

# Spatial genetic mark-recapture methods applied to the Swedish brown bear survey to analyze the problem relating to borders.

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# Introduction

## The bear inventory.

For several years now the population size and trends of brown bears in four regions of Sweden have and continues to be monitored. The total population and how it changes over time is important for conservation efforts and the setting of hunting quotas. If the hunting quotas are too large the survival of the brown bear species could be in jeopardy. On the opposite if it is too low the population could grow large enough to cause problems in the eco-system or for the local human population.

The monitoring and estimation of the bear population is done through the collection of scat samples. The collection is done by volunteers and genotypes are identified through DNA analysis and used to get an estimate of the number of bears from which a scat sample has been obtained. We also expect that for a certain number of bears no samples will be found and as such the population of such bears must be estimated statistically.

The collection of spill samples takes place over 5 years in which spill samples are collected in one region each year in order with the fifth year is an off year when no collection takes place. The samples are collected over 11 weeks in which the volunteers notes down the location of the spill and collects a small piece to send in for DNA analysis.

Region 1 consists of both Gävleborg and Dalarna, Region 2 is Västerbottenslän, Region 3 consists of both Västernorrlandslän and Jämtland, and Region 4 is Norrbottenslän

The estimation of the total bear population is currently modeled using the Capture-Mark-Recapture method. Traditionally the Capture-Mark-Recapture method involved physically capturing the animals in question but with advancements in DNA analysis it is now possible to perform the analysis by just “capturing” the DNA of the animals instead. While similar the underlying models at work are quite different. When collecting scat samples for example there is no beforehand known upper limit to the number of “captures” like there might be when using traps. A thorough explanation of this “genetic mark-recapture” method we use can be found in the article “*A new method for estimating the size of small populations from genetic mark-recapture data*” by Miller, Joyce, and Waits (2005).

A full explanation of the methods used in the Swedish survey be found in “*Estimating population size and trends of the Swedish brown bear *Ursus arctos* population*” Kindberg et al. (2011).

A problem with the division of Sweden into regions in this way is that brown bears do not care for these arbitrary borders. A bear could be found on one side of the border one year and the other in another year. Should this happen the bear would be counted twice for the census of the total population in Sweden which introduces bias to the estimation.

Another problem with this is deciding which region a bear belongs to. One could assume that each bear has a territory throughout which it wanders regularly. Whichever region contains the largest share of this territory or that contains the territories midpoint could be considered the bears home region. Another method would be counting the bear as the ratio of its territory that lies within each region. Male brown bears, especially young ones are known to wander freely and it is not unthinkable that their territory changes dramatically between years.

Trying to estimate a bears territory only using the location of scat samples is difficult. For bears which only a single sample has been found you can only get a rough idea of where that bears territory is located. For the bears that no samples were discovered there is no way to assign them a territory.

Another complication with the border problem is how it affects the numbers of samples found for each bear. To estimate the number of bears for which zero samples are found the rate at which samples are found needs to be estimated. The rate is assumed to be constant for each bear but due to the way the collection of samples is performed only samples inside the region currently being sampled can be found. As such a bear that has its territory close to the border is going to have their samples found at a lower rate causing bias

in the estimation of the rate and therefore also in the estimation of the number of bears with zero samples found.

The impact of these various sources of bias on the estimate of the bear populations do vary depending on what the actual rate of samples found and the size of the bears territories are. Should the rate of found samples be very high the number of bears for which zero samples are found will be close to zero. If bears have very small territories then the probability that a bears territory will span several regions is also very low.

The method capture-recapture methods that take the positions of animals into account is referred to as spacial capture-recapture and in this case it would specifically be spatial genetic mark-recapture methods. A thorough explanation of why and how spatial methods are useful can be found in “*Unifying population and landscape ecology with spatial capture–recapture*” Royle, Fuller, and Sutherland (2018).

To analyse how the border problem affects the estimation of the bear population we have performed a simulation study. By simulating a random number of bears over a created region and varying the rate at which samples are found and the size of bears territories the bias can be measured and illustrated.

The simulation values will be chosen based on the values observed for the Swedish survey samples. A calculation heavy method will also be utilized on the Swedish survey samples as well to get an alternative estimate for the population. which can be compared to the bias observed for the simulated samples.

## Conclusions

Using the simulation study we concluded that the bias in the population estimate scales close to linearly with the size of the bears territories. For very small territories the population estimate exceeds the true population by somewhere between 5 and 10 percent with only minor differences in bias for different simulated rates of discovered samples. Should however the territory be much larger the population estimate could exceed the true population by over 60%.

The main source of this bias comes from the bears from outside the inventoried region. The amount of bears from outside that are observed grow as territory sizes grow and the among all observed bears between 5 to 40% of them could be from outside. The amount of outside bears also increases noticeably as the rate of found samples increase.

Estimating the size of the territories as well as the rate at which samples are left by bears was found to be biased as well. As the rate of samples found and as the bears territories increase, the bias in the estimates increase as well. Since we can't get an accurate estimate of these parameters it is difficult to make an exact estimate of the mean population estimate bias from a real world sample in which the rate is unknown.

Applying the results of the simulation study to the Swedish survey the bias for each region was estimated to lay somewhere inbetween 5-13%

## Acknowledgments

I would like to thank Martin Sköld for his advice and guidance.

## Method

We will be using R (R Core Team (2021)) as programming language to perform the simulations and analysis. The R package sf (Pebesma (2018)) will be used to create polygonal areas for the spatial part of the analysis. The R package polyCub (Meyer (2019)) will be used to numerically calculate integrals of bivariate normally distributed distribution functions over polygonal areas.

## Statistical models and assumptions

For any area we are performing an inventory on  $S$ , we define the area that lies within distance  $l$  from the border of  $S$  as  $O$  and  $W$  as the union of  $S$  and  $O$ . Both  $S$  and  $O$  have different bear populations but with the same population density.

In Miller, Joyce, and Waits (2005) a Multinomial distribution is used as a model for the samples. The idea is that we condition on the number of samples observed and for each sample assume that each bear has an equal probability of expelling the sample in question. As such the number of samples left by any bear is  $B(M, 1/N)$  where  $M$  is the total number of samples and  $N$  is the total population of bears in the region. However the multinomial distribution is slightly difficult to work with especially as due to spatial reasons the number of samples we expect to observe from each bear is not equal for all bears. As it is easier to work with each bear having its own independent distribution for the number of samples it leaves we will instead assume each bear leaves samples based on the  $B(M, 1/N)$  distribution. Since the observed values for  $M$  is relatively large and  $1/N$  is relatively small we can approximate the binomial distribution with the poisson distribution  $Poisson(M/N) = Poisson(\lambda_0)$ .

A thorough explanation of approximating the multinomial distribution with the poisson distribution can be read in “On the Poisson approximation to the multinomial distribution” McDonald (1980).

The number of samples that bear number  $i$  leaves is  $K_i \sim Poisson(\lambda_0)$ . For each bear that has had a sample observed the sample  $k_{ij}, j = 1, \dots, n$  has a location that is bivariate normally distributed  $N(\mu_i, \sigma I)$  and we let  $T_i(\mathbf{x})$  be the probability distribution function for this distribution. We also use  $T_i$  to describe bear  $i$ 's territory. The amount of time that a bear spends during the inventory period in any area  $A$  is  $\int_A T_i(\mathbf{x}) d\mathbf{x}$ .

