A semi-automated method to study family size and age structure of the Eurasian Beaver *Castor fiber*

Master thesis, Science Faculty, University of Bern

2026

handed in by

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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 1922 (Stocker, 1985). Based on this timeline, much of our knowledge about the species was gained during a time of marked population growth well below carrying capacity (D. J. Halley et al., 2021). 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?

Here, our focus lies specifically on the family size and age structure of beaver families at high territory densities. Using a specific configuration of three camera traps per territory, we were able to identify and age beavers based on traits of the beaver tail. However, identification based on scars and colouring anomalies of the tail requires considerable manual work and expertise. Hence, we developed methods to reduce the manual work involved by using a series of algorithms and machine learning. Going from an almost fully manual analysis-pipeline to a computer-assisted workflow enabled us to more efficiently identify individuals and thus allow analysis on a larger scale.

Overall, we investigated a system of 30 territories found in the area of the highest beaver density in Switzerland. With an average of 6.6 individuals per territory, the observed family size was larger than expected. In some territories, we could observe up to 16 individuals with strong overlap with other territories. Our assumption of a saturated population is further underlined by the high ratio of adult beavers as well as the observation of floaters, visiting up to 5 territories across the study site. All in all, this study identifies several factors in the beaver's life history which could be linked to density-dependence and could benefit the stability of a population at 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). Yet the interplay of driving forces behind it is far more complex than the principle itself. By studying density-dependence of the family structure, we tried to isolate one particular component that is potentially linked to slowing down population growth of the Eurasian beaver *Castor fiber*. The semi-aquatic mammal nearly went extinct in the early 19th century and our knowledge mostly comes from the time after its reintroduction, when the species was growing nearly exponentially.

In the field of conservation biology, the Eurasian beaver is often regarded as among the best comeback stories (Halley et al., 2012). At its lowest point in the early 1800s, the population was estimated at around 1,200 individuals, scattered across eight isolated subpopulations across Europe (Halley et al., 2021). Since then, the Eurasian beaver has reclaimed large parts of its original distribution. In Switzerland, where the beaver was absent for more than a century, the beaver has largely repopulated the Swiss plateau, with a current estimate from the national beaver survey in 2022 of around 4,900 beavers (Angst et al., 2023).

Benefits and conflicts

The increase in beavers is not welcomed by everyone (Kaphegyi et al., 2015). With the growing population, there has also been an increase in conflicts caused by or related to beavers (Angst et al., 2023). By building dens under or inside infrastructure such as flood protection dams or roads, their stability, stability can be undermined. Additional conflicts can arise by flooding of agricultural land or through direct feeding damage (Angst et al., 2023).

On the bright side, numerous cases have demonstrated that the beaver has a positive effect on many different species groups. As an ecosystem engineer, the Eurasian beaver can construct habitats according to its own preferences by building dams in small rivers (Rosell et al., 2005; Rozhkova-Timina et al., 2018). The modulation of the riverine habitats has a significant impact on biotic and abiotic characteristics in the surroundings, which can benefit a wide range of taxonomic and functional groups, including, but not limited to, terrestrial and aquatic invertebrates, fish, amphibians, birds and water plants (Rosell et al., 2005). Damming of rivers by beavers has also been shown to benefit water management as it helps in retaining water upstream, thus reducing the risk of both severe floods and droughts (Puttock et al., 2021).

Such direct and indirect benefits for nature and humans provided by the presence of beavers have long been recognized. Today, conservation strategies can even include the beaver as a helping force for habitat restoration (Castro et al., 2017, Angst & Auberson in prep.). Yet, given the broad spectrum of benefits and problems caused by beavers, it should be no surprise that the species is currently the object of controversial debates (Kaphegyi et al., 2015). In winter 2025, the federal hunting ordinance was revised, allowing the culling of beavers if they cause considerable damage that cannot be prevented with reasonable protective measures (Schweizerischer Bundesrat, 2024). Since such interventions are „individual measures“ on single beavers, indicating a certain number of animals from a local population, it is crucial to know how many animals are to be removed. However, to sustain a healthy population, such actions should stem from well-informed decisions. Exact estimates of the population size and dynamics are therefore a necessary foundation for informed, rational management decisions.

Knowledge gap

Up to this date, much of the knowledge about the Eurasian beaver was gained during a period in which the species was expanding throughout Europe (Halley et al., 2021). Now that, as of 2026, the population is reaching carrying capacity in some regions, the question arises whether increasing density might cause shifts in life history and ecology. The knowledge about such changes would be in the interest of understanding density dependence but also future management decisions, especially when these management decisions include lethal measures.

In Switzerland, the current population estimate from the 2022 national survey (Angst et al., 2023) is based on indirect observations of signs of beavers. Territories are differentiated into individual/ couples territories or family territories. Individual/ couples territories are estimated to hold 1.5 individuals, whereas family territories are estimated to consist of five individuals on average (Angst, 2010), comprising two adults and two generations of offspring. These estimates have been defined in accordance with the general knowledge of the family structure in the Eurasian beaver (Rosell & Campbell-Palmer, 2022).

However, a recent study conducted in Norway suggest that in areas with high population density, offspring might delay dispersal beyond the typical two years (Mayer et al., 2017c). With the offspring staying around longer in the territory, family size could increase under high population density (Rosell & Campbell-Palmer, 2022; Runge, 1999). Under such conditions, we would then also expect to observe more than two adults. The population model of Molini et al. (1980) additionally suggests that at high density, a population could consist of up to 20% of floaters. These individuals do not belong to a specific family but move across territories, a dynamic observed in several studies (Crawford et al., 2008; Havens, 2006; Svendsen, 1980). However, the overall behaviour of floaters remains poorly characterized, not only for beavers but for animals with complex social structures in general (Huck & Fernandez-Duque, 2023).

In Switzerland, Meier (2023) compared family sizes in regions with high and low population densities using camera traps. Families were larger at high population densities; however, the average family size at both densities was lower than the five individuals used as an estimate by the national survey (Angst et al., 2023). Additionally, with an average of 2.3 adults per family at high population density, the study found no substantial evidence for delayed dispersal. However, as the study did not investigate all adjacent territories at a site and the families were only sampled for 10 days, some individuals might have been missed or misassigned.

