Family size and age structure of the Eurasian Beaver *Castor fiber* under density dependence

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Abstract

After the Eurasian beaver (*Castor fiber* Linnaeus, 1758) was nearly driven to extinction in the early 19th century, the species has flourished ever since it has been re-introduced in large parts of Central Europe, starting in 1956. Based on this timeline, much of our knowledge about the species was gained during a time of marked population growth well below carrying capacity. Now that the species is approaching said capacity in some areas, the question arises, what and to what extent do we see change in the life history and ecology of the beaver?

In this study we focus mainly on the family size and age structure in a system of beaver territories located in an area with very high territory density (Belpauen in the Swiss canton of Bern). Using a specific configuration of three camera traps per territory, we were able to identify and age beaver individuals based on traits of the beaver tail. Visual identification of scars and colouring anomalies of the tail were used for individual identification, while tail dimensions were extracted semi-automatically to group the beavers in three distinct age-classes. In the five occupied territories that we observed, we found an average of 6.2 individuals per family, with the largest family consisting of 9 beavers. More notably, we found a shift in age structure towards an increased number of adult beavers per family compared to the two dominant adults found in common literature. This stands in accordance with observations made in Norway, where offspring could delay dispersal for several years. We also witnessed a surprising number of individuals venturing beyond their territory borders often crossing several other territories in the process.

Therefore, at least in our study area - where the beaver reaches its highest density of Switzerland - our results suggest that life history may in fact change when approaching carrying capacity.

Keywords: Eurasian beaver, family size, age structure, density-dependence, life history, carrying capacity

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1. Introduction

Growth is not unlimited – a concept that is well known and widely applicable in ecology (Solomon, 1949). If a population expands beyond a certain, unseen threshold, negative selection pressures will increase, ultimately bringing population growth to a halt. As universally recognized this concept - some might call it law of nature - is, the more diverse the driving forces behind it are. In this thesis, we try to shine light into potential drivers slowing down the population growth of a semi-aquatic mammal, the Eurasian beaver *Castor fiber*. A species that has nearly gone extinct and our knowledge of only comes from a time where the species was growing nearly exponentially.

In the field of conservation biology, the Eurasian beaver is often regarded as among the best comeback stories (D. Halley et al., 2012). The species was nearly extirpated in the early 19th century, with the population being down to around 1'200 individuals in 8 isolated subpopulations (D. J. Halley et al., 2021). In Switzerland, the last beaver was extirpated in the beginning of the 19th century. Individuals were first re-introduced in 1922 in Sweden (Stocker, 1985), in Switzerland re-introductions started in 1956. Up until 1977 a total of 141 beavers were introduced in Switzerland alone (Stocker, 1985). Since its reintroduction, the European beaver has repopulated the Swiss plateau to a large extent with current counts from the national beaver survey in 2022 of almost 1'400 territories with an estimated population size of around 4'900 beavers (Angst et al., 2023).

However, the increase in beavers in Switzerland is not well conceived by some (Kaphegyi et al., 2015). With the increase in population size, there has also been an uprisal of conflicts that are caused by beavers (Angst et al., 2023). This includes building dens underneath infrastructures such as flood protection damns or roads leading them to destabilize, flooding of agricultural land or direct feeding damage in maize, carrot and sugar beet fields as well as orchards (Angst et al., 2023).

On the bright side, it has been shown in numerous cases that the beaver has a positive effect on many different species groups. As an ecosystem engineer, the Eurasian beaver is able to construct habitats according to its own preferences by building dams into small rivers. The modulation of the riverine habitats has a significant impact on the biotic and abiotic factors in the vicinity, which can benefit a wide range of species groups including but not limited to terrestrial and aquatic invertebrates, fish, amphibians, birds and water plants (Rosell et al., 2005). In Germany, Orazi et al. (2022) found more species of conservation concern at beaver ponds than comparable habitats. Damming of rivers has also been shown to benefit water management as it helps in retaining water upstream, thus reducing the risk of severe floods but also droughts (Puttock et al., 2021). The direct and indirect benefits for nature and humans, provided by the presence of beavers has long been recognized and today, conservation strategies can even include the beaver as a helping force for habitat restorations (Castro et al., 2017, Angst & Auberson in prep.).

As shown through the benefits and problems caused by the beaver, it should be of no surprise that the species is currently controversly discussed (Kaphegyi et al., 2015). As of summer 2024, the government of Switzerland is discussing a relaxation of the beavers' conservation policies and making it easier to remove potentially problematic beavers through lethal methods (Schweizerischer Bundesrat, 2024). However, this action should be well informed in order to sustain a (genetically) healthy population. Having exact estimates of the population size and its dynamics is therefore a necessary foundation for well-reasoned and educated management decisions.

In general, much of the knowledge about the Eurasian beaver was gained during a period where the Eurasian Beaver was expanding throughout Europe (D. J. Halley et al., 2021). Now that the population is reaching saturation in some regions, this poses the question, whether there might be differences in life history and the beavers ecology. The knowledge about such changes would not only be in the interest of understanding density dependence but also key for future management decisions, especially when these management decisions include lethal forces.

In Switzerland, the current population estimate from the national survey done in 2022 (Angst et al., 2023), is based on indirect observations of signs of beavers. All territories are differentiated into individual/ couple territories or family territories where individual territories are estimated to hold 1.5 and family territories five individuals (Angst, 2010). The latter consisting of two adults and two generations of offspring. However, recent studies conducted in Norway have suggested that in areas with a high population density, the offspring might delay dispersal and stay longer with the family than the suggested two years (Mayer et al., 2017). This in turn could then lead to increased family size under high population density (Rosell & Campbell-Palmer, 2022).

Meier (2023) investigated this suggestion in more detail in Switzerland and studied family sizes in regions with high and low territory densities. Two camera traps per territory were set up near the beaver den, usually situated in the middle of the territory. With this specific camera trap setup, Meier could identify each individual beaver which enabled counting the visiting beavers without the risk for double counting (Schwaiger & Schwemmer, 2012). While she found a tendency towards larger families in high territory densities, neither high nor low territory densities had an average of five individuals per family, used as an estimate by the national survey (Angst et al., 2023). Instead, average family size was at 2.53 individuals for low density and 3.59 for high density (Meier, 2023). While the study looked at multiple territories per site, not all adjacent territories were covered and thus, it could only be assumed that the photographed individuals actually belonged to the territory. Possibly visiting neighbors could have been identified as family member and as this could be more likely to happen in highly populated areas, the family size would wrongfully increase in relation to less populated areas.

In this study, we specifically look at a system of beaver territories in an optimized grouping of camera traps to identify visiting beavers and possibly solidify the prior results of family size and age structure by Meier (2023). Furthermore, this study is aimed at further improving the use of camera traps to study spatial dynamics of beaver individuals.

In detail, this study aims to answer how large families can grow in areas in Switzerland with high population densities. In accordance with Angst et al. (2023) we would expect to see on average 5 or slightly more individuals per family, which stands in contrast to the overall findings of Meier (2023) where regardless of density, the average family size was smaller than five. However, as we are studying family size in the densest area of Switzerland and Meier (2023) also observed families with up to eight individuals this would indicate that large family size might only happen in very high densities. Subsequently, this would indicate that the current population size estimates do not need a re-evaluation as large family size in very densely populated areas would be buffered by the smaller family size in low density areas.

Additionally, we look into answering the question whether intrusions of a conspecific's territory is a common phenomenon in the Eurasian beaver during the winter months. As the beaver is a highly territorial animal (Graf et al., 2016), we do not expect members of beaver families that live in close proximity to each other regularly cross their respective territory borders. This would be in accordance with the findings of (Graf et al., 2016; Herr & Rosell, 2004) which has shown that beavers only rarely spend time beyond their territory borders. This should be even more the case during the study period in the winter where home ranges are reduced (Korbelová et al., 2016).

Lastly, we also want to give input about the reliability of the method used to study territory and family dynamics in the Eurasian beaver. We expect the method to feed us reliable and otherwise inaccessible information about the Eurasian beaver while remaining with a fully non-invasive method, to avoid interfering with the study results or more importantly harming the beavers in any way. As Mortensen & Rosell (2020) could show, capturing and handling beavers can have significant effects on body mass and fitness of individuals, hence this non-invasive approach to inhibit any negative impact on the species.

2. Methods

2.1. Searching suitable beaver territories

Study area

Based on the national beaver survey by Angst et al. (2023) and on the recommendation of C. Angst, we chose an area with a high density of beaver territories. In fact, the chosen study area has the highest territory density in Switzerland. The area is located in the Belpauen, between Belp and Rubigen, just adjacent to the western bank of the river Aare but separated from it by a dam, to protect it against major flooding. The area is subject to moderate continental climate with cold winters and warm summers (MeteoSchweiz).