If  $k_{ij} \in S$  then it will be observed with probability  $p$  and if  $k_{ij} \notin S$  then the probability of it being observed is zero. Let  $I_i = \int_S T_i d\mathbf{x}$  then the number of samples that bear number  $i$  leaves inside  $S$  is  $K_{Si} \sim Poisson(I_i \lambda_0)$  distributed. Since these samples are only observed with probability  $p$  the distribution for the number of samples observed by bear number  $i$  is binomially distributed  $B(K_{Si}, p)$  which is a conditional distribution. The binomial distribution where the number of repetitions is conditioned on the outcome of a poisson distributed variable is also poisson distributed so  $B(K_{Si}, p) \sim Poisson(p I_i \lambda_0)$ . As we are not specifically interested in neither  $p$  nor  $\lambda_0$  we can replace  $p \lambda_0$  with  $\lambda$  and focus only on the rate at which samples are observed. Therefore the number of observed samples left by bear number  $i$  is  $O_i \sim Poisson(I_i \lambda)$ .

## Simulation

For this simulation  $W$  is a 9 x 9 square with centre in origo of the two dimensional Cartesian plane and  $S$  is the 2 x 2 square centred around origo. We want  $S$  and  $O$  to have the same average population density and since  $S$  has an area of 4 square units and  $W$  has an area of 36 that is 9 times larger we simulate the population of  $W$  from a  $poisson(9\mu)$  distribution where  $\mu$  is the mean population size of  $S$ .

For the location of bears midpoints in  $W$  we choose to use a homogeneous poisson process throughout the plane. As such each simulated bear number  $i$  has a territory midpoint  $\mu_i = (X_i, Y_i) \sim (U_{-3,3}, U_{-3,3})$ . Any bear whose midpoint lies within  $S$  is marked as a “True Bear” and the rest as “False bears.” The total number of “True bears”  $N$  is what we are trying to estimate so for each simulation we include this total. For each simulated bear we simulate the number of samples they leave from a  $Poisson(\lambda)$  distribution. Each simulated sample then has its location simulated from the bivariate normal distribution  $N(\mu_i, \sigma I)$ . Any sample that is not contained in  $S$  is then removed and then any bear with zero remaining samples is also

removed and the remaining samples are considered observed. The number of True bears and False Bears for which at least one sample has been observed is then counted.

$\lambda$  is estimated using the maximum likelihood estimate for a zero truncated poisson distribution since we cannot observe the bears with zero samples observed.

Let  $N_{Obs}$   $N^{\text{obs}}$  be the number of bears observed,  $N_T^{\text{obs}}$  be the number of bears observed whose midpoint actually belong to  $S$  and  $N_F^{\text{obs}}$  be the number of bears observed whose midpoint does not belong to  $S$ .

Since the probability that an outcome of a  $Poisson(\lambda)$  distribution is 1 or larger is  $(1 - e^{-\lambda})$  then we have

$$N(1 - e^{-\lambda}) = E(N^{\text{obs}})$$

The estimate for the total number of bears in  $S$  is then.

$$\hat{N} = \frac{N^{\text{obs}}}{1 - e^{-\hat{\lambda}}}$$

However this is done under the assumption that  $N^{\text{obs}} = N_T^{\text{obs}}$ . However in our case

$$N^{\text{obs}} = N_T^{\text{obs}} + N_F^{\text{obs}}$$

Which means that

$$\hat{N}^{\text{obs}} = \frac{N_T^{\text{obs}} + N_F^{\text{obs}}}{1 - e^{-\hat{\lambda}}}$$

Which we could rewrite as

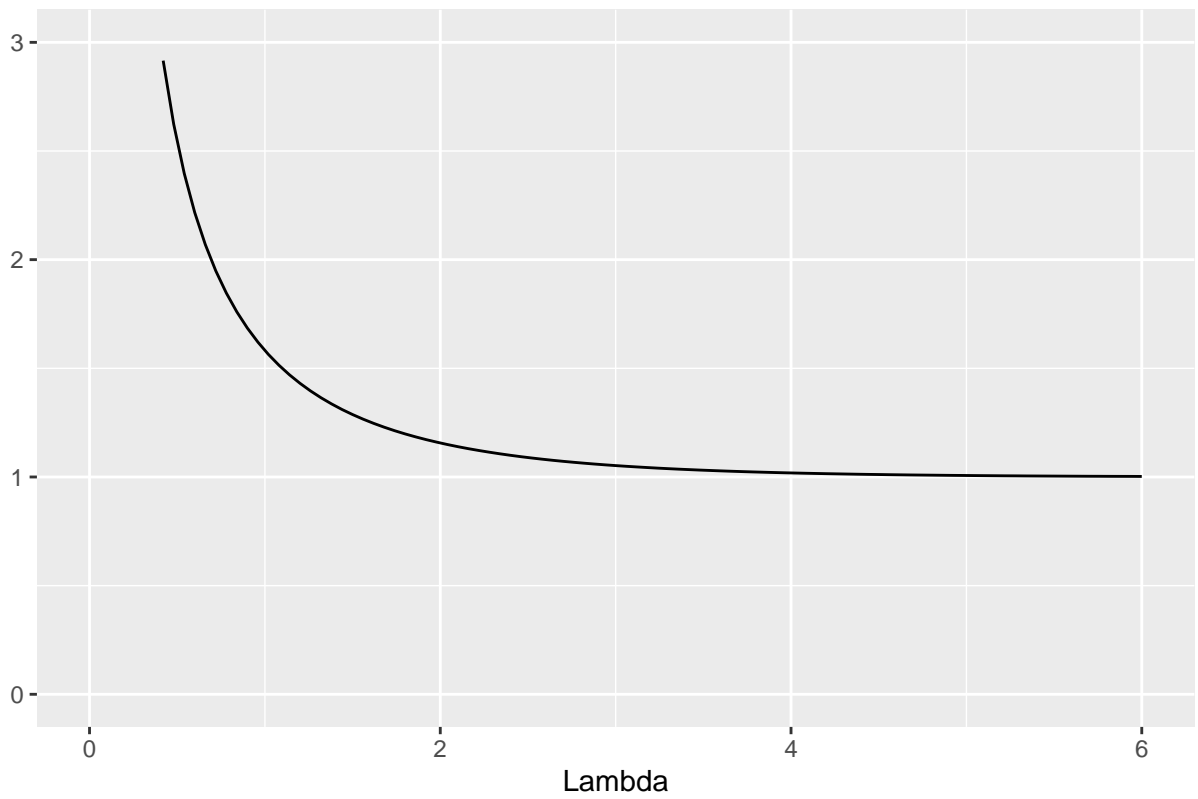
$$\hat{N}^{\text{obs}} = \frac{N_T^{\text{obs}} + N_F^{\text{obs}}}{N_T^{\text{obs}}} \frac{N_T^{\text{obs}}}{1 - e^{-\hat{\lambda}}}$$