To address these limitations and obtain a more reliable estimate of family size and dynamics at high population densities, we examined a system of adjacent beaver territories. By using an optimized method to capture and identify all individuals, we could then distinguish between family members and visiting beavers.



Figure 1: An adult beaver swimming along the shoreline. *Beavers are easily recognized by the flat surface area and the lack of nose hair (in contrast to Nutria).*

Working with camera trap data

As capturing and handling beavers can have significant effects on body mass and fitness, a non-invasive approach is preferable (Mortensen & Rosell, 2020). Beavers are highly territorial animals, and intra-specific aggression is common, often resulting in scars, specifically on the tail. The resulting scars, along with the scale pattern of the tail, can be used for visual identification. Schwaiger & Schwemmer (2012) and Minnig et al. (2022) previously developed a method to capture tail traits using camera traps. However, this method also comes with challenges, mainly due to the large amount of manual work involved in this process. As image quality was severely limited due to methodological constraints, individual identification relied on large scars, and individuals with less obvious marks were difficult to distinguish. Additionally, there was no software available to create an efficient workflow for beaver identification, which became particularly apparent with larger numbers of images.

This challenge applies not only to Eurasian beavers, but to most projects working with the output of camera traps, highlighting the need for efficient solutions (Beery et al., 2019; Greenberg, 2020; Leorna & Brinkman, 2022). The rise of artificial intelligence (AI) in recent years promises to significantly reduce the amount of manual work involved. There are now a variety of algorithms that can classify camera trap images (or videos) and identify species and even different individuals.

To alleviate the task of individual recognition, computer vision has been used for several years now, especially with species that have rather clear and unique patterns. Some of the more common examples include amphibians such as the yellow-bellied toad *Bombina variegata* (Cruickshank & Schmidt, 2017) and mammals such as big cats (Cheema & Anand, 2017; Shi et al., 2023; Wattegedera et al., 2022) or giraffes (Lee et al., 2022). For animals with less clear patterns, there has been a recent push towards more advanced algorithms, such as (deep) convolutional neural networks which have, for example, been applied to facial identification of bears (Clapham et al., 2020; Jangid et al., 2024).

Hinds et al. (2023) showed that individual identification of beavers is also possible, using computer vision on pictures of the beaver's tail. However, the demonstration was limited to photos of stuffed beaver tails, captured using a digital single-lens reflex (DSLR) camera under controlled soft lighting. The information for the matching algorithm was therefore of much better quality than what can be expected from a camera trap deployed in the field, which faces several additional challenges (Table 2).

Here we set out to further develop the methods both in the field and in the data analysis. With several adjustments to the camera traps and their setup, we aimed to first improve the quality of data(photos). We then followed this by developing a more efficient data analysis pipeline, applying computer vision in multiple steps. The resulting methodological improvements, along with our data analysis software, therefore allowed us to carry out the present study on a large number of territories, and more generally provide a framework for easier and more efficient follow-up studies.

Objectives of the study

This study aimed to answer questions of both ecological nature and regarding methodological issues. To study family size and age structure we were reliant on a more optimized methodology. By reducing the quantity of manual work involved, we aimed to overcome limitations of prior beaver studies using camera traps, allowing us to study the selected life history traits at larger scales.

2. Materials & Methods

2.1. Study site

For the study, we selected the area with the highest density of beaver territories in Switzerland (Figure 2), which, according to the national beaver survey, is found between Bern, Belp and Rubigen (Angst et al., 2023). The area is subject to a moderate continental climate with cold winters and warm summers (MeteoSchweiz, 2026) with the elevation of the water bodies ranging between 500 and 600 m a.s.l. (Table 1). The Aare as the main water body runs through the study area from south to north with several arms of the Giesse and Gürbe running in parallel to the Aare. These streams then eventually merge with the Aare at the North-eastern end of the study area.

To a large extent, the study area is part of the BLN[1] (*Aarelandschaft zwischen Thun und Bern*), although only some isolated parts at the northern and southern end of the area are under strict protection and not accessible to leisure activities. The permit to access and place camera traps in the area was granted by the Canton of Bern and the Stiftung Hunzikenau.

Table 1: Details of study area. *The measurements are from the weather station in Bern / Zollikofen located northwest of the study area (MeteoSchweiz, 2026).*

Name	Belpauen
WGS coordinates	46° 53' 49.47" N 7° 31' 49.78" E
LV95 coordinates	2'607'000, 1'194'000
Mean elevation m.a.s.l.	515 m a.s.l.
Average daily temperature	7.7 °C
In winter (90 days)	-0.4 °C
In summer (90 days)	16.0 °C
Annual precipitation	1107 mm

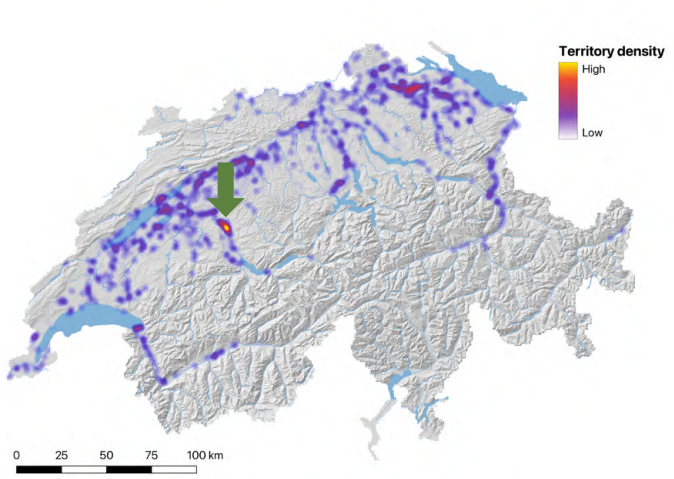

Figure 2: Population density of C. fiber in Switzerland. *The study area is marked with a green arrow. The data was provided by Angst et al. (2023) and visualized in QGIS (using a heat map with Kernel shape bi-quadratic with a radius of 3 km and a weighting for individual to family territories of 1:5). Background: ©Swisstopo*

[1] Bundesinventar der Landschaften und Naturdenkmäler von nationaler Bedeutung

2.2. Study design

Finding territories

Before deploying the camera traps in the field, we located all active territories in the study area. We conducted a daytime survey in late autumn to initially identify all active beaver territories based on occupied lodges and signs of activity in the vicinity. Additionally, areas with high levels of activity within each territory needed to be located, to ensure that the camera traps would capture substantial activity.