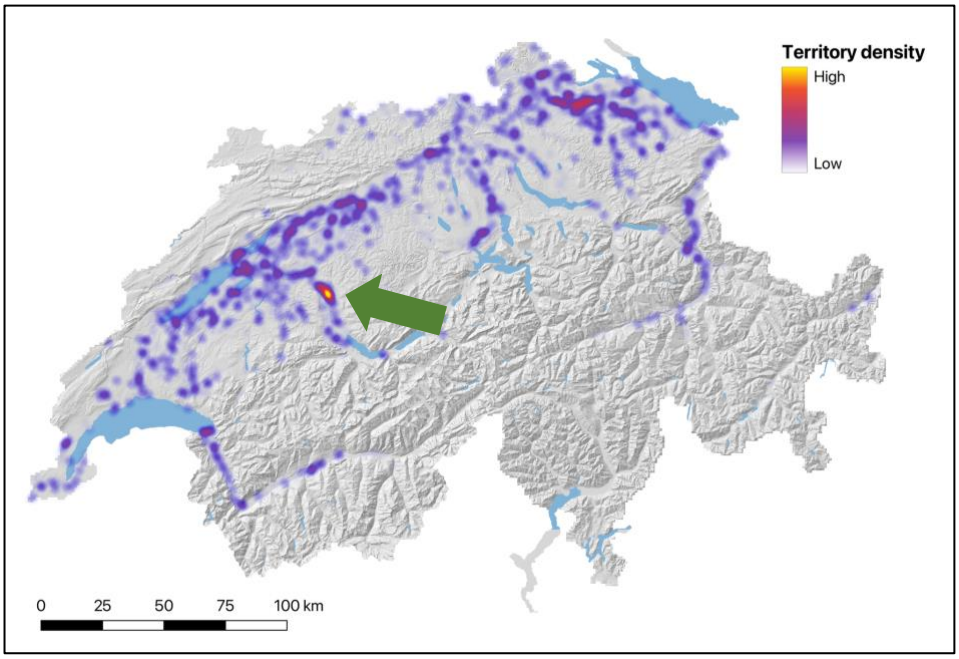

Figure 1: Population density of C. fiber in Switzerland. The study area is marked with a green arrow. The data was provided by Angst et al. (2023) and visualized in QGIS using heat map with Kernel shape bi-quadratic with a radius of 3 km and a weighting for individual to family territories of 1:5. Background: ©Swisstopo

The study area is part of the Bundesinventar der Landschaften und Naturdenkmäler von nationaler Bedeutung (BLN) site number 1314 (*Aarelandschaft zwischen Thun und Bern*), Bundesinventar der Auengebiete von nationaler Bedeutung site number 69 (*Belper Giessen*) and Bundesinventar der Amphibienlaichgebiete von nationaler Bedeutung site number BE973 (*Belpau*) and BE968 (*Aareaue bei Belp*). The land is owned by the Burgergemeinde Belp which granted us the permit to use the access roads by car as well as mapping the area and setting up the camera traps.

Table 1: Details of study area, measurements taken from the weather station of Bern Airport just adjacent to the northwestern border of the territory (MeteoSchweiz).

Name	Belpauen
WGS coordinates of site center	46°88'99.28", 7°53'38.39"
LV95 coordinates of site center	2'607'255.89, 1'193'205.73
Mean elevation m.a.s.l.	515 m.a.s.l.
Average daily temperature	7.7 °C
In winter (90 days)	-0.35 °C
In summer (90 days)	16.01 °C
Annual precipitation	1107.05 mm

Survey

As the beaver is active during the night, we used an indirect survey conducted during the day to initially identify all active beaver territories (occupied lodges and signs of activity in the vicinity). The survey locates beaver lodges and the respective territory boundaries using various traces (see Figure 2). While the beaver lodges usually prevail rather stationary for longer periods of time, the territory boundaries change dynamically. As the last beaver survey was done in 2022 (Angst et al., 2023), we did a separate survey in the chosen area in order to check, whether the lodges were still actively used and to update the territory borders.

A

B

C

D

E

F

Figure 2 (A-F): Examples of beaver traces found during the mapping. A: Typical gnawing mark. B: Leftovers at a feeding place. Differently sized marks of the teeth are helpful to find juveniles and thus identify territories as family territory. C: Typical lodge of C. fiber at the shore. D: In front of the lodge, C. fiber often builds up a pile of branches as a winter reserve, indicating, that this lodge is actively used. E: Traces of C. fiber feeding on grass in agricultural land. F: A small beaver dam to maintain the water level in the upper part of the river where the lodge is situated.

The survey was conducted in late December across 2 days (25. and 27.12.2023). The weather was stable before and during these days and, most importantly, the floods from earlier that winter were already more than a week ago and therefore, it could be assumed that there would already be a lot of beaver traces along the riverbed. With the exception of a small area in the north of the study area, all sections of the waterbodies could be accessed to sample traces of the beaver. The absence of traces in an area can therefore be taken as true absence-data (not part of a beaver territory) with the exception of the marked area (orange striped polygon).

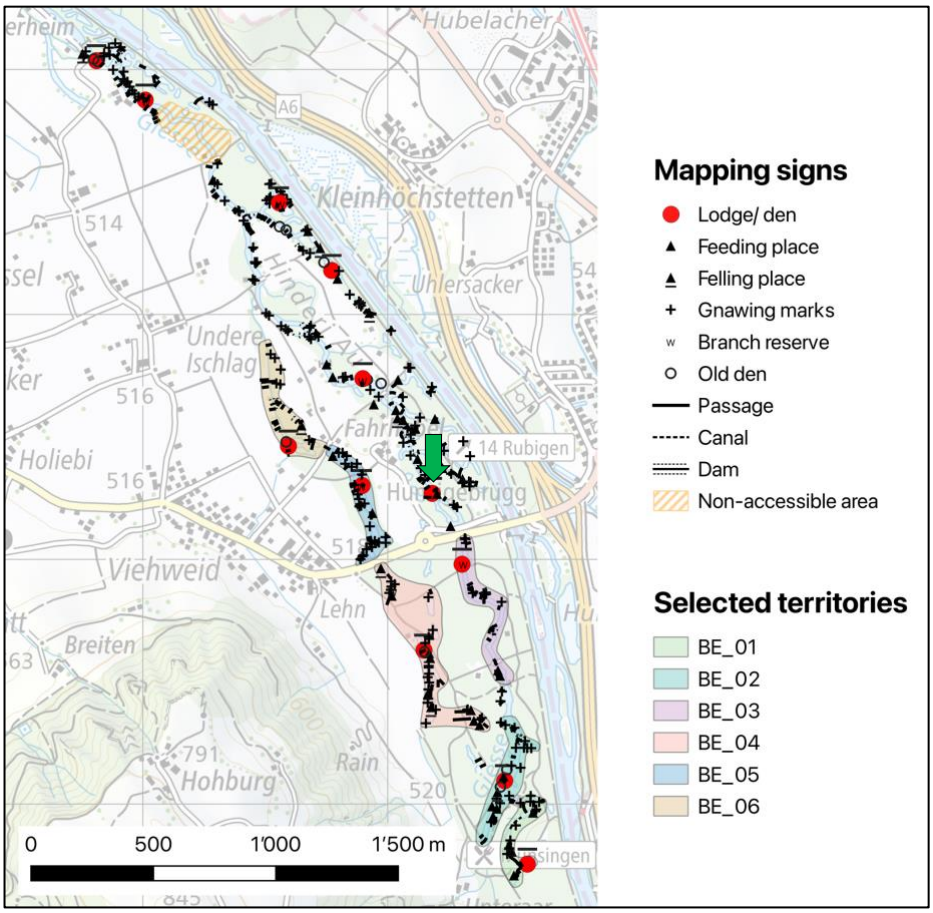

Figure 3: Mapping of all beaver traces found in the study site. The territories which were selected for the following steps are indicated as green polygons. The den whose activity remained unclear is indicated with a green arrow. The section which was inaccessible for the survey is marked with an orange striped polygon. Background: © Swisstopo

All lodges and markings were first noted on printed maps at the 1:10 000 scale (© Swisstopo) and then digitalized using QGIS (Figure 3). The collected data was then evaluated to assert the territory boundaries. To make sure, the found territories were used by families and not individual beavers, we used a variety of select traits, such as abundance of traces and also variance of teeth size in gnawing marks. Adult beavers have teeth with a width of 10 mm ± 3.2 mm while juvenile have widths of 5.6 mm ± 1.0 mm (Angst et al., 2023). As the differences can be marginal, we only counted a territory as family territory, if we found both wide and small teeth marks. This was to make sure, we do not interpret the gnawing marks of an individual adult beaver with small teeth as juvenile and subsequently the territory wrongly as family territory.

In total, 415 different traces of beaver were found. Besides 11 active lodges we found 9 abandoned lodges while the activity in one den remained unclear (green arrow). In contrary to the other lodges, this den consisted of a burrow into a steep riverside but without any winter reserves. Due to the activity in the vicinity, it was still scored as an active den/ territory, but as we were not sure whether we actually found the actively used den of this particular territory, we decided against using it for our further study.

2.2. Installation of the camera traps

Based on the preliminary survey we then chose territories where we set up camera traps. In each territory we installed three camera traps. One camera trap was positioned near the active beaver lodge. For all the cameras placed at the lodge, we positioned the camera along a path created by the beaver itself. Often this path was mainly used to get to the top of the burrow. The other two camera traps were each installed near the expected territory boundaries. These cameras were placed at locations where we expected beaver activity to be high. Points of high activity are for example exits out of the water, paths leading the beaver into the forest, territory markings, feeding places or crossings between two water bodies.

With a total of 18 available cameras (all model Reconyx Hyperfire 2) and three cameras needed for each territory, we were limited to six territories in total. Since activity can fluctuate considerably and the cameras were left in the field for 45 days, it was not feasible to re-locate the camera traps to another territory to increase sample size. In previous studies, the camera traps were left for 10 days. As we were also interested in the visiting beavers and not only the family members, we decided to use a longer study duration, mainly because we expected these visits to be rather rare.

Figure 4: The camera trap setup to identify the beavers by its tail. The camera traps were secured with a cable and a small lock. Additionally, information about the study with contact details was attached to each metal frame.

To increase trapping rate at the territory centers, sugar beets were added to the camera traps located close to the lodge. Per camera, around 5 kg of sugar beets were added once on day 34 and again on day 39. To avoid attracting beavers of opposing territories to the same camera and possibly instigating territorial fights, sugar beets were only added to the cameras at the respective territory centers (lodges). Thus, adding sugar beets was only aimed at helping to resolve each individual's territory but not it's movement across camera traps.

As it is rather difficult to identify sex and age in beavers, let alone identify them, a specific camera trap setup is needed. We used a method first proposed by Schwaiger & Schwemmer (2012) and then further optimized by Minnig et al. (2016). The cameras are situated along paths that the beavers use on land, elevated to a height of 1.8 m using a metal construction and point vertically to the ground in order to get a near-planar image of the beaver's tail. We placed a ruler on the ground which is part of the captured image to get various measures of the tail. Cameras were secured with a lock and an information note was added to the camera mount.

The cameras were set to capture images day and night with a sensitivity setting of "Very high". For some cameras that were particularly exposed to gusts of wind, this setting was later re-adjusted to "medium". All cameras were set to take 5-image series in the rapidfire interval. A wait time of 10 seconds was used, and the cameras were set to take an additional timelapse series to get periodic measurements of the temperature.