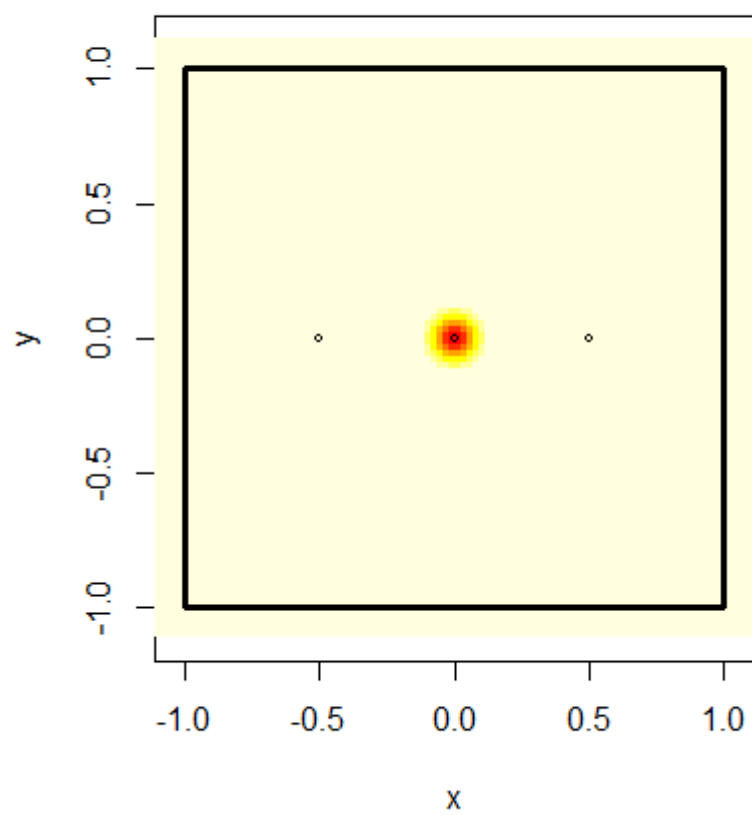
Which gives us two factors of which the left depends on the problem related to the number of false bears observed and the right depends on the error in the estimation of  $\lambda$ .

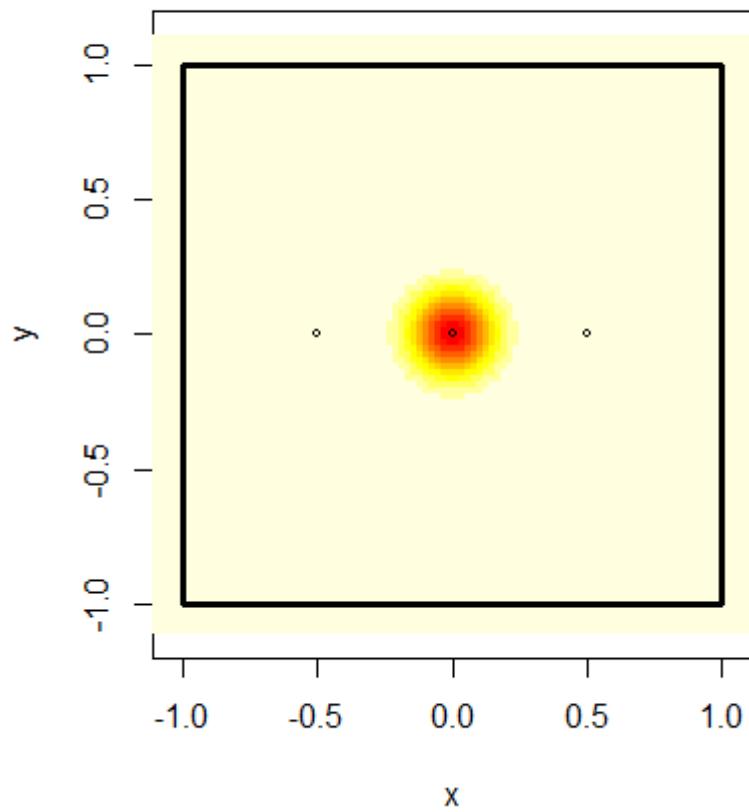
Since we measure the true value of  $N$  we can measure the bias  $\hat{N} - N$  and analyse it.

For  $\lambda$  we use values 2, 3 and 4 and for  $\sigma$  we use 0.025, 0.05, 0.075, and 0.1. These values were chosen because they are close to the ones estimated for the Swedish sample. There is little reason to use  $\lambda$  values higher than 4 because in our estimate of the total population size we use the transformation  $1/(1 - e^{-\lambda})$  instead of just  $\lambda$  by itself. When  $\lambda$  is larger than 4 the transformations value changes very little as can be seen in Function Graph 1.

Function Graph 1: The function graph for the transformed lambda.



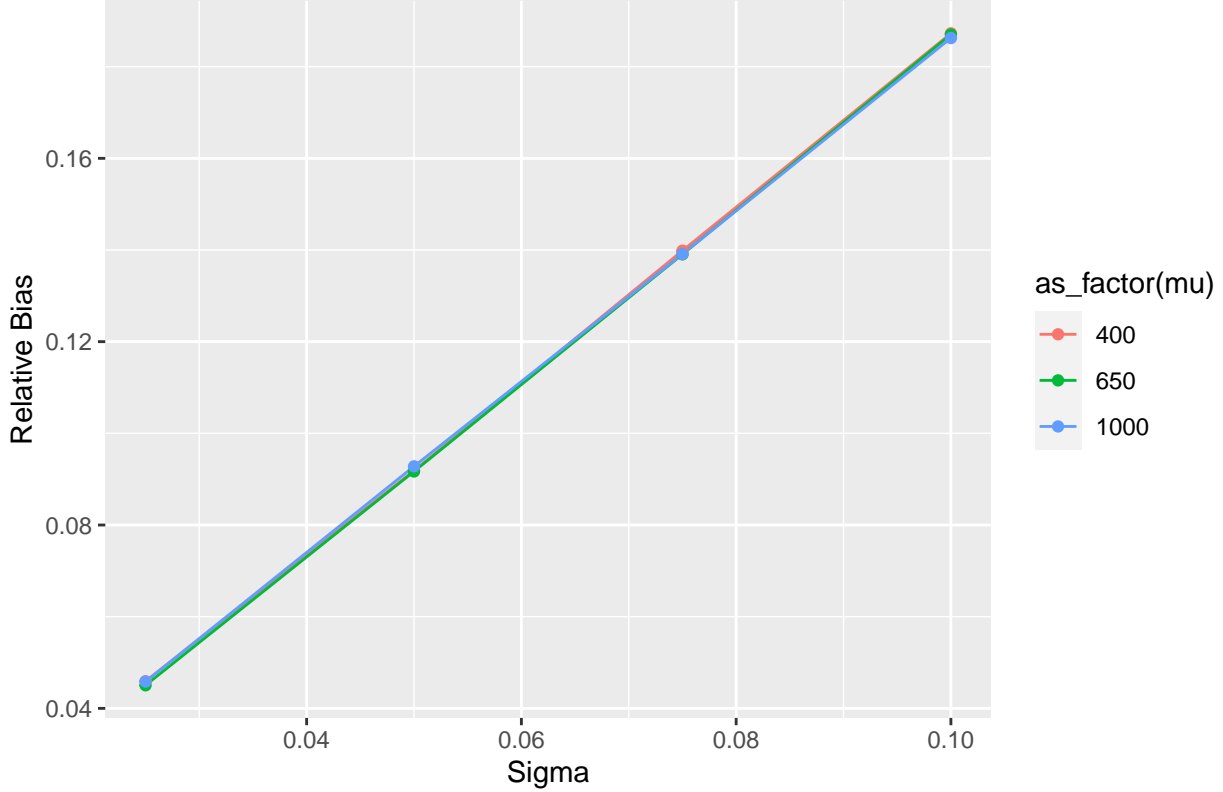




We choose to keep  $\mu$  at a constant value of 500 as the relative bias in the population estimate does not change with different average populations. A simulation was run to illustrate this and the results can be seen in FIGURE 1.