While we based our search for territories on the national survey that took place in 2022, we more generally searched all water bodies inside the study area that we considered large enough to accommodate beavers. All signs of beavers - including lodges, dams, territory markings and feeding signs – were logged in the field using QField version 4.0.0 (*QField for QGIS*, 2025). Based on the density of beaver signs and its decline with distance from the beaver lodges, we then manually delineated the territories in QGIS 3.34.3 (QGIS Development Team, 2026). This manual assignment was done under the assumption that each active lodge belonged to a separate territory, even if they were spaced closely together. We defined an active lodge by the presence of winter reserves or fresh branches in the immediate surroundings of the lodge.

A B





C D





Figure 3 (A-D): Examples of beaver traces found during the mapping*. A: Typical gnawing mark. B: Typical lodge of C. fiber at the shore. C: Traces of C. fiber feeding on grass in agricultural land. D: A small beaver dam to maintain the water level in the upper part of the river where the lodge is situated.*

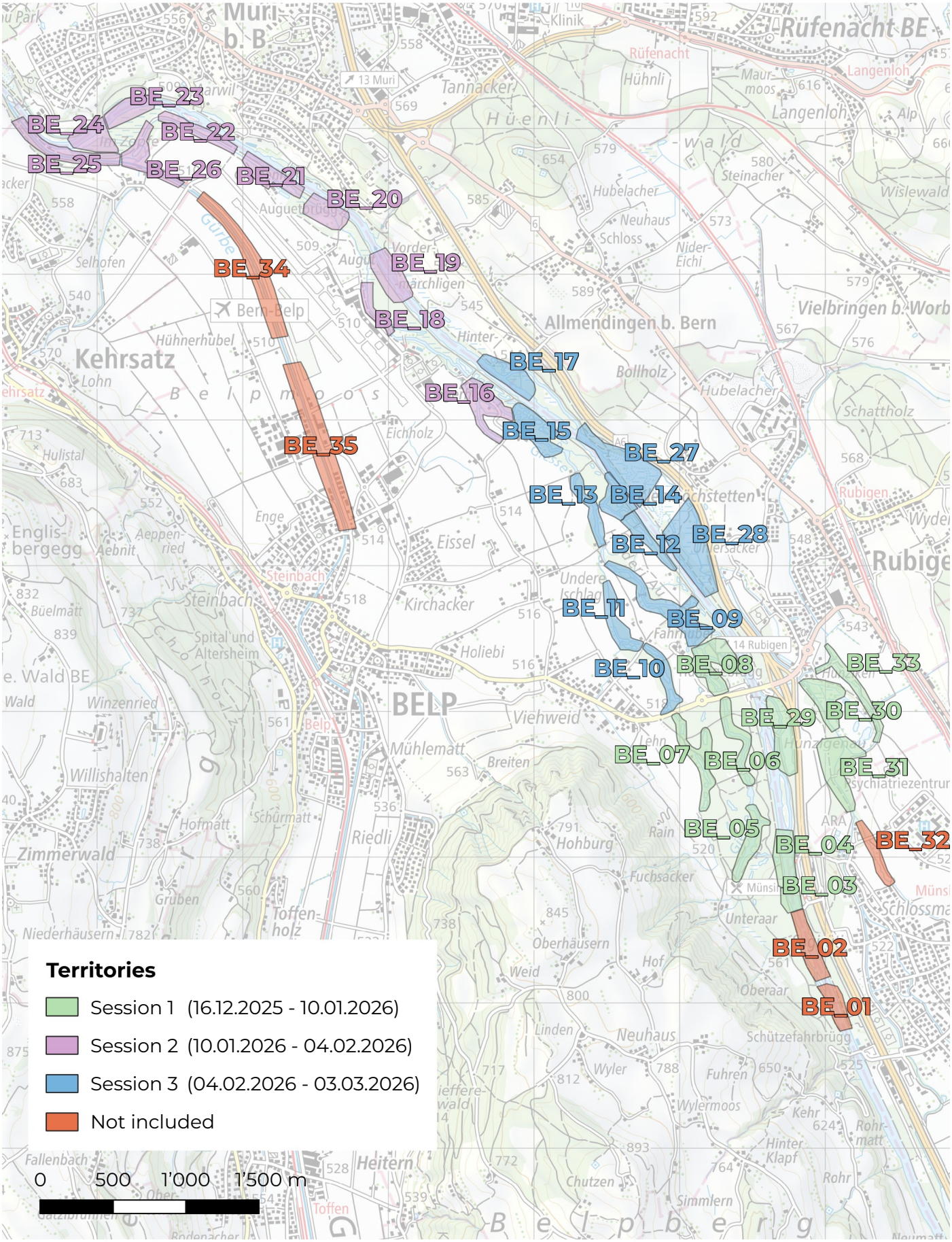

Figure 4: The map of all territories in the study area. *Each territory is coloured according to the camera trap session. Territories in orange were surveyed but eventually not chosen for the camera trap sampling, due to a limited number of available camera traps.*

Camera traps in the territories

Based on the preliminary survey, we chose 30 adjacent territories inside the study area. Within each territory, we set up three camera traps. One camera trap was positioned near the active beaver lodge, while the other two camera traps were installed closer to the expected territory boundaries.

The cameras were placed at points of high expected activity, including crossings between two water bodies, exits out of the water, paths leading beavers into the forest, territory markings or feeding places. Where possible, the cameras were placed at crossings between water bodies as these were deemed the most promising in preceding pilot studies. Additionally, individuals on extra-territorial forays tend to spend most of their time in the water and only emerge when strictly necessary, i.e. having to cross water bodies (Mayer et al., 2017b).

The camera traps in each territory were deployed for a total of 24 days. According to our pilot studies, we estimated that after this period, all individuals belonging to the family would have been captured at least once. After the 24 days, the cameras were repositioned to a new territory. We changed territories twice to cover a total of three groups of ten territories. This allowed us to capture 30 territories, making the most use of our 30 available cameras within the winter season, as recommended by Meier (2023).