2.3. Camera trap images

The resulting batch of images was first stripped of all empty frames, caused by faulty camera settings, gusts of wind or strong heat haze. Using Megadetector (Beery et al., 2019) and the software Timelapse (Greenberg, 2020), we selected all 5-image series where an animal was detected with a certainty of 80% in at least one image.

In the next step, all photographed species were manually annotated, together with other information (see Table 2), using Timelapse (Greenberg, 2020). Lastly, the images were also aggregated to events. If an animal passing underneath the camera would trigger the camera a second time, after the sleep timer reset, the two separate image series were aggregated to one single event. This was also the case, if a beaver would pass in front of the camera and then again within a 10-minute interval.

Table 2: Data recorded for every camera trap event. The images were annotated individually in Timelapse. The individual data annotations were then aggregated into the distinct events using R Studio.

Location	Location (territory and position) of the camera trap	**Species**	Manually annotated species seen on the image.
Time	Time and date, extracted from the camera's metadata	**Direction**	Direction of the animal (where it came from and where it is headed towards)
Temperature	Extracted from the camera's metadata (°C)	**Individual**	Beaver individual annotated
Duration	Duration of the event from the first image with a beaver visible until the beaver leaves the camera frame again.	**Tail**	Manually set for images of an event that have the tail of the beaver fully visible (middle of the image frame and flat on the ground)

All events of beaver were then evaluated further to identify each individual using several traits of the tail. We used scars from territorial fights, colouring anomalies of the scales as well as the shape and fat percentage (visibility of the vertebra) of the tail to distinguish between individuals.

The size of the tail was used to differentiate between the age classes: juvenile (younger than one year), sub-adult (younger than two years) and adult (two years and older). Secondly, we also used these measurements to control for possible false identifications. Images used to measure the beaver's tail were first selected on three conditions:

- The tail was fully inside the cameras field of view (no clipping with the edge of the frame)
- The tail was near the center in order to minimize skewing due to perspective
- The tail was flat on the ground and not elevated, turned or angled in any way

Using a python script (Van Rossum & Drake, 2009) adjusted from Eppel (2022) based on Fast R-CNN (He et al., 2017), a commonly used algorithm for instance segmentation, we could extract several measurements of the beaver's tail semi-automatically. The algorithm was trained with 376 images from the study of Meier (2023). Semantic maps for beaver and its tails were created using CVAT.ai (CVAT.ai Corporation, 2023) and the algorithm was then trained over 26'000 training steps. The trained algorithm could then detect the beaver tails automatically and measure the length of the tail and the width at 20 positions (see Figure 5 for a detailed explanation). In the case of the algorithm not recognizing the tail accurately, manual corrections were made. Using the ruler placed on the ground, the images could then be scaled to actual measures (pixels to cm) using Fiji/ ImageJ (Schindelin et al., 2012).

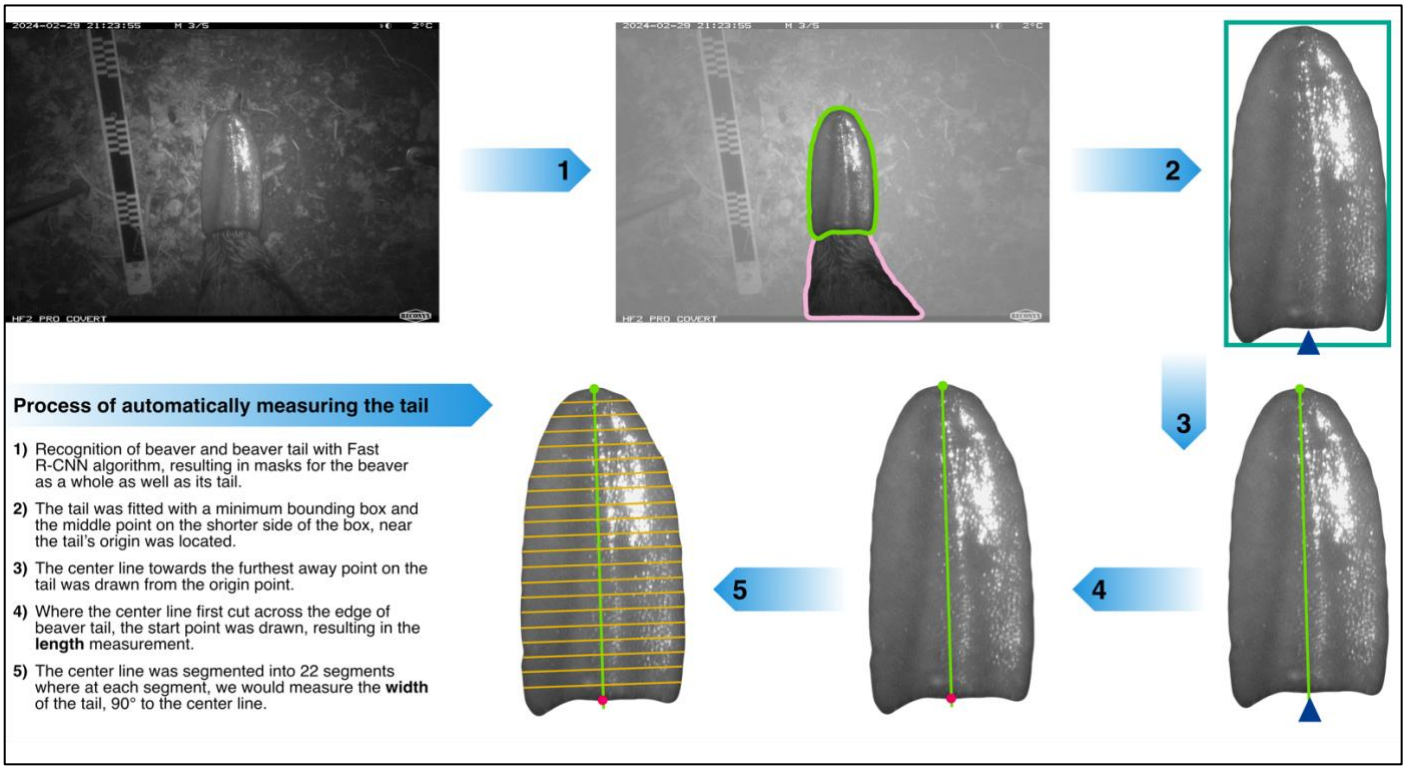

Figure 5: Description of processing steps to calculate length and widths of the beaver tail.

2.4. Data

All statistical analyses were carried out in R Studio 2024.04.0+735 (R Core Team, 2024) with R version 4.4.0.

Temperature data

The temperature measurements of camera traps located at the upper border of BE_01 and lower border of BE_05 were extracted from the timelapse images taken at an interval of one hour. The measurement was averaged between both camera traps before the mean of each day was calculated. As these two cameras were placed at opposite ends of the study area, we judged the mean of their measurements should be representative of values across the whole area.

Tail measurements

The measurements of the tail were used for two purposes: first, they were used to control for potentially false identifications. Width measurements were averaged across all width measurements bar the five at the start of the tail and the four at the end of the tail to reduce measurement error. The width was then plotted against the length of the tail and coloured by the annotated individual. All the images for which the measurements did not match the rest of the cluster were then re-evaluated a second time (see Figure 6).

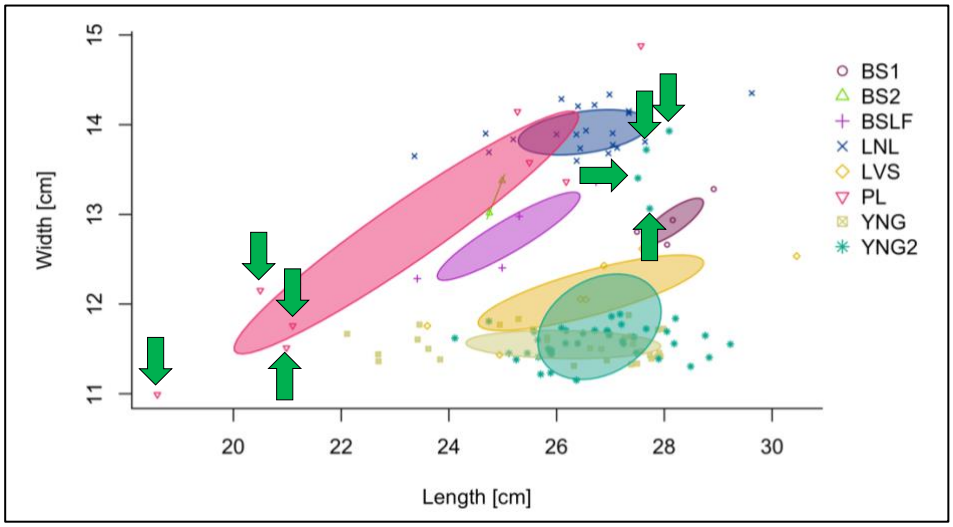

Figure 6: Re-evaluation of measurements. Indicated by the green arrows are measurements that were re-evaluated using the respective images.

Secondly, the average and confidence interval of each individuals' measurements were then used to assign the beavers to an age class (Table 3). Our classification criteria slightly deviate from the suggested values by Rosell & Pedersen (1999). This is owed to the fact, that we did not just take one measurement across the middle point of the tail but instead, an average across about 50% of the tail in the middle area. The tail dimensions were then both plotted as a scatterplot and by calculating a PCA using the factoextra package (Kassambara & Mundt, 2020).

Table 3: Measurements of tail of the 3 age classes, adjusted from Rosell & Pedersen (1999).

Age class	Length	Average width
Juvenile	< 24 cm	< 11 cm
Sub-adult	24-27 cm	11-14 cm
Adult	> 27 cm	> 14 cm

Territory assignment

Based on each individual's capture history across the camera trap locations, an origin territory was assigned. If the beaver was captured at a camera trap in the territory center, the individual would be directly assigned to this territory. If a beaver was never recorded at a territory center, it was assigned to the territory in which it was most often found in. In the rare case of a beaver being found at two territory centers or across multiple territories in equal abundances, the temporal history was taken into account. In such a case, assignment priority was given to the territory which had sightings across more nights.