Figure X: Relative bias does not change with the total population.



## Application to the Swedish survey

The idea with the alternative model is to take the positions of the bears into account when making the estimations of the underlying parameters. Since the bears territories are binormally distributed, estimating how much of the territories lies within a certain region requires integrating over some irregularly shaped intersections between the territories and the region in question the integrals needs to be performed numerically. These numerical methods will then also be used in combination with an optimizing functions which causes the calculations to take a very large time when they need to be repeated thousands of times in a simulation to get an estimate for their effectiveness. As such these methods will only be used on the real samples and their effect will need to be trusted based on their soundness.

For the real data we assume that all the assumptions of the simulation are true. Since male bears are known to wander further than female bears and as such would have very different values of  $\sigma$  we choose to estimate their populations separately.  $\sigma$  is estimated by removing all bears that only have 1 samples discovered and then using the pooled sample variance method. To make comparisons between the real data and the simulated data we also want to get a normalized value for them both. For this we choose to use  $\sigma/\sqrt{RegionArea}$ . Since the area in the simulation is 4 we can use the value of  $2\sigma/\sqrt{RegionArea}$  to make comparisons between the real data and the simulation.

The midpoint coordinates of each bear is estimated as the mean of the samples lateral and longitudinal coordinates. The midpoints are going to be biased since all samples are located inside the region so to account for that we will apply an optimizing function to each bear. We find the midpoint  $\mu$  that optimize the function

$$l(\mu) = \sum_1^n \log(\phi((x_i - \mu)/\sigma)) / \int_S \phi((x - \mu)/\sigma) dx$$

where  $x_i$  is the location of the bear in questions sample  $i$  and  $\phi$  is the standard bivariate normal distribution. The function applies a penalty to midpoints further from the border which allows midpoints from outside the region in question to be possible outcomes.

After each bears midpoint has been adjusted we can calculate  $I_i$  (The integral of the bears territory over the Region) and then get the maximum likelihood estimate for  $\lambda$  where each bears number of samples found is assumed to be a outcome of  $Poisson(I_i\lambda_0)$ .

For the estimate of the bear population we have thought of two different methods for the estimate. The first is to simply remove any bear whose midpoint was adjusted to lie outside the region and then use  $\hat{\lambda}$  to estimate the number of bears for which zero samples were discovered. The second is instead of summing up the discovered bears, we instead sum up  $I_i$  which means we are counting the fraction of the bears estimated territory that lies within the region and assume that the remainder  $1 - I_i$  belongs to another region. The number of bears for which zero samples were found is then estimated the same as in the first method.

# Results

## Simulation results

In Figure 1 we can see how the bias in the population estimate bias grows seemingly linearly as  $\sigma$  grows while changes in  $\lambda$  adjusts the slope coefficient. As  $\sigma$  approaches zero each bears territory converges towards a single point, that being the midpoint of the territory. When the bears territories are that small the probability that a any bears territory will intersect with a region that the bear does not belong to is negligible and all bears will only leave spills inside their own region. However for large  $\sigma$  the relative bias is quite high with the estimate possibly being more than 60% larger than the true population.

In Figure 2 we see that the mean number of false bears that are observed in each sample also grows seemingly linearly with  $\sigma$  and again  $\lambda$  adjusts the slope coefficient. Even for relatively small  $\sigma$  the number of observed bears that are false can be as large as 10% of the observed population.

Using the results of the simulation it would theoretically be possible to estimate the bias for any estimation made using this method. However to do this we would need to be able to accurately estimate the underlying parameters  $\lambda$  and  $\sigma$ . In figure 3 we can see the bias for the pooled sample variance estimate of  $\sigma$  and how it varies depending on  $\lambda$  and  $\sigma$ . The magnitude of the relative bias does increase linearly with  $\sigma$  but for smaller values the estimate is relatively close. The bias is seemingly not influenced at all by the value of  $\lambda$ .

For the estimate of  $\lambda$  we instead choose to look at the bias in the transformed version  $1/(1 - e^{-\lambda})$  as it also factor that we multiply the number of observed bears with to make our total population estimate. We can see from figure 4 how the bias grows in magnitude with as  $\sigma$  grows. The estimate is also biased for all values of  $\sigma$ . Since both the estimate for  $\sigma$  and  $\lambda$  are biased we cannot use the mean bias estimated through the simulation to make an exact adjustment of a real samples population estimate.

Figure 1: Mean bias of the simulated population estimate.

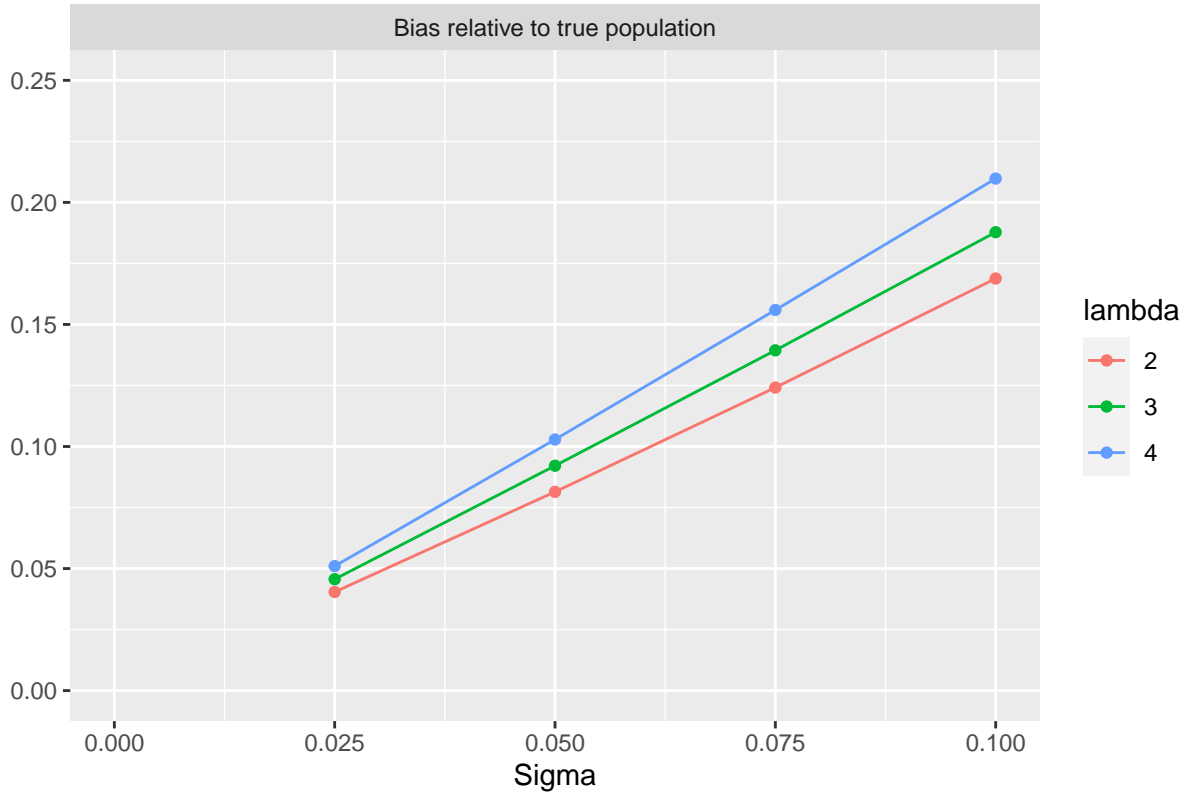


Figure 1 shows how the mean bias in the population estimate grows seemingly linearly as  $\sigma$  (The size of

the bears territories) grows. The mean bias grows faster as the value of  $\lambda$  (The rate at which samples are discovered) increases.