To increase the likelihood of capturing all individuals of a territory, sugar beets were placed near the camera at the territory center. The sugar beets were exclusively added at the territory center to only attract beavers from the corresponding territory. No sugar beets were placed at the territory borders to avoid artificially attracting beavers from other territories and provoking territorial fights. In total around 10-15 kg of sugar beets were added to the camera traps in two rations. The first half of the sugar beets were placed upon installation of the camera traps, with the second one following 10 days later.

Due to extreme weather events some of the camera traps remained for up to 26 days in a territory as we were forced to reschedule field work several times. All the cameras froze over in early January (6th – 8th of January) and there was strong wind at the start of February (3rd of February), making it too dangerous to access the forests. As these extreme events probably also decreased the activity of the beavers, we decided to keep the data of the additional days, likely compensating for the reduced activity in previous nights.

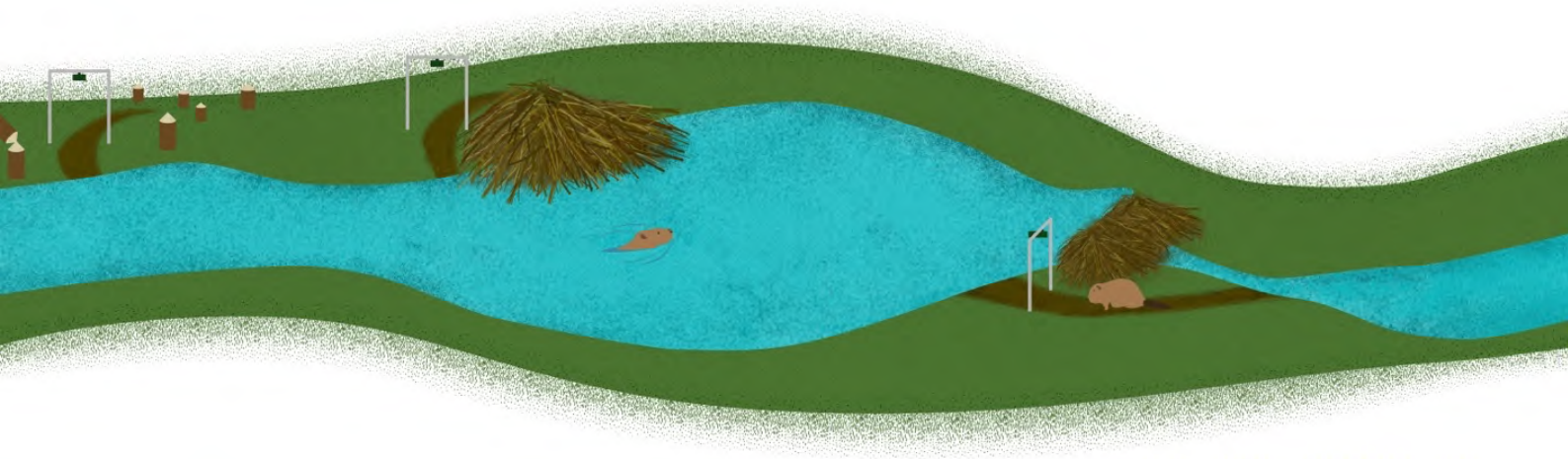

Figure 5: The camera trap setup on the territory scale. *Per territory, three camera traps were placed each. One camera was placed in the territory center in the vicinity of the beaver lodge. Two camera traps were placed upstream and downstream of the lodge.*

Camera trap setup

To visually identify beavers using tail traits, we used a specific camera trap setup first proposed by Schwaiger & Schwemmer (2012) and then optimized by Minnig et al. (2016), which specifically photographs the beaver's tail and captures a variety of tail traits for individual identification. We then further improved the method with several modifications, in order to mitigate some of the issues that we identified in our pilot study (Table 2).

Table 2: A list of challenges and issues that we observed using camera traps to individually identify beavers*. While some can be solved quite easily, some other challenges are simply related to the methodology in general.*

Issue	Description
Image quality	In camera traps, the image resolution is usually very limited, especially at nighttime. In case of camera traps with higher Megapixel counts, this often is caused by interpolation which doesn't result in net gains in image quality.
Focus	The focus of camera traps is set by the manufacturer and usually cannot be changed in the camera itself. In most camera traps, the range between ~2 m to Infinity is in focus. Placing the camera closer to the subject results in loss of detail.
Movement	As the animals move past the camera trap, the subject – in our case the beaver tail – can be in a variety of positions in or only partly in the frame. Using multiple images per series this can be compensated to some extent, however it is then also necessary to choose the most representative image.
Motion blur	As beavers can move swiftly, the sharpness might also be lower due to motion blur. Higher shutter speeds are available in some camera traps, which then however might come at the cost of image quality due to a higher sensitivity setting (ISO).
Rolling shutter	Movements can also become an issue as the image sensor reads the image line by line. If an animal moves swiftly across the camera trap, the tail might be skewed due to the upper part being scanned first while the lower part is captured a short moment later.
Lighting	Due to the nocturnal nature of the beaver, images are captured at night using an infrared flash to illuminate the scene. However the flash is built into the camera trap which results in lighting conditions that do not yield the optimum information due to reflections and reduced shading.
Tail position	As the beaver's tail is a highly agile organ, the positioning of the tail can vary from image to image. This is mostly an issue when it comes to measurements of the tail which can vary with how the tail is positioned.
Water (reflections)	Depending on whether an individual just emerged from the water or was foraging in the forest, the wetness of the tail can vary a lot which then also results in strong differences in the reflections.
Dirt	Foraging beavers can often pick up dirt and leaves which can partly cover the tail or appear as if it were a mark on the tail. Beavers carrying bigger branches also often have their tail obstructed to a greater extent.
Changes	Marks on the tail can change over time with the addition of new marks due to injuries from territorial fights but through healing of wounds.