Individual history/ movement

For every individual, the history of movement was recreated using the recordings of the camera traps. Under the assumption that the individual would always return to its home lodge (territory center) during the day, we could re-create a simplified history across the study period.

Based on the coordinates of the camera traps, using the Swiss CRS LV95, the distance between each camera was then calculated. The calculations used the shortest path between the two points and did not take into account habitat permeability (see Figure 7). In combination with the individual's history, we could then calculate an approximate measure of the distance covered across all nights.

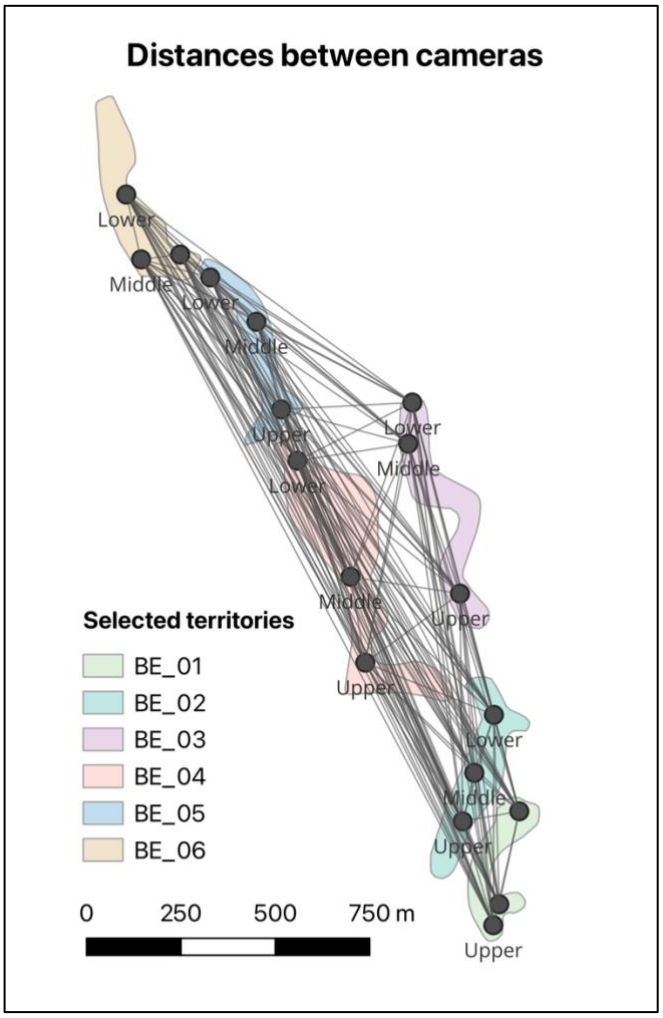

Figure 7: Network of all distances between cameras. Habitat permeability was not taken into account and thus, the distance between cameras was measured by shortest distance between them.

3. Results

Over the course of 45 days, a total of 145'000 images were captured by the cameras. Excluding empty images and events triggered by mice, a total of 1'703 events were recorded. Beavers were the most abundant animal with 856 events (Table 4). This was followed by humans, dogs & cats, moorhen and blackbird. More notably, otters were recorded seven times at four different locations and the European polecat was recorded 42 times at 11 different locations.

Table 4: Camera trap events per species, descending order from top to bottom and left to right. Images of mice were not counted and are thus not included in this list.

Beaver *Castor fiber*	856	Mallard *Anas platyrhynchos*	13
Dog *Canis familiaris*	156	Great tit *Parus major*	9
Human *Homo sapiens*	155	Otter *Lutra lutra*	7
Moorhen *Gallinula chloropus*	68	Robin *Erithacus rubecula*	5
Blackbird *Turdus merula*	49	Carrion crow *Corvus corone*	4
Polecat *Mustela putorius*	42	Eurasian jay *Garrulus glandarius*	4
Cat *Felis catus*	40	Roe deer *Capreolus capreolus*	2
Marten *Martes sp.*	32	Stoat *Mustela erminea*	1
Badger *Meles meles*	26	Chaffinch *Fringilla coelebs*	1
Human & Dog	19	Hedgehog *Erinaceus europaeus*	1
Red fox *Vulpes vulpes*	15	Songthrush *Turdus philomelos*	1

Looking at the trapping rate of the beaver, there was an average of 13 (± 8) events per night across all territories and cameras in the first 33 days (Figure 8). After the addition of sugar beets at the territory centers on day 34, we see a significant increase of the trapping rate to 34 (± 14) events per night ($t = -4.8916$, $df = 13.692$, $p = 0.00025$). In regard to the impact of temperature on the activity of the beaver, we found no significant correlation between the daily mean temperature and the activity of the beavers ($R^2 = 0.04779$, $p = 0.2216$) as seen in Figure 9.

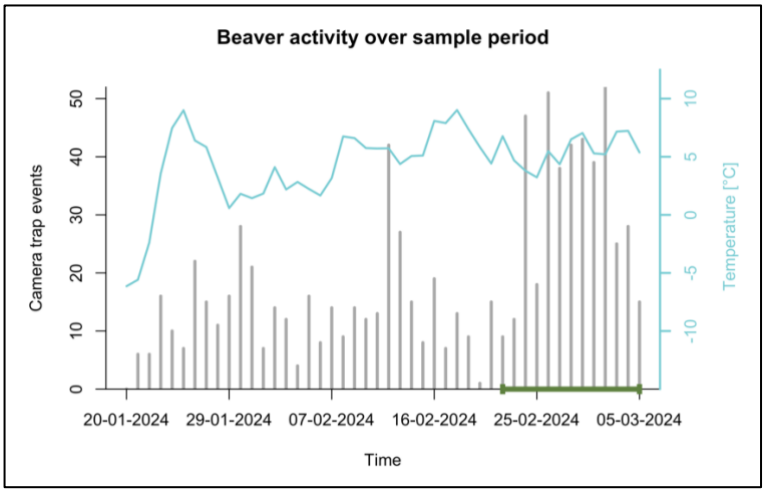

Figure 8: Beaver activity across the study period. The activity is approximated by camera trap events of beavers. In light blue, the average daily temperature is shown, measured by the camera traps located at the upper border of BE_01 and the lower border of BE_05. Sugar beets were added on day 34 and 39. The period where sugar beets were present at the territory centers is indicated by the green bar.

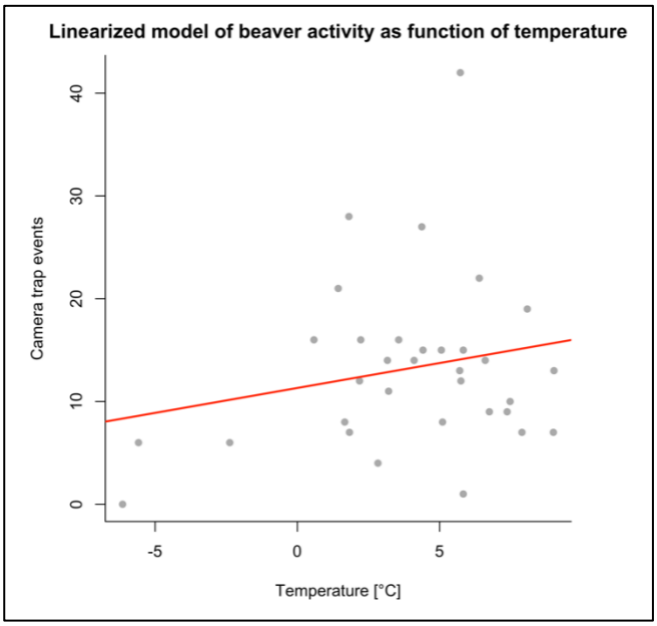

Figure 9: Beaver activity (number of camera events per night) as a function of temperature during the first 33 days (R^2 = 0.04551, p = 0.2332).

There were significant differences in the beaver activity in different territories (X^2 = 318.61, df = 5, p < 2.2E-16). The territories BE_04 and BE_01 had the lowest activity with only 12 beaver events for territory BE_04 and 72 events for BE_01 (Table 5). For territory BE_01, the events were only recorded at the lower territory border but not at the upper border nor at the center of that territory. BE_04 had no captures of beaver events at the center but events at both territory borders. All other territories had significantly more events distributed across all 3 cameras, the most being recorded in territory BE_03.

Table 5: Distribution of beaver recordings across territories and cameras. Numbers in bold indicate the total number of events across the whole 45 days. The differentiation between the first 33 days to the last 12 days where sugar beets were added to the territory centers are indicated in parentheses.

Territory	Upper Border	Center	Lower Border	Total
BE_01	**0** (0-0)	**0** (0-0)	**72** (39-33)	**72** (39-33)
BE_02	**5** (2-3)	**53** (7-46)	**190** (136-54)	**248** (145-103)
BE_03	**221** (164-57)	**10** (2-8)	**20** (13-7)	**251** (179-72)
BE_04	**10** (9-1)	**0** (0-0)	**2** (2-0)	**12** (11-1)
BE_05	**21** (11-10)	**64** (0-64)	**67** (16-51)	**152** (27-125)
BE_06	**70** (48-22)	**39** (0-39)	**12** (9-3)	**121** (57-64)

Of the 856 events involving beavers 697 (81.4%) could be individually identified. In the other cases, the beaver would trigger the camera, but no images of the tail were captured. This could be the case when:

- The beaver passed beneath the camera too quickly or just outside the field of view.
- The tail was angled or covered in snow so no marks could be identified.
- The beaver passed the camera too slowly or waited at the edge of the frame, thus when ultimately the tail would have been in the field of view, the camera was in the sleep timer.
- In some rare cases, the beaver investigated the metal posts of the trap before turning around.

Over the course of the 45 days, where the cameras were in the field, a total of 31 individuals were identified (see Figure 10 for examples).