Figure 2: Bias divided into False bear and Lambda bias.

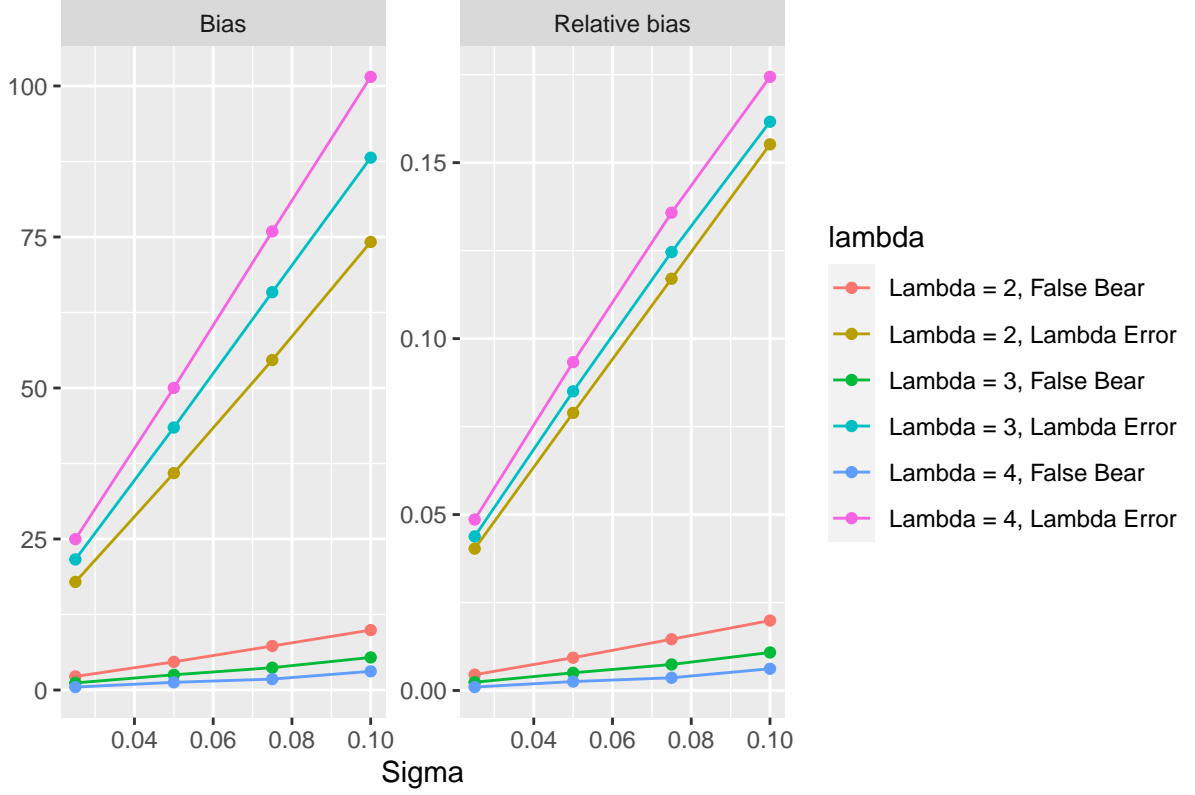


Figure 2 shows the bias divided into 2 categories. The lambda error  $\frac{N_T^{\text{obs}}}{1-e^\lambda} - N$  which is the mean bias in the population estimate we would have if only true bears were observed. The false bear error is  $\frac{N_F^{\text{obs}}}{1-e^\lambda}$  which is the number of false bears observed in the sample further amplified by the factor we use to estimate the bears for which no samples were discovered.

We can observe how the majority of the bias in population estimate can be attributed to the number of false bears observed and how it grows much faster than the error caused by the bias in the estimate of  $\lambda$ . If all false bears could be eliminated from the sample the remaining relative bias would not exceed 2.5%.

Figure 3: Bias in the estimation of the parameters.

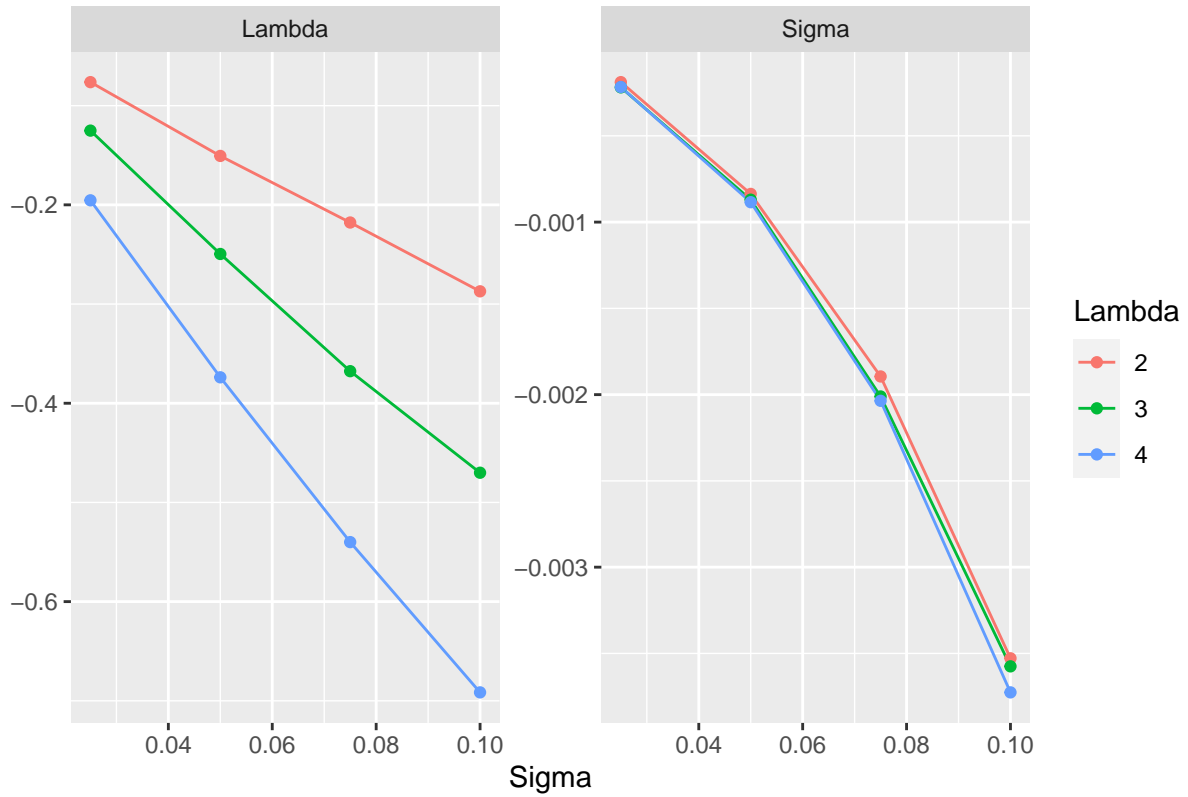


Figure 3 shows the bias when estimating the underlying parameters of the simulation. The methods utilized always underestimate both of the parameters and the bias grows along with  $\sigma$ . As both parameters are biased we cannot directly use the simulated data to get an exact estimation of the mean bias in a sample for which the underlying parameters are unknown.