As shown in Figure 6, the cameras were installed along beaver paths, using a metal frame to elevate them to a height of 80 cm and have them point vertically downward. We used Reconyx Hyperfire 2 camera models, with a +1.5-diopter lens added to the front of the camera trap to accommodate for the close focusing distance. The camera was then set to capture a series of 15 images per motion trigger using the highest framerate possible (around 2 images per second). This ensured a high likelihood that the beaver tail was fully visible in at least one image.

The resulting, near-planar images yield information useful for identification (scars, other marks and scale pattern) as well as for aging (dimensions). To get accurate measurements of the tail dimensions, a grid was placed at the time of installation of the camera traps. After installing the camera, we then triggered the camera to take a series of reference images of the grid, before removing it again. The reference images were then used in our software to calibrate the images for both size reference and the perspective.



Figure 6: The camera trap setup to identify the beavers by their tails. *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. The grid is placed underneath the camera upon installation of the camera trap but is then removed so it doesn't disturb passing animals.*

2.3. Developing a pipeline to efficiently work with images: BeaverFindr

With the number of cameras left in the field for several months, the number of images can quickly reach tens to hundreds of thousands of images. While there are a variety of camera trapping data pipelines available to deal with this abundance of images, at the time of our study there was no suitable software available that also allowed us to efficiently measure and identify tail images. We therefore decided to develop our own software, to tailor each step to our specific needs. Overall, the software is split into four separate modules, as depicted in Figure 7.

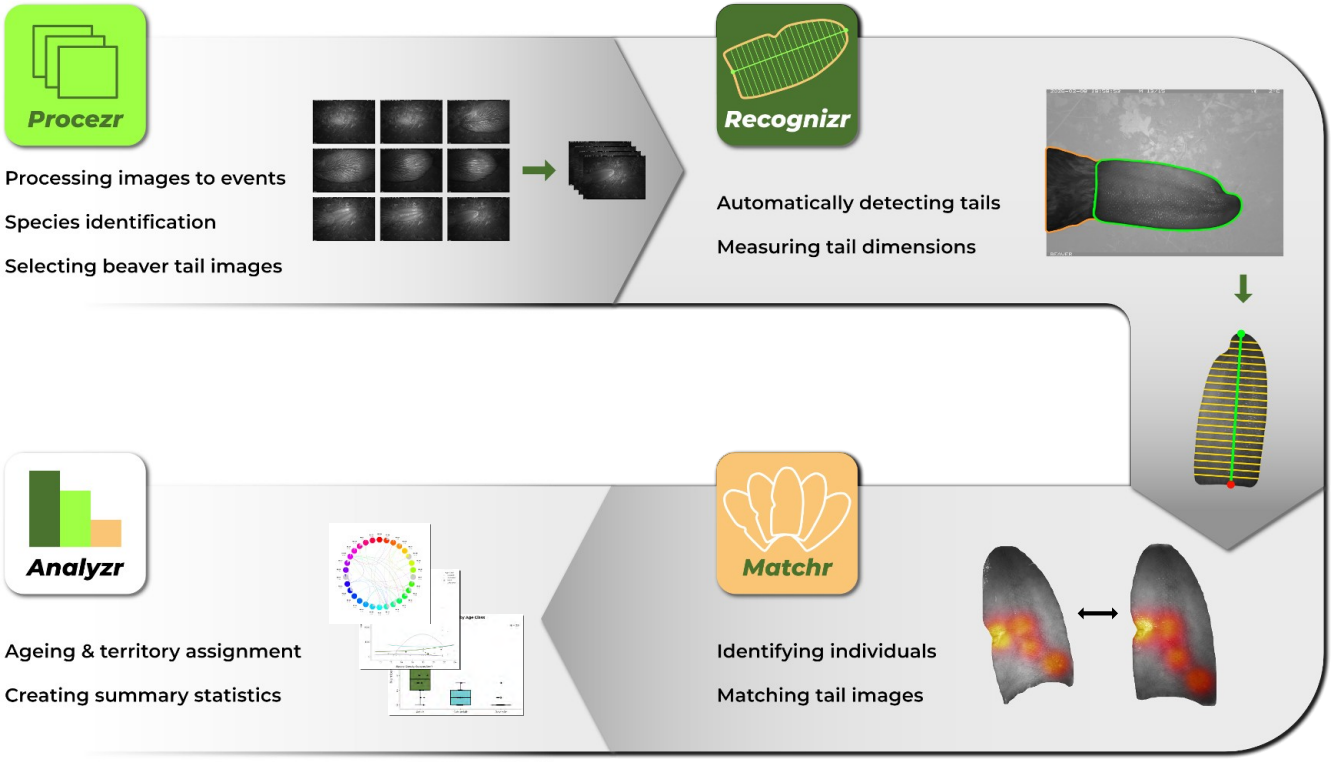

***Figure 7: Flowchart of the modules used in BeaverFindr**. Images are first processed to events in Procezr. Images of the tails are then measured and matched in Recognizr and Matchr. Analyzr is used to age and assign each individual to a territory. Analyzr can then immediately output a variety of summary statistics.*

Processing images to select beaver tails

The first module of the pipeline was used to sort the large quantity of images into camera trap events, filter out the species of interest, and the relevant images that can be used for identification. Additionally, we used ExifTool (Harvey, 2026) to extract metadata from the camera traps to gather temperature data as well as other camera-specific information.

For our study, we defined camera trap events to consist of a series of images, all triggered by one individual moving past the camera trap. If multiple individuals were captured in a single image series, this was manually split into separate events.

For the identification of species, we used the DeepFaune algorithm (Dussert et al., 2025) via AddaxAI (van Lunteren, 2023). DeepFaune is run on individual images, and the classifications are then aggregated for each event, using a threshold of 0.7 to remove uncertain classifications with low confidence scores. Although these steps made classifications more robust, all classifications were manually verified and adjusted if necessary.