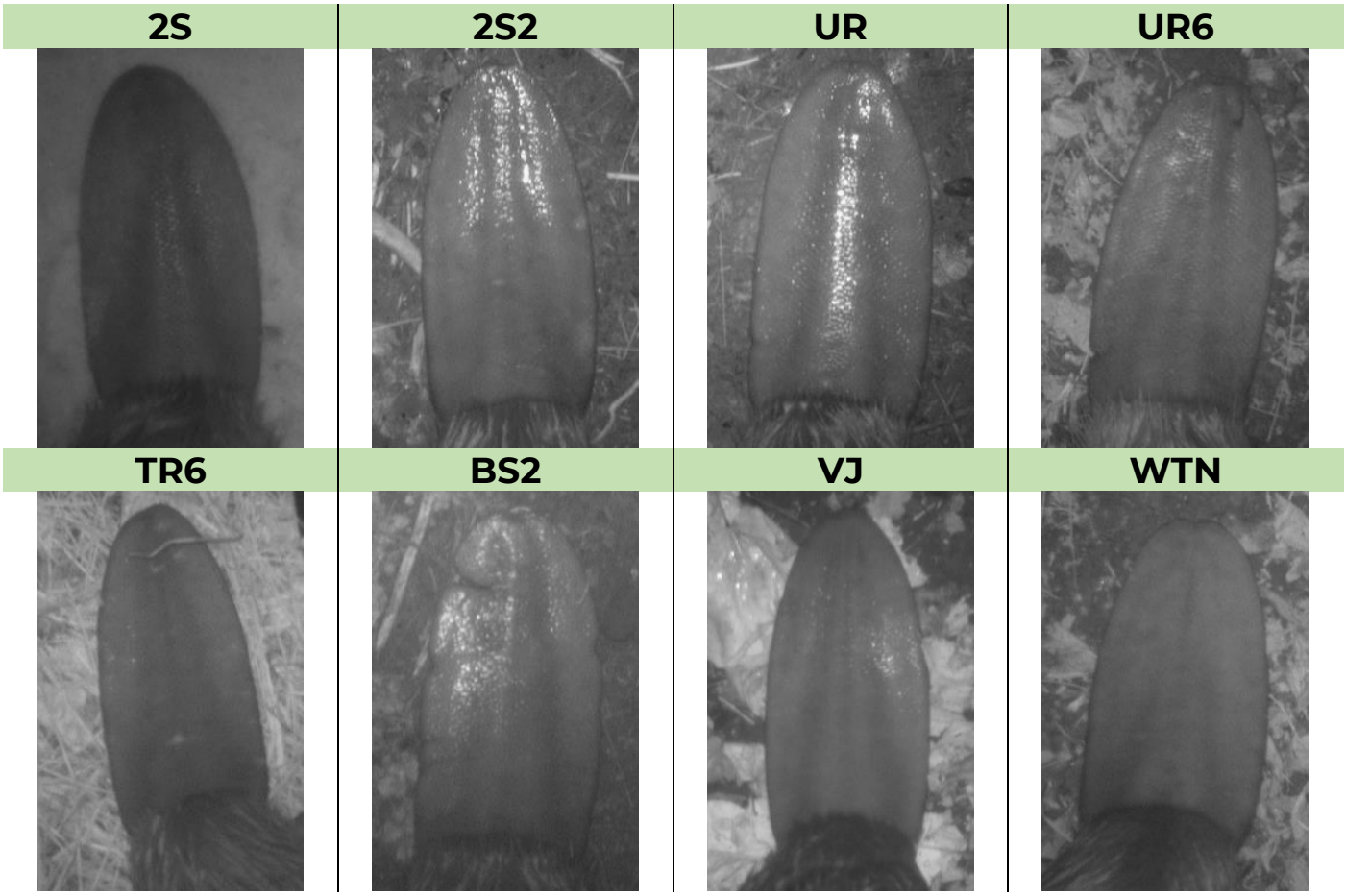

Figure 10: Overview of some of the observed individuals (8 out of a total of 31).

In the first 10 days, on average 0.48 new individuals were recorded per territory during each night (Figure 11). After this initial phase, new individuals were added at a lower but consistent rate of 0.16 new individuals per territory per night. The last new individual for a territory was recorded on day 44. As intended, the addition of sugar beets did not attract new individuals to the territories, as seen by the absence of a strong increase in the number of new individuals after day 33.

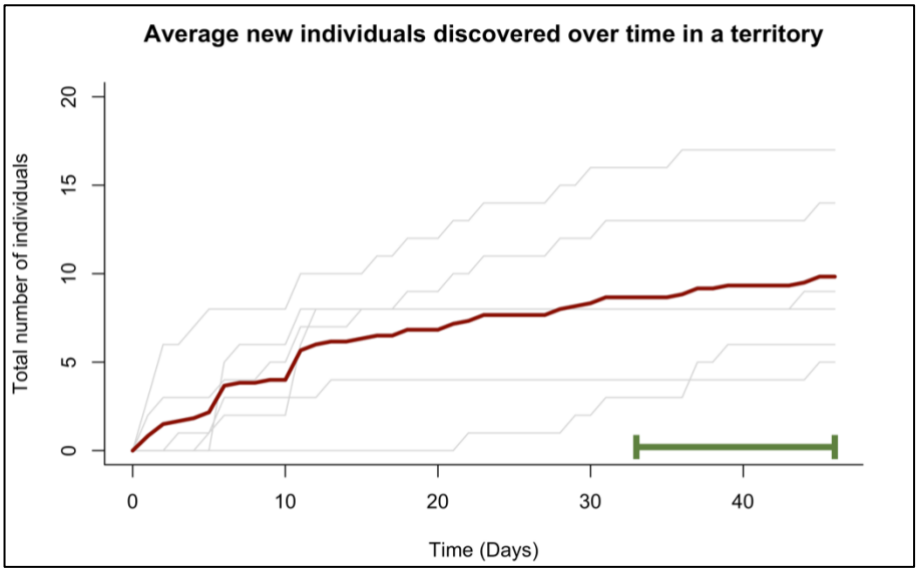

Figure 11: Average new individuals per territory over time. The average over all territories is indicated by the red line. Individual territories are indicated by the grey lines. The period of added sugar beets is marked by the green bar.

A total of 533 images were classified as usable for measuring the tail of the beavers. In total we found 2 juvenile beavers, 10 sub-adults and 18 adults. For one individual, no images of the tail were available to retrieve measurements. Age classes could be separated into 3 clusters with some overlap between the adult and sub-adults (Figure 12 and Figure 13). The length of the tail was on average 27.6 cm for adults, 25.4 cm for sub-adults and 22.0 cm for juveniles. The width was on average 14.2 cm, 12.5 cm and 9.5 cm respectively.

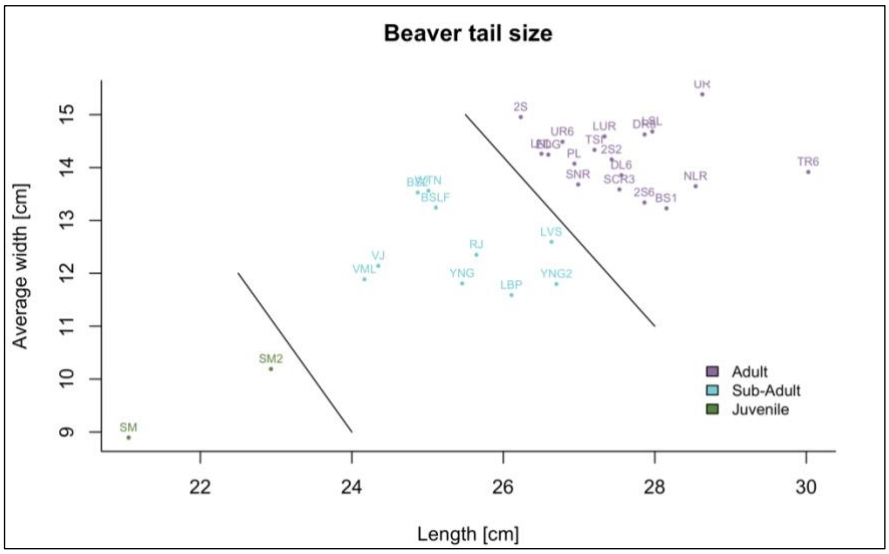

Figure 12: Scatterplot of each individual's tail dimensions. The width was averaged across the 11 innermost measurements. All measurements of an individual were then averaged.

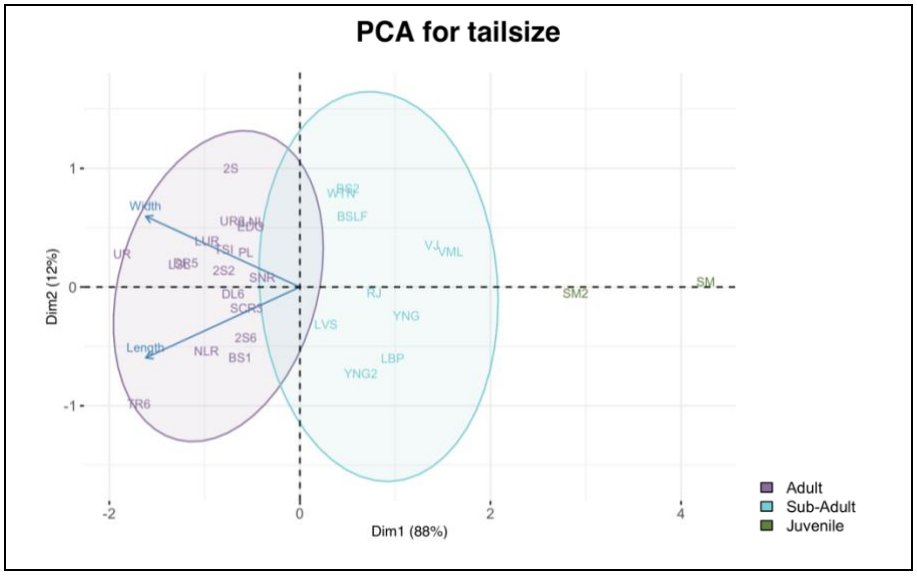

Figure 13: PCA for tail size. Calculation of the ellipse for juveniles was not possible due to only having 2 individuals.