Figure 4: Comparing bias in the population estimate between the two meth

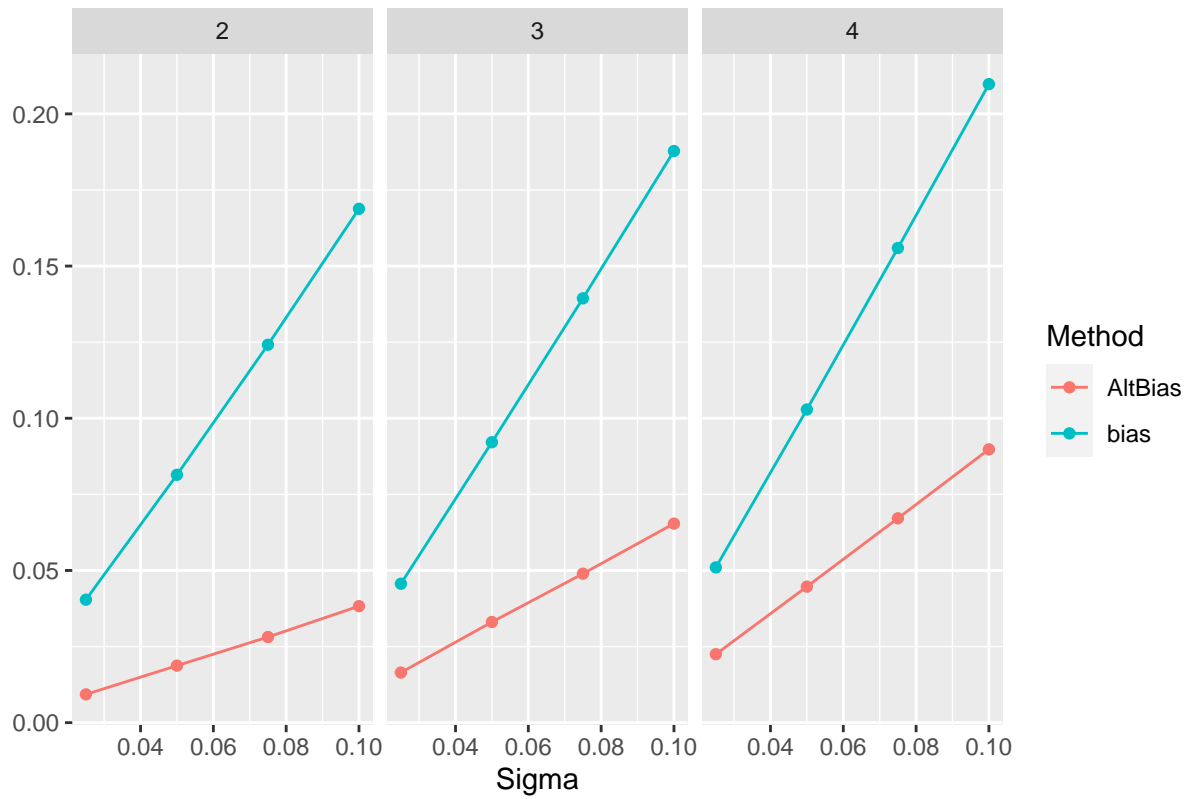
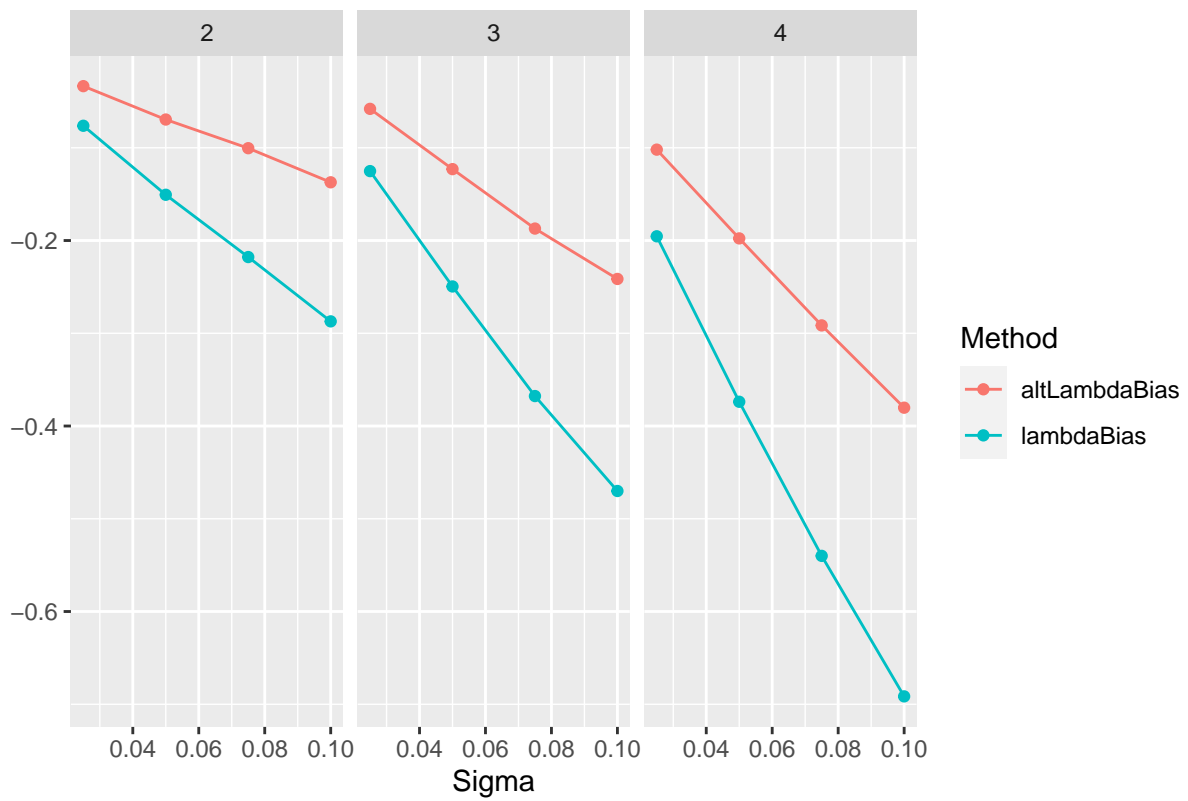