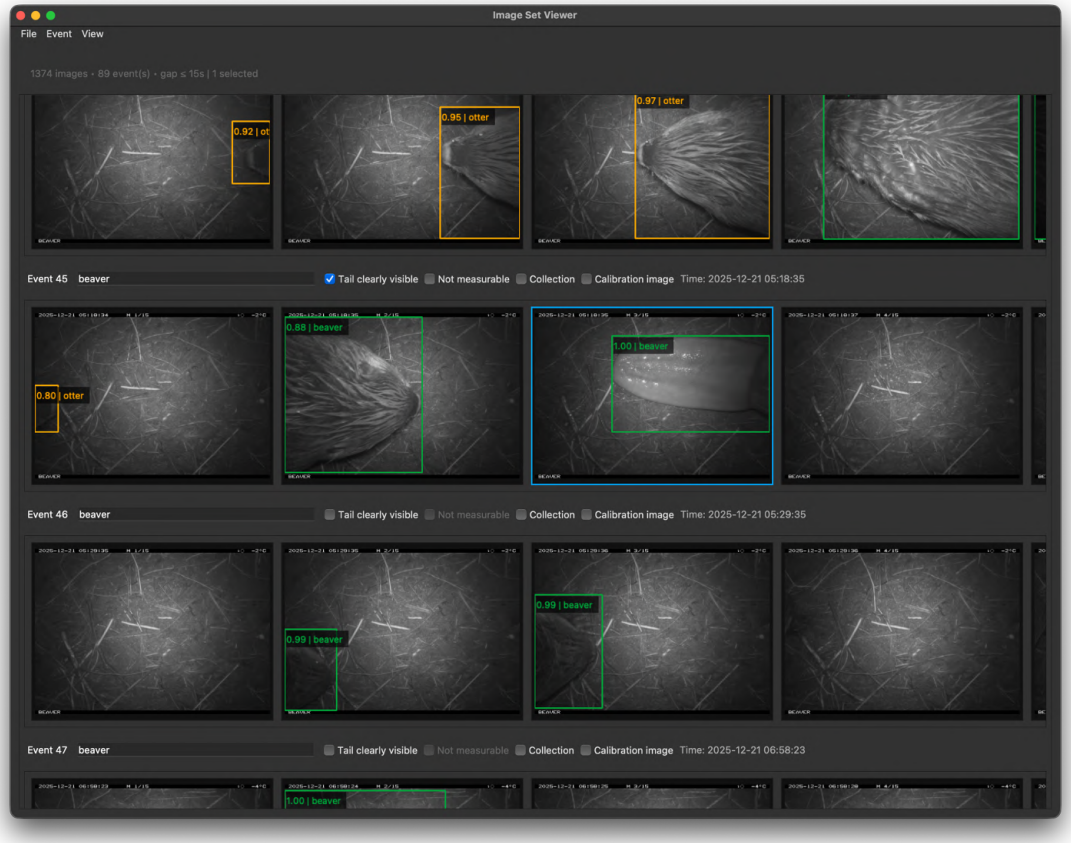

Figure 8: Screenshot from the first module "Procezr". *Individual camera trap events are represented as rows with a corresponding annotation bar for each row. Bounding boxes with species classifications are directly imported from AddaxAI using the DeepFaune algorithm. As seen in the screenshot, even though individual images can be falsely identified, aggregating classifications can mitigate these errors.*

The module is also used to select images where the beaver's tail is visible. As the images of the tail are also measured, we marked whether the given image was eligible for measurement. As this process is very sensitive to the positioning and orientation of the tail, measurable images were chosen conservatively.

Additionally, we selected the calibration images captured during installation of the camera traps. These images were used to maintain accuracy of the tail measurements across all camera traps, ensuring that we could compare measurements between locations.

Automatically recognize and measure beaver tails

All images of beaver tails as well as the calibration images that were selected in the previous step were then passed on to the next module (Recognizr), where the tails were automatically segmented and measured. As a first step, a calibration image of the grid was used to correct for the perspective warp and to set up a reference for subsequent measurements.

With the calibration profile applied, a YOLO26 segmentation algorithm was then run on all the images of beaver tails (Jocher & Qiu, 2026). The algorithm was trained on 580 images from previous studies and returned the segmented tails, which were then stored with the background removed. Additionally, the tails were also measured if they had been marked as measurable in the previous module. Measurements included length, area and circumference of the tail, as well as 20 width measurements at 20 points along the longitudinal axis of the tail (Figure 9). In case of false or inaccurate detection of the tail, the program also allowed for manual adjustments to ensure accurate measurements.