3.1. Family size and age structure

Based on the locations of each recorded event, the individuals were then assigned to a certain territory (see Figure 14). Based on the observations made, territory BE_01 was abandoned with zero individuals. In BE_04 two adult beavers were recorded. BE_02 had eight individuals recorded consisting of three adults and five sub-adults. In BE_05 we observed the largest family size with four adults, two sub-adults, two juveniles as well as one individual of unknown age. In BE_03, we recorded three adults and two sub-adults. In BE_06, we recorded six adults and one sub-adult. Excluding the abandoned territory BE_01, we found on average 6.2 individuals per territory. We might not have found all individuals in BE_04; if we also exclude this territory, the average would increase to 7.25 individuals per territory.

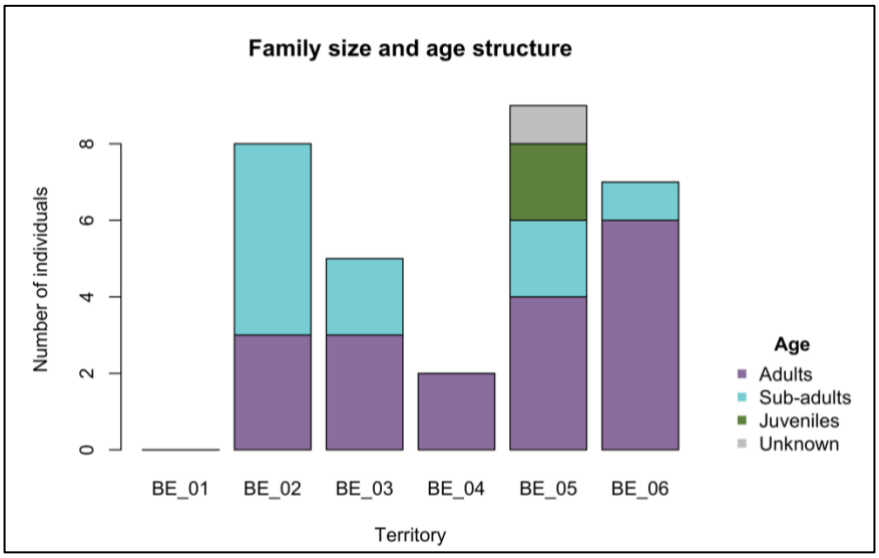

Figure 14: Family size and age structure found in the territories.

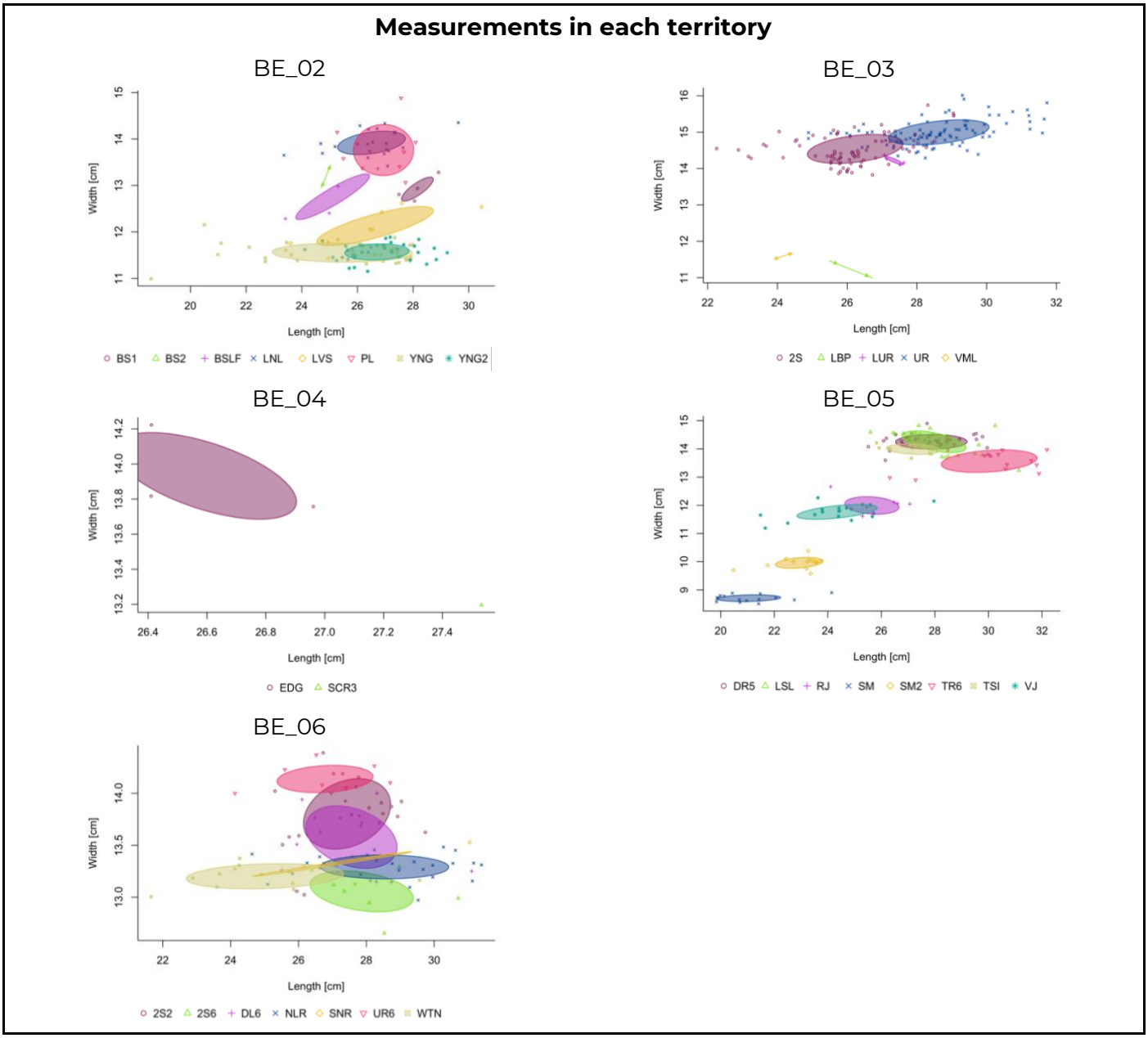

Figure 15 (A-E): Beaver tail measurements per territory. Differently coloured and shaped dots represent a different individual. Coloured ellipses represent the 95% confidence area of one individual's measurements.

3.2. Movement and territoriality

Combining the assigned territories with the observations made at each camera trap, we can identify potential territory overlaps (Figure 16). We looked at the origin territory of each individual, that was captured at a camera trap location to get the relative frequencies of each family at a certain location.

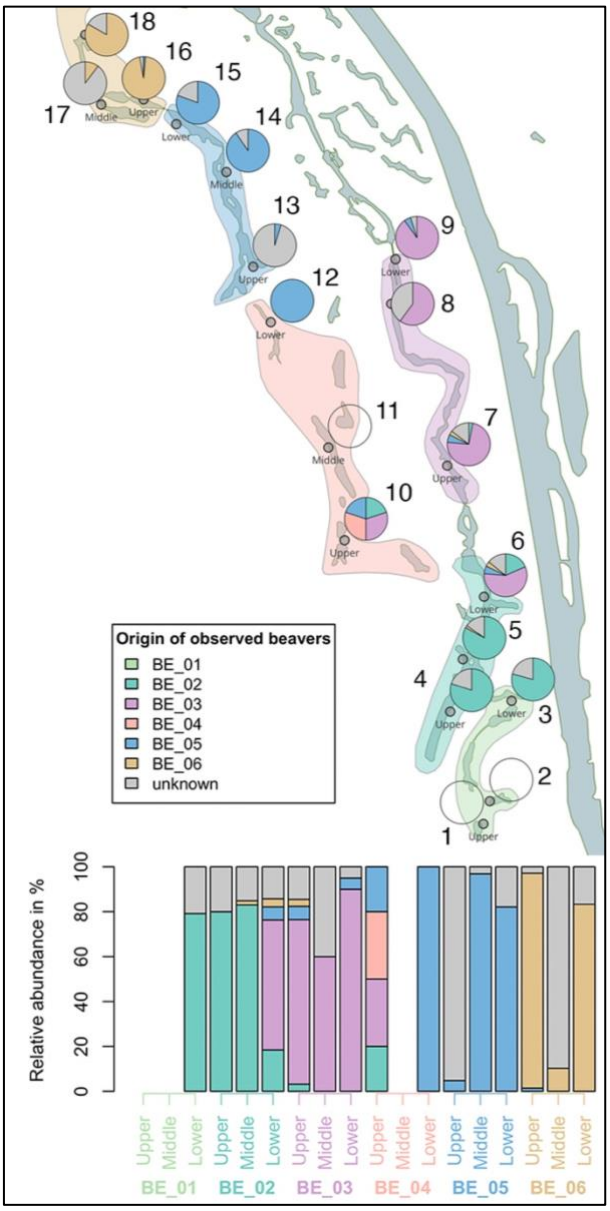

Figure 16: Territory overlap across camera traps. The bars represent, the relative frequencies of each family captured at the camera trap regardless of which individual we have seen specifically. Cameras without a bar (BE_01 Lower and Middle as well as BE_04 Middle) did not have recordings of beavers throughout the study period. Grey bars represent the frequency of beavers that could not be identified and thus, we do not know the origin of.

Individuals of BE_02 were almost equally abundant at the camera traps BE_01 Lower (camera 3 in Figure 16), BE_02 Upper (4) and BE_02 Middle (5). In BE_02 Lower (6) we recorded mostly individuals from territory BE_03 but there were also visits from BE_02, BE_05 and BE_06. At BE_03 Upper (7), which was located downstream of BE_02 Lower, the distribution of origin territories was about the same with lower abundance of BE_02. At BE_03 Middle (8) and Lower (9), we exclusively recorded individuals from this territory. At BE_04 Upper (10), we found a mix of individuals from territory BE_02, BE_03, BE_04 and BE_05. BE_04 Middle (11) had no beaver recordings while there were only 2 passings of an individual of BE_05 at BE_04 Lower (12). Recordings of camera traps at BE_05 were exclusively from individuals belonging to this territory while in territory BE_06 there was only one intrusion from an individual of BE_05 at BE_06 Upper (16).

