	30	± 57.6	Jolly-Seber
1972 Autumn	38.9	± 49.8	Jolly-Seber
1973 Spring	29.3	± 20.4	Jolly-Seber
1973 Autumn	33	± 61.8	Jolly-Seber
1973 Autumn	33	± 61.8	Jolly-Seber
2022 Spring	224	± 170.925	Lincoln-Petersen

Table E.2. Population size and Confident interval 95 % of adult grass snakes (Natrix natrix) in the study area of Nacka nature reserve from spring 1945 to autumn 2002. estimated from the Jolly-Seber model.

Period	Estimate	Confident interval 95 %
1945 Spring	51.6	± 13.2
1945 Autumn	161.7	± 167.8
1946 Spring	95.5	± 29.2
1947 Spring	102.0	± 29.6
1947 Autumn	70.2	± 73.1
1948 Spring	72.8	± 20.7

1948 Autumn	67.1	± 42.5
1949 Spring	94.6	± 57.7
1949 Autumn	112.0	± 99.5
1950 Spring	74.2	± 42.7
1950 Autumn	77.5	± 123.0
1951 Spring	69.3	± 119.3
1952 Spring	80.0	± 50.2
1953 Spring	19.0	± 0.0
1953 Autumn	48.0	± 82.0
1954 Spring	36.7	± 18.8
1954 Autumn	54.0	± 113.4
1955 Spring	32.5	± 22.4
1956 Spring	32.0	± 54.0
1956 Autumn	44.1	± 28.5
1957 Spring	65.0	± 26.0
1957 Autumn	48.9	± 50.5
1958 Spring	51.7	± 10.5
1958 Autumn	47.5	± 69.0
1959 Spring	38.7	± 15.0
1959 Autumn	47.0	± 77.9
1960 Spring	36.3	± 22.4
1960 Autumn	23.2	± 14.6
1961 Spring	18.0	± 19.2
1962 Spring	35.1	± 40.6
1963 Spring	27.6	± 31.4
1966 Autumn	19.2	± 32.5
1967 Spring	15.3	± 22.7
1968 Spring	32.0	± 26.3
1969 Autumn	51.6	± 56.1
1970 Spring	81.2	± 42.7
1970 Autumn	85.9	± 44.5
1971 Spring	115.2	± 41.9
1971 Autumn	87.6	± 43.3
1972 Spring	104.0	± 35.0
1972 Autumn	123.7	± 60.4
1973 Spring	131.4	± 35.4
1973 Autumn	154.3	± 102.7
1974 Spring	199.1	± 58.5
1974 Autumn	291.2	± 367.4
1975 Spring	148.5	± 37.1
1975 Autumn	195.2	± 201.9

1976 Spring	135.2	± 45.3
1977 Spring	119.1	± 74.0
1977 Autumn	95.3	± 73.5
1978 Spring	124.2	± 108.0
1978 Autumn	35.0	± 53.6
1979 Spring	31.6	± 16.3
1979 Autumn	17.0	± 9.0
1980 Spring	26.2	± 46.0
1981 Spring	31.9	± 53.7
1981 Autumn	21.8	± 37.8
1982 Spring	12.3	± 8.6
1982 Autumn	105.0	± 207.0
1983 Autumn	39.1	± 40.3
1984 Spring	28.4	± 15.6
1985 Spring	24.9	± 15.8
1985 Autumn	24.3	± 17.4
1986 Spring	35.5	± 22.5
1986 Autumn	21.0	± 22.6
1987 Spring	41.2	± 23.0
1987 Autumn	19.2	± 6.6
1988 Spring	28.0	± 9.7
1988 Autumn	13.0	± 0.0
1989 Spring	34.3	± 25.1
1990 Spring	18.0	± 10.0
1990 Autumn	18.7	± 11.8
1991 Spring	40.0	± 18.7
1991 Autumn	48.6	± 38.5
1992 Spring	41.1	± 22.4
1992 Autumn	63.1	± 51.2
1993 Spring	28.3	± 11.7
1993 Autumn	30.0	± 14.5
1994 Spring	67.7	± 41.9
1994 Autumn	88.2	± 55.3
1995 Spring	77.7	± 34.3
1995 Autumn	98.6	± 50.8
1996 Spring	106.5	± 62.1
1996 Autumn	124.0	± 63.9
1997 Spring	92.6	± 37.3
1997 Autumn	325.0	± 614.1
1998 Spring	130.6	± 64.9
1998 Autumn	208.4	± 247.2

1999 Spring	119.8	± 77.9
1999 Autumn	240.0	± 355.6
2000 Spring	79.0	± 37.2
2000 Autumn	255.7	± 193.4
2001 Autumn	426.7	± 888.6
2002 Spring	67.2	± 132.4
2002 Autumn	193.2	± 491.8