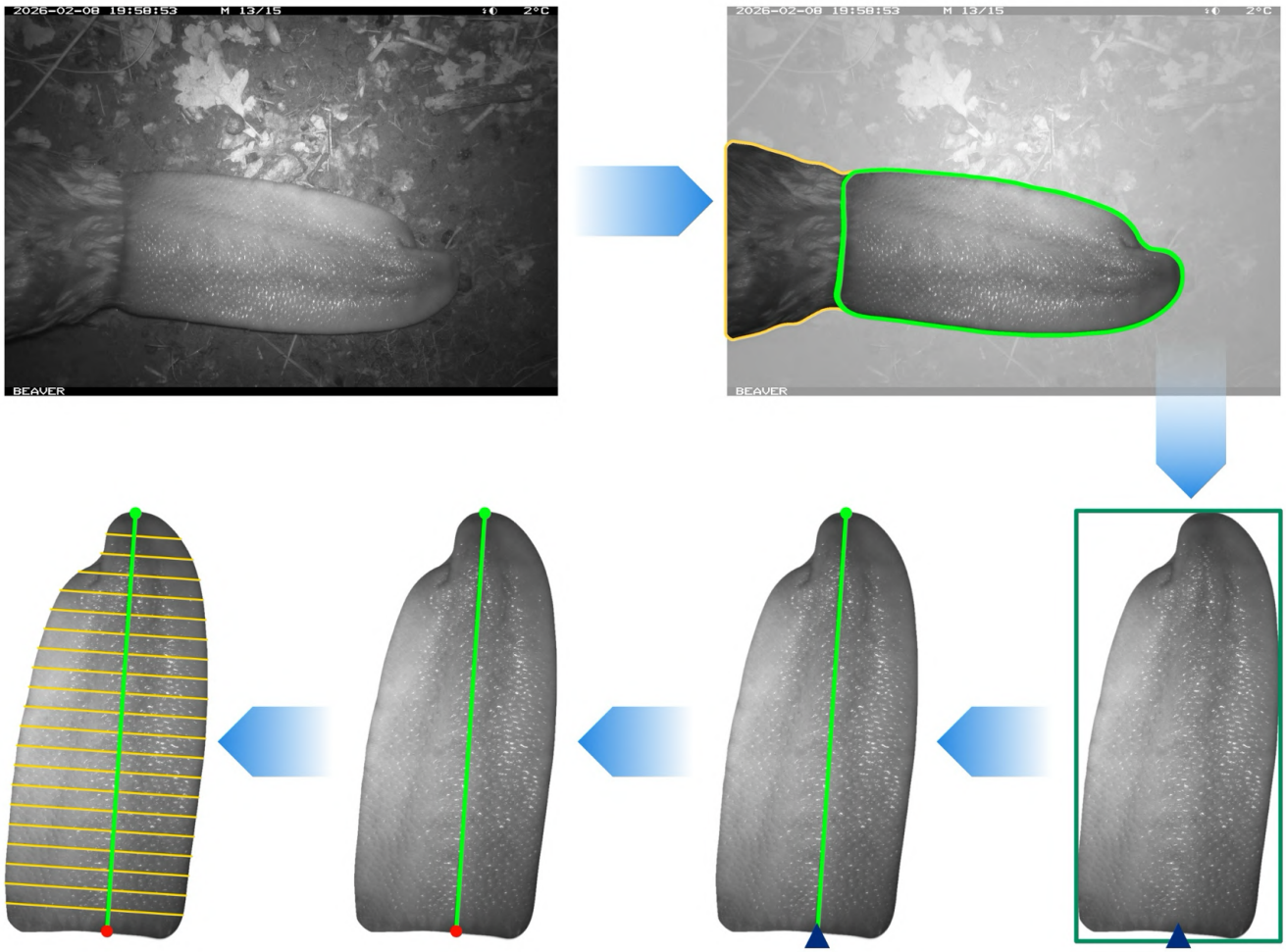

Figure 9: Description of processing steps to calculate length and widths of the beaver tail. *The tail image is first segmented by YOLO26 which returns an image with the background removed. As it also detects the beaver's fur, we can infer the direction in which the beaver is heading. From the base of the tail the program then draws a line towards the furthest point along the tail. This longitudinal line is then made sure to start and end at the border of the tail while 20 lines are drawn at a 90° angle representing the 20 width measurements. These are equally spread across the length line and start at the base of the tail.*

SIFT Algorithm for individual identification

In the subsequent module (Matchr), the images of the beaver tails were matched against each other and assigned to individuals. To distinguish the individuals, scars, colouring anomalies, scale pattern, and tail shape were used. While the matching was done manually, to support the matching process we used specific image processing, a SIFT-matching algorithm, and the tail dimensions.

To improve the visibility of marks on the tail, the images were processed. First a high pass filter was run on the image of the tail. This image was then inverted and blended with an original copy of the image by keeping the lighter pixel from each pair. The resulting image was then finally adjusted with an increase in contrast.

In addition to specialized image processing to highlight scars and the scale pattern, we used a SIFT (Scale-Invariant Feature Transform) algorithm to propose likely matches. Likely matches were sorted by the number of SIFT matches and displayed using a heatmap (Figure 10). By searching through the candidates, we were able to select the best match if there was a match in the dataset.

Independent of the SIFT-matching, the tail dimensions were also used to calculate a similarity score based on the Mahalanobis distance between each candidate pair. For this, we used a multi-dimensional trait space not only consisting of the raw measurements but also of derived shape ratios (**Table 3**). The resulting similarity score was used to verify the visual matching process, whenever the measurements were available for both candidate images. This step added a guardrail to prevent accidental false-matches, further refining the accuracy of our matching process.

Table 3: Measurements of tail. *All 15 measurements were used in combination to calculate the Mahalanobis distance between candidate pairs (if both had measurements available). Entries in* ***bold*** *are based on raw measurements while others represent shape (ratios).*

1. **Total tail length (cm)**
2. **Tail surface area (cm²)**
3. **Tail perimeter/circumference (cm)**
4. **Mean of all width measurements**
5. Standard deviation of all width measurements
6. Ratio of area to circumference
7. Ratio of area to length
8. Ratio of area to mean width
9. Mean narrowing rate across the last 6 width measurements (tail tip)
10. Standard deviation of narrowing rate across the last 6 width measurements
11. Count of width measurements within 1 cm of the first (base) width
12. **Mean of the first 5 width measurements**
13. **Standard deviation of the first 5 width measurements**
14. **Mean of the last 5 width measurements**
15. **Standard deviation of the last 5 width measurements**