Looking at the territoriality of the individuals (frequency of getting captured inside their territory) throughout the whole study period, juveniles were captured always inside the territory borders. On average, sub-adults were captured most often beyond the home range, while, of all captures of adult beavers, 85% were made inside their home range (Figure 17). However, looking at individual records, there were several adults that had a lower territoriality than the lowest of the sub-adults.

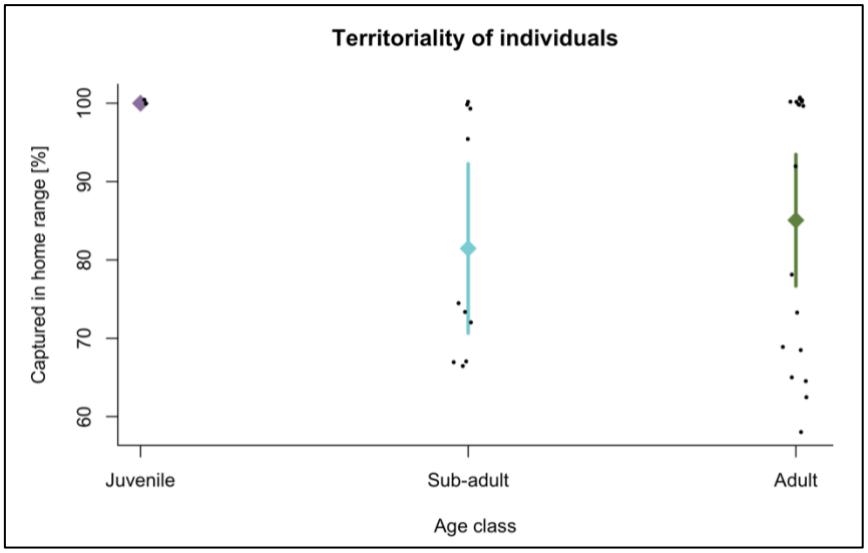

Figure 17: Territoriality of individuals of different age classes. The mean for each age-class is given by the coloured diamond with its 95% confidence. Individual measurements are represented by the black dots (scattered for better visibility).

Based on the individual's history, the distance covered during each night when the individual was seen, was then calculated. Juvenile beavers covered the least amount of distance with an average of 21.13 m (N = 2). This distance is particularly low, as juveniles were only once captured at a location different to their territory center. Sub-adults covered on average 593 m (N = 10) while adults covered around 612 m (N = 18). The largest distances covered during one single night were recorded by the subadult WTN and the adult 2S2 with 3439 m and 3115 m respectively. The adult 2S covered, on average, the largest distance per night with 1465 m, being recorded during 41 nights.

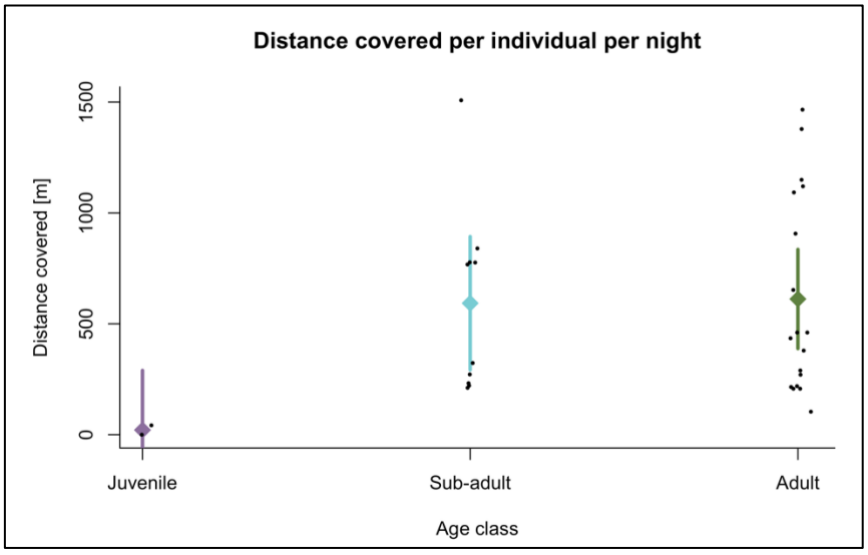

Figure 18: Distance covered by age classes. The mean for each age-class is given by the coloured diamond with it's 95% confidence. Individual measurements are represented by the black dots (scattered for better visibility).

4. Discussion

4.1. Survey of territories in the study area

Our survey conducted in the winter of 2023/ 2024 was in large part in accordance with the mapping of 2022 by Angst et al. (2023). The differences included two new territories while the other territories remained. In one territory, activity was unclear, and the exact location of the den could not be found for certain. This territory was therefore not used for all further steps. As seen later by the help of the camera traps, territory BE_01 turned out to be inactive, judging by the fact that no beaver camera events were recorded at the center and the upper territory border. As the lower territory border is frequented by individuals belonging to the adjacent territory BE_02, it is possible that the territory has been taken over. This would be in accordance with the many camera trap recordings of territorial fights along the border between the two territories (Kurt Grossenbacher, *personal communication*). Some of these video sequences during the winter just prior to the beginning of the study showed a female with significant injuries. The sudden disappearance of this individual leads us to believe it succumbed to its injuries, which would further reinforce the potential explanation that territory BE_01 was abandoned only shortly before we set up our camera traps there.

As expected, the territory boundaries were more fluctuating than the location of the lodge itself and, in general, more difficult to determine. As we judged the territories by the presence of signs, the territory boundaries were set where the number of signs was markedly lower between two occupied beaver lodges. In a system of beaver territories where the territory density is high, there is less of a gradient in sign abundance by distance from the lodge. As seen in some areas of our survey, there is an almost continuous density of signs across a water body, where multiple territories are placed. Determining the territory border at the right place can thus be challenging and the set boundaries should therefore be taken with caution. Our camera trap records suggest that at least some borders might have not been placed at the correct location to at least some extent.

4.2. Activity at camera traps

In regard to our proposed results, the location of the cameras is the most sensitive variable of the used method. We found significant differences in beaver activity not only across territories, but also across locations inside a particular territory. In territory BE_04, activity was in general very low. For the camera at the lower boundary, this could potentially be explained by the fact that the camera was placed beyond the actual territory boundary and beavers only venture out that far when exploring. In fact, at that particular place, only an adult from another territory was recorded by this camera twice. The camera which was located at the lodge of BE_04 did not record any beavers throughout the study period. One potential explanation is that the path around the lodge, where the camera was placed was only rarely used by the beavers. Since they were not attracted by the sugar beets either, the alternative explanation is that this was not actually the active lodge and/ or the beavers never caught on the bait. Due to the thick vegetation, accessibility and visibility along the pond was limited and the actual lodge could therefore have been missed.

For future studies using this method, we suggest that camera traps are placed preferably between waterbodies where the passing of the beavers is constrained to very narrow pathways. If this sort of location is not available, activity at the site should especially be tested in advance. As the beaver's activity pattern can fluctuate and are predominantly dictated by resource availability, there is a small chance remaining that even with a prolonged test phase, the camera traps do not cover a lot of activity.

Nevertheless we suggest at least two nights of preliminary tests with camera trapping before finally settling on a site. This test period should however be prolonged if the temperatures drop significantly below zero, as activity could change with the water bodies freezing.

In our study period, we only had sub-zero temperatures for the first few days. This meant that the ponds froze and movement for the beavers was therefore constricted to running water bodies (Korbelová et al., 2016). As the most active territories were situated along running water bodies that did not freeze completely, there was a negligible impact on the observed beaver activity in lower temperatures. This was confirmed by the non-significant correlation in the linear model in Figure 9. However, if there were more days with low temperatures and the territories were located at stationary water bodies, the activity of the beavers might have a stronger positive correlation with temperature. This would be in accordance with the study on seasonal variation by Bartra Cabré et al. (2020) and Korbelová et al. (2016). The chance of the water body freezing over should therefore be taken into account when deciding on a study duration for this method.

Temperature and weather patterns in general are obviously difficult to predict over several days and weeks, so we would recommend future studies encompass longer study periods, at least longer than 10 days. Our study period did not include any major storms, strong or prolonged precipitation or flooding, so we cannot comment on the effect those might have on results. For example, Bartra Cabré et al. (2020) showed that beavers had increased daily activity periods under wetter weather conditions. On the other hand, floods might negatively impact activity. As shown in Figure 11, the saturation of new individuals found in a territory is reached after around 20 to 30 days. However, there were some differences across the territories. Ultimately, the length of the study period should reflect the main purpose of the study. If the interest lies mainly in finding all individuals belonging to the territory, study duration can be reduced while sugar beets or apples can be added to increase the trapping rate as done in previous studies (Meier, 2023). We emphasize the importance of only baiting at camera traps close to the lodge. Adding bait to camera traps at the territory borders could instigate territorial fights by luring conspecifics into the territory. By baiting at the territory centers, we might also influence the movement of individuals as foraging movements are reduced. Thus, this leads to the loss of information of the movement of individuals across territories and the relationship between territories. Since we were not only interested in the family size but also in the movement across territories, we split the study period in a longer, un-baited period of 33 days, followed by a 12-day period with baiting at the territory centers.

4.3. Identification and ageing

Recently, there have been efforts from multiple ecologists and managers to move from invasive methods of studying beaver movement to non-invasive methods such as camera trapping, using features of the tail for individual (and automated) identification. Hinds et al. (2023) focused on the pattern of scales on the beaver's tail using a SIFT algorithm. However, the nocturnal habits of the beaver imply several challenges for this method. As the camera traps use infrared to not to disturb the animals, they do not provide information about colour. More importantly, these cameras often suffer of low resolution, especially when fine details such as the scales of the beaver's tail are important. While it has been shown that the scales of the beaver (Hinds et al., 2023) could be a reliable parameter for automated identification, the need for good images might make it not robust enough as a single factor in identification.