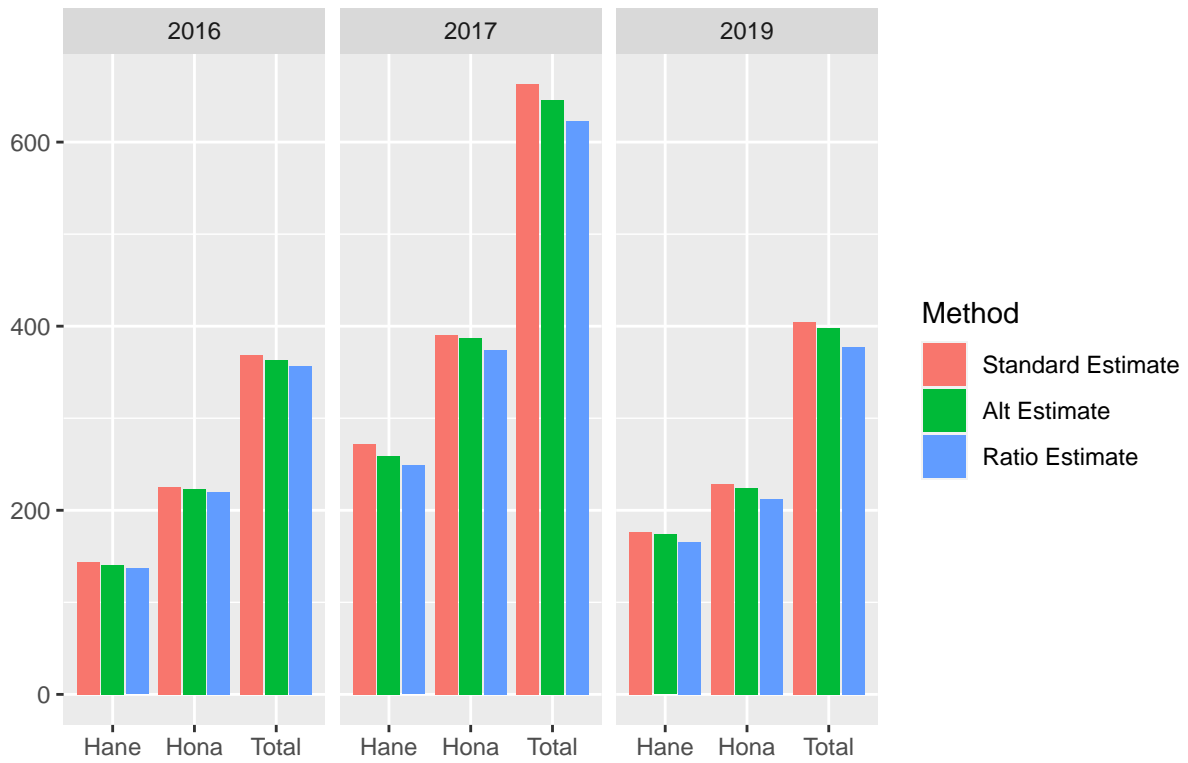
Figure 5: Comparing bias in the estimate of lambda between the two meth



## Swedish survey results

SwedishBearPopulationEstimateFigure1

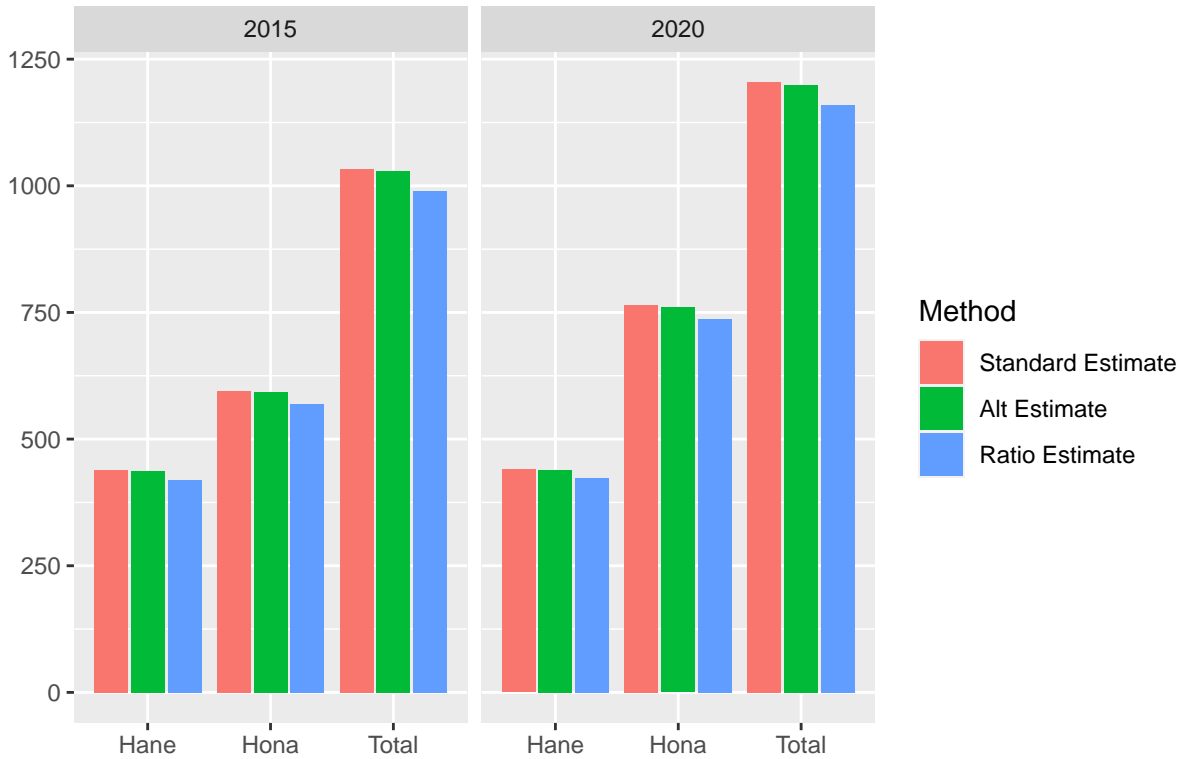
Figure 6: Estimation of the Swedish bear population in 3 different regions.



SwedishBearPopulationEstimateFigure2



Figure 7: Estimation of the Swedish bear population in the same region tw



In figure 4 we can see the estimates of the bear population for 5 years of the Swedish survey. Year 2015 and 2020 were performed on the same region. The standard estimate is the one that is made without taking the location of the samples into accounts.

The alternative estimate is the one in which the bears midpoints were re-evaluated and the bears whose midpoints ended up outside the region were removed. The method also improves the estimation of  $\lambda$  by taking into account that bears closer to the borders will have fewer mean number of samples observed.

The Ratio estimate instead of counting each bear observed as one bear instead counts the estimated ratio of the bears territory that lies inside the surveyed region along with the alternative estimation of  $\lambda$ .

The Simulated Unbiased Estimate assumes that the estimated values of  $\sigma$  and  $\lambda$  are true and reduce the standard estimate by the simulated mean bias for the corresponding parameter values. As the parameters are on average underestimated and the mean bias grows as the parameters grow we expect this estimate to overestimate the bear population if all the assumptions of the simulation are true.

The alternative estimate does not differ much from the standard estimate. The Ratio estimate is noticeably lower than the standard estimate and the simulated unbiased estimate is even lower.

## Discussion

### What conclusions can we draw from results?

The bias in the population estimate grows as the parameters of the distribution functions used in the simulation  $\lambda$  (The rate at which samples are found) and  $\sigma$  (The size of the bears territories) grows.

This bias can be attributed to the false bears for which samples have been observed and to the bias in the estimation of  $\lambda$ . However the bias introduced by the false bears vastly exceeds the bias from the estimation of  $\lambda$ .

The mean bias in the population estimate can be seen as a function of the underlying parameters  $\lambda$  and  $\sigma$  that defines the size of a bears territory. As such if we could calculate an expression for this bias function and knew the values of these parameters for a collection of samples we could get an estimate of the bias in that collection. However for a real collection of samples these parameters must also be estimated first which is a problem since the estimates for them are biased and the bias is larger the larger the values for the parameters are.

### Swedish samples

The population estimate of the alternative estimation method when applied to the Swedish samples did not differ dramatically from the normal method that does not take the bears positions into account.