In our study, we looked at other factors of the tails such as its scars and dimensions. Identification of beavers using the various features of their tail was possible in around 80% of all events. The other 20% that could not be identified was mostly due to the beavers crossing the camera too fast, in between the sleep timer, or outside the image frame. In general, our annotations were all done

manually and relied mainly on marks and coloring anomalies. The shape of the tail was only used in rare instances as a characteristic attribute, while the tail size was only used as a control of the visual identifications. Identification was more difficult for beavers that lacked any sort of nicks and marks on the tail. This was mostly the case for sub-adult and especially juvenile beavers. With increasing age, nicks and marks are more common and therefore, adult beavers were generally easier to recognize and with a higher certainty. Overall, identification should be appropriately accurate, especially in the light that adult beavers are the most interesting to recognize.

Out of all images submitted for measuring the dimension of the tail, approximately 75% could be measured fully automatically using our algorithm based on Fast R-CNN. Thanks to a semi-automated workflow, which allowed user input in case recognition failed, all images could be processed quickly. The measurements were used to annotate one of three age classes for each individual. As we measured an average width of the tail and not the width at the middle point, our measurements for each age-class differed slightly from the measurements proposed by Rosell & Pedersen (1999). To some extent, the observed size difference could also be due to regional differences. Regardless, three distinct clusters could be identified, which allowed the ageing of all but one individual. For this individual, we were not able to retrieve any images that allowed accurate measuring.

While the tail dimensions were appropriate to age the beavers, using them as a way to identify beavers was not feasible. This was mainly caused by the marked variation in tail length between but also within cameras traps. As the width measurements were substantially less variable, we can rule out false calibration or false identification to some extent. We argue that instead, this method of measuring the size of the beaver tail is prone to measurement error if the tail is not flat on the ground or the camera itself is not aligned properly to the ground plane. Either possibility results in a skewed image of the beaver tail in the Y- but not the X-axis. With a conservative method of selecting the images that are measured, we limited the measurement error in length to some extent, but it was still significantly larger than the width measurement, even when accounting for the larger measurement itself.

As a single measure, the dimensions of the tail are therefore not sufficient to identify beavers yet accurate enough to age the beavers. We argue however, that in combination with scale pattern recognition, nicks and colouring anomalies, automated identification based on camera trap images could be possible, especially with increasing computing power. The ideal solution is yet to be found and thus further research is necessary, mainly in how to integrate scale pattern recognition in a real-world scenario with camera trap images. It possibly necessitates improving the quality of images and the measurements through better controlling of the environment. For example, one could try to add a wooden panel on the ground with a raster to correct for skewing due to perspective in retrospect. This would also significantly improve the measurements and help with automated recognition of the tails. On the contrary, we argue that it could be difficult to implement this as it is difficult to add a large wooden plane at some of the camera trap locations due to the size needed. It would also need some testing on whether the beavers would actually walk over the wooden plane or divert to natural ground.

Additionally, as tested by Dytkowicz et al. (2023), adding an external lens to the camera trap could help further improving the image quality. In their study, Dytkowicz et al. used a camera height of 1 m with an external +1 diopter attached. Based on the problems we encountered with perspective skewing, we suggest trying at a more elevated position with a stronger magnification. This should provide a higher resolution of the scales while maintaining the less skewed perspective.

4.4. Family size & age structure & movement

Of the six territories that we studied, five were actually occupied. On average, 6.2 individuals were found in these five remaining territories. In territory BE_04, the camera traps were seemingly not positioned ideally, as seen by the low trapping rate throughout the territory. Judging by observations made by Kurt Grossenbacher (*personal communication*), it is likely that we missed some individuals in this territory. If we exclude this territory too, the average across the remaining four territories increases to 7.25 individuals. Regardless of whether we include this territory or not, our average family size is slightly higher than the estimate used in the national survey (Angst et al., 2023) and even more so, the average found by Meier (2023).

Meier (2023) also found family sizes up to eight individuals, suggesting there is a possibility that we captured three very large families by chance. Since the territories are located in the highest beaver territory density of Switzerland, our observations would also be in accordance with the study of Mayer et al. (2017) indicating that the delay of dispersal could lead to larger family sizes and are subsequently a natural consequence of very high densities. Looking at the age structure of the families, we found a trend towards more than two adults. Of all occupied territories, all but the territory BE_04 held more than two adults. Most notably, territory BE_06 consisted of six adult and one sub-adult beavers further complementing the hypothesis by Mayer et al. (2017).

We recognize our sample size was relatively small, and thus these results could just be an exception, but we still consider it of interest to further clarifications. A family consisting of 6-7 fully grown adults will likely consume more resources and potentially also differ in feeding strategy (Zahner et al., 2020). This would also generally indicate a significant change in the life history of the beaver and is further hinted at by the low number of juveniles observed in the territories. However, this could also be due to the fact that juveniles tend to be shier and thus less likely to get caught by our camera traps. As they were attracted to the cameras at territory BE_05 using sugar beets, it is likely that there were simply no juveniles around in the other families. This would be in line with observations made across the study site, where no juveniles were observed throughout the year (Kurt Grossenbacher, *personal communication*).

A change in life history could also mean significant changes in spatial and territorial dynamics. Our results of territoriality and movement remain very simplistic due to limitations by the number of camera trap locations and trapping rate. Nevertheless, we could show that there can be a strong overlap between territories and some individuals roam exceptional distances across several territory borders. Juveniles in general are expected to roam the least, as they mostly stay close to the lodge. The fact that territoriality and movement for adults and sub-adults were similar in our study could be explained by the fact that many adults still lack the dominant status and thus still roam more freely beyond territory borders, in search of their own territory. Again, this would support the hypothesis by Mayer et al. (2017) that offspring delays dispersal as there is no free territory available. Overall, though, to study the beavers' movement pattern in more detail, more camera traps per territory would be necessary as we lack in spatial resolution.

It remains to be determined whether camera traps are the more effective solution in absolute terms, as opposed to invasive methods such as radio tagging the individuals. We argue that with the on-going improvements in camera trap and automated recognition of individuals, the non-invasive method should be preferred, in accordance with the 3R-principle (Russell et al., 1959). Invasive methods might still be necessary for specific instances where there was a need for a more continuous resolution both temporally and spatially.

4.5. Bigger picture

Beavers have rapidly increased in number across Europe after their widespread reintroduction. In some areas, the population is, however, slowly approaching carrying capacity. With that, less and less territories are up for grabs and thus, it is becoming increasingly difficult for offspring to find areas to disperse to. As shown by Mayer et al. (2017), beavers can delay their dispersal for up to 7 years, increasing their likelihood of establishing a territory of their own successfully at the cost of the overall reproductive rate.

As a natural consequence of the increase in beavers, there has also been an increase in conflicts between humans and beavers. In face of the decision by the Swiss government to allow easier lethal removements of the beaver in conflict zones (Angst, 2010; Angst et al., 2023), we highlight that especially in areas of high territory density, this measure will likely only be of short effect. As seen by the frequent movements across territories by sub-ordinate adults and as observed following actual removals in Bayern (Angst, 2010), newly available territories will most likely get re-occupied within a short period, thus highlighting the need for more durable and long-term solutions. Such measures include protecting fields or trees, regulating beaver dams or protecting important infrastructure (Angst, 2010). Effective and sustainable long-term measures should be informed by accurate and precise demographic data, to allow us to leverage the benefits that beavers provide to their ecosystems, adding a valuable component to conservation (Angst & Auberson, in prep.). We thus highlight the importance of maintaining a scientific focus on the Eurasian beaver even though it is not under imminent threat itself. Understanding the beaver better is key in restoring and maintaining river corridors.

5. Conclusion

Using three specially mounted camera traps per territory in a system of six adjacent territories proved to be an effective method to measure size and age structure of beaver families. The dense packing of cameras in the area allowed us to gain insight into rare events such as the venturing of individuals beyond their territory borders. Across the 5 occupied territories, we found an average of 6.2 individuals per family. Seeing that for one territory we possibly did not find all individuals, our family sizes are bigger than previous estimates for family size in Switzerland. Furthermore, we also found a shift in age structure of the families, with up to 6 adults in a family. As our study system is located in the area with the highest density of Switzerland, our findings are in line with the findings in Norway, where offspring delays dispersal for multiple years. Additionally, we have found evidence that the delay of the offspring's dispersal could lead to an increase in family size.

Nevertheless, our findings do not yet justify re-evaluating the estimate of 5 individuals per family that was used for the national beaver survey. As found in a previous study, family size is significantly smaller in low territory density, which balances out the large family size in high density. By our optimized set-up of camera traps in a system of territories, we were able to mitigate previous uncertainties on intrusions of individuals of adjacent families. Overlap of territories and intrusions into and even across territories was captured surprisingly often, considering that the beaver is a territorial species.

Our findings generally point towards changes not only in the life history of the beaver but also its ecology as a whole. Density-dependence is often the cause of slower population growth, but it is rare to be able to study this phenomenon in the wild on a large mammal. Further studies on this change are therefore not only in the interest of understanding the beaver better to leverage its conservation benefits, but also for a better understanding of basic ecological dynamics.

6. Acknowledgments

I would like to thank my supervisor Stefano Canessa for the support throughout the project and Christof Angst who not only provided me with the idea for the project to begin with, but also helped me massively in all aspects of the project. I also want to thank Silvan Minnig as well as Christof who provided me with part of the materials, namely camera traps and the metal frames to mount them. I want to thank Manon Meier whose work I could continue and profit from, namely in providing me with the camera trap images that I could use to train the algorithm on. I want to thank Kurt Grossenbacher for the insightful discussions and that he was willing to share his incredible knowledge of the beaver territories in the Belpauen. This work would not have been possible without the generous helping hands of friends and family. Thanks to Shaquille Mathys, Michael Wyss, Janis Steiner, Dominik Epli, Valeria Benz and my dad Bernhard Stettler for helping in the field. Another big thanks goes out to Markus Lüscher who provided me with all the sugar beets. Last but not least, I want to thank my mother, Caroline Kan, for her invaluable corrections to my thesis.

7. Literature

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