For each of the 4 regions in Sweden  $\sigma$  is estimated to lie somewhere inbetween 0.05 and 0.08 which from the simulation estimates would suggest that the relative bias for the regions lies in-between 8 and 13 percent. However the Swedish regions do differ from the simulation in certain ways. For example part of each Swedish region borders the Baltic Ocean in which brown bears are not known to live. As such the assumption that the population density of the outside region is the same as in the inside region does not hold for any of the Swedish regions. A better approximation of the bias could be achieved by multiplying the bias by the ratio of the border that does not touch the Baltic ocean. Furthermore the bear population is not consistent across the inside of the region either as bears are not known to wander freely throughout larger human settlements.

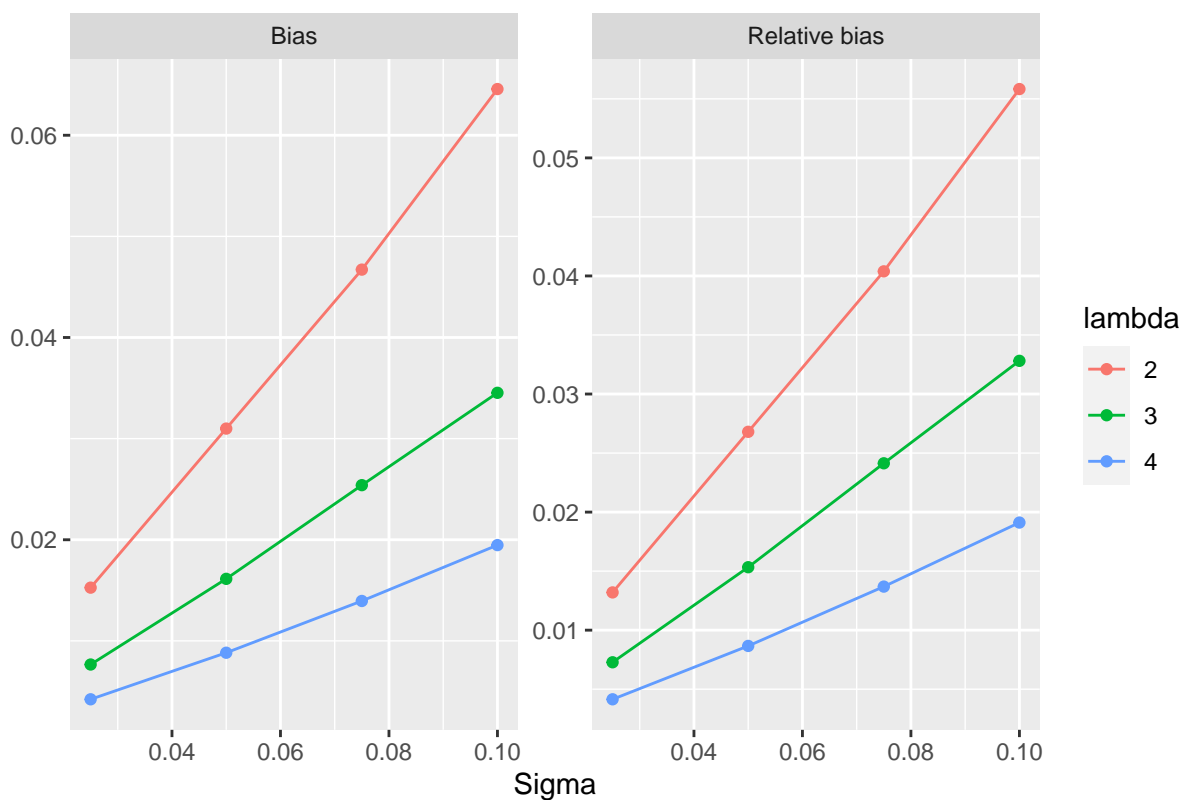
While the simulation most likely differs quite a lot from the Swedish survey it does seem likely that the methods currently being utilized will on average overestimate the bear population but by exactly how much is not known. While better estimations could be made using different methods on the samples observed, changing the current surveying methods to better take the border problem into account would be more likely to get better results.

### Future directions for research.

A way to get a better understanding of the border problem would be to extend the search for samples to some distance outside of the region currently being investigated. Not only would we have an easier time identifying bears from outside regions, we could also get a better estimate of the rate at which bear samples are observed by removing bears for which all samples lie very close to the new extended border without losing too much information about the region currently being surveyed.

## Appendix

Figure 5: Bias for the multiplication factor.



year	sex	Standard Estimate	Alt Estimate	Ratio Estimate	Standard Lambda	Alt Lambda	Normalized Sigma
2015	Hane	438.9666	437.2374	419.2321	4.706508	4.905714	0.0762118
2015	Hona	594.2778	592.4432	569.7841	3.801252	3.946863	0.0574793
2015	Total	1033.2444	1029.6805	989.0162	NA	NA	NA
2016	Hane	143.5283	140.1657	136.7642	2.438544	2.529981	0.0654466
2016	Hona	225.3331	223.2975	219.6450	2.405327	2.448531	0.0432451
2016	Total	368.8614	363.4631	356.4092	NA	NA	NA
2017	Hane	272.2243	259.0285	248.5888	3.188547	3.356554	0.0669158
2017	Hona	390.7397	386.9825	374.3613	3.211857	3.320572	0.0518495
2017	Total	662.9639	646.0110	622.9501	NA	NA	NA
2019	Hane	176.2526	173.7480	165.3290	2.025502	2.125154	0.0915389
2019	Hona	228.2444	224.1914	212.1645	1.840133	1.940800	0.0656059
2019	Total	404.4969	397.9395	377.4935	NA	NA	NA
2020	Hane	440.1865	438.4731	422.6845	3.434908	3.559724	0.0657033
2020	Hona	764.4728	759.9292	736.3503	3.042619	3.138866	0.0439210
2020	Total	1204.6593	1198.4023	1159.0348	NA	NA	NA

year	sex	Standard Estimate	Alt Estimate	Ratio Estimate	Simulated Unbiased Estimate	Estimated Simulated Bias	Simulated Bias Estimate
2015	Hane	438.9666	437.2374	419.2321	375.1851	63.78148	0.17
2015	Hona	594.2778	592.4432	569.7841	530.6052	63.67262	0.12
2015	Total	1033.2444	1029.6805	989.0162	905.7903	127.45410	NA
2016	Hane	143.5283	140.1657	136.7642	128.1502	15.37803	0.12
2016	Hona	225.3331	223.2975	219.6450	210.5917	14.74142	0.07
2016	Total	368.8614	363.4631	356.4092	338.7420	30.11945	NA
2017	Hane	272.2243	259.0285	248.5888	240.9064	31.31784	0.13
2017	Hona	390.7397	386.9825	374.3613	358.4768	32.26291	0.09
2017	Total	662.9639	646.0110	622.9501	599.3832	63.58075	NA
2019	Hane	176.2526	173.7480	165.3290	153.2631	22.98947	0.15
2019	Hona	228.2444	224.1914	212.1645	207.4949	20.74949	0.10
2019	Total	404.4969	397.9395	377.4935	360.7580	43.73895	NA
2020	Hane	440.1865	438.4731	422.6845	389.5456	50.64092	0.13
2020	Hona	764.4728	759.9292	736.3503	701.3512	63.12161	0.09
2020	Total	1204.6593	1198.4023	1159.0348	1090.8968	113.76253	NA

Link to github repository containing the code and materials used.

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