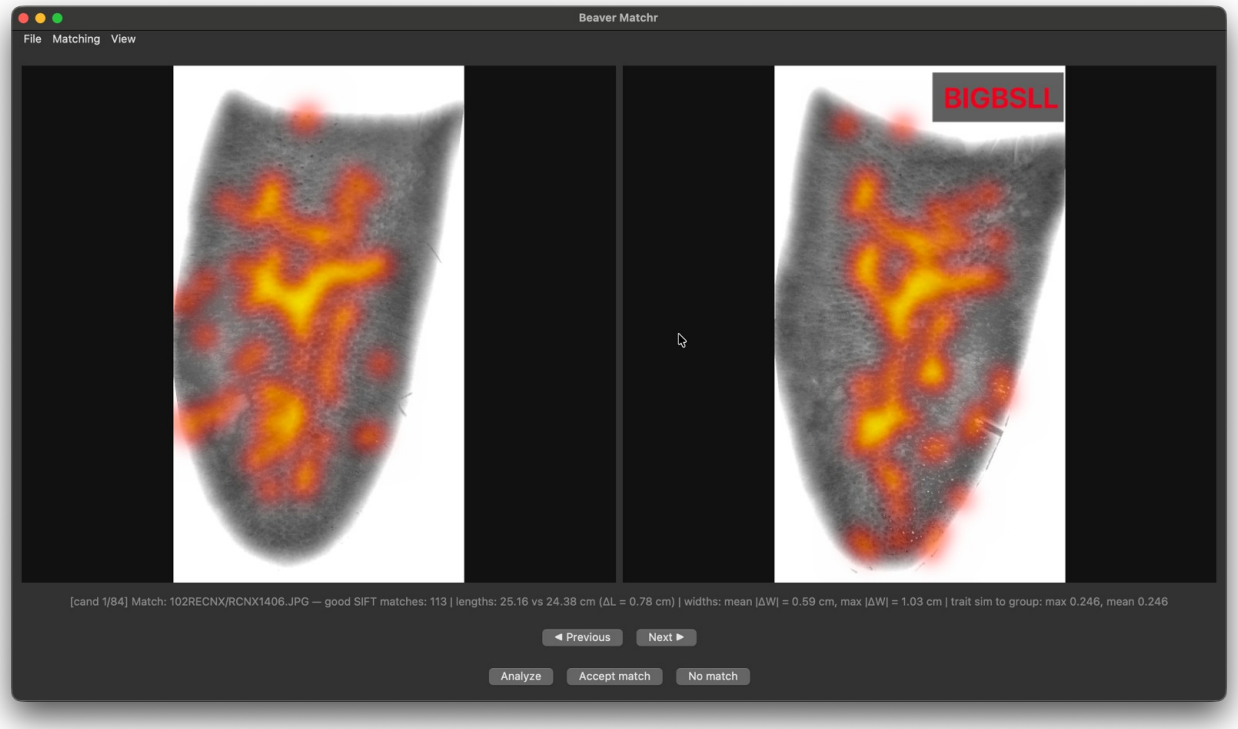

Figure 10: Screenshot of the Matchr module. *Images that are matched against the database appear on the left, whereas the best matches are shown on the right as candidates. The heatmap indicates which area of the tail shows a particularly high match.*

Territory and age class assignment

In the "Analyzr" module, all the events across the camera traps were then combined to recreate the capture history of each individual. The resulting capture histories could then be used to assign each individual to a territory, ultimately allowing us to define family size and age structure. If an individual was captured at a camera trap in the territory center, it was directly assigned to this territory. If it was never recorded at a territory center, the individual was assigned to the territory in which it was found most often. In the rare case of a beaver being found at two territory centers or across multiple territories with equal frequencies, the temporal history was taken into account. In such a case, assignment priority was given to the territory that had sightings across the highest number of nights.

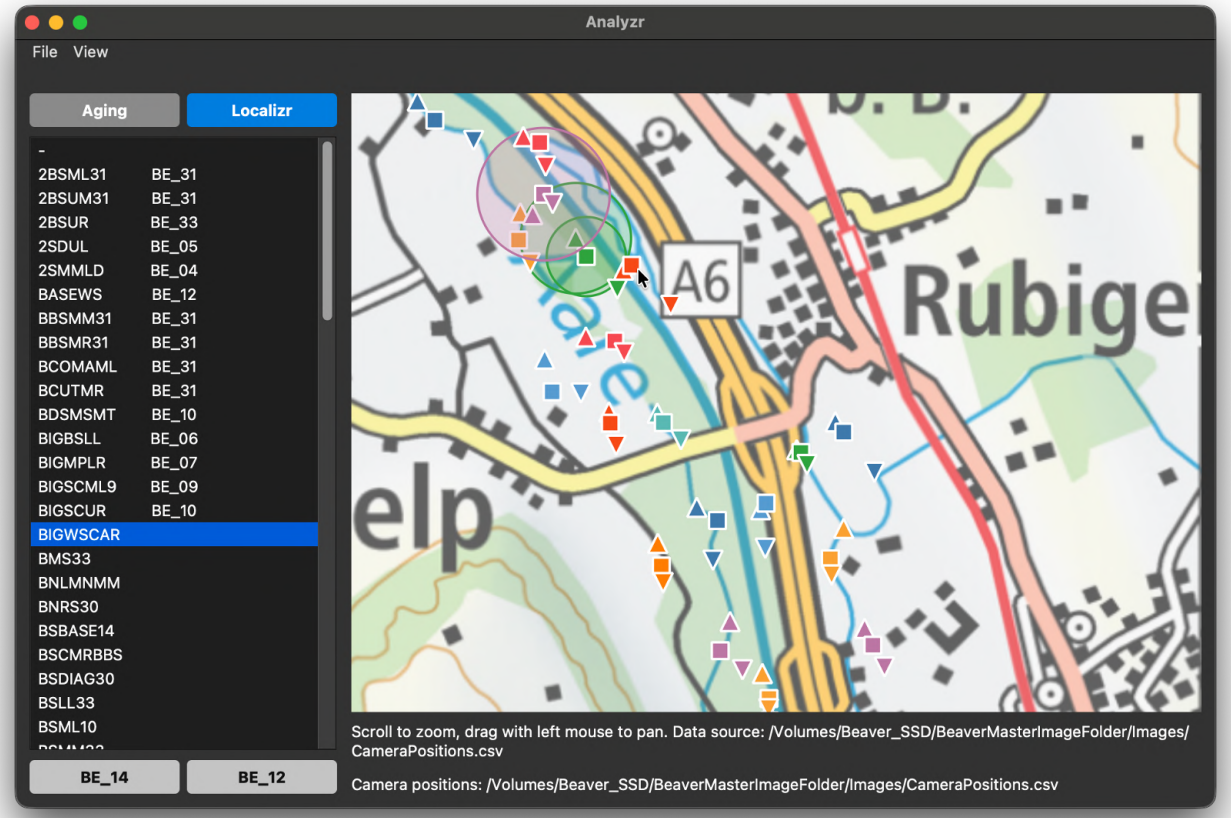

Figure 11: A screenshot from the Analyzr module where the individual's trapping rate is displayed across the study area. *Based on the trapping history, the individuals could be assigned to a specific territory.*

In the last step, the tail measurements were used to assign each individual to one of the three age classes (Table 4). Following the classifications of Rosell & Pedersen (1999), we used both the length and the average width of the tail to infer the individual's age. Generally, we used the mean of all available measurements for each individual. However, we also visually inspected all individual measurements in order to identify possible outliers which could have affected the mean tail dimensions.

Table 4: Tail measurement thresholds for the three age classes. *The classifications follow the suggestions of (Rosell & Pedersen, 1999).*

Age class	Length	Average width
Juvenile	< 22 cm	< 8 cm
Sub-adult	22-27 cm	8-11 cm
Adult	> 27 cm	> 11 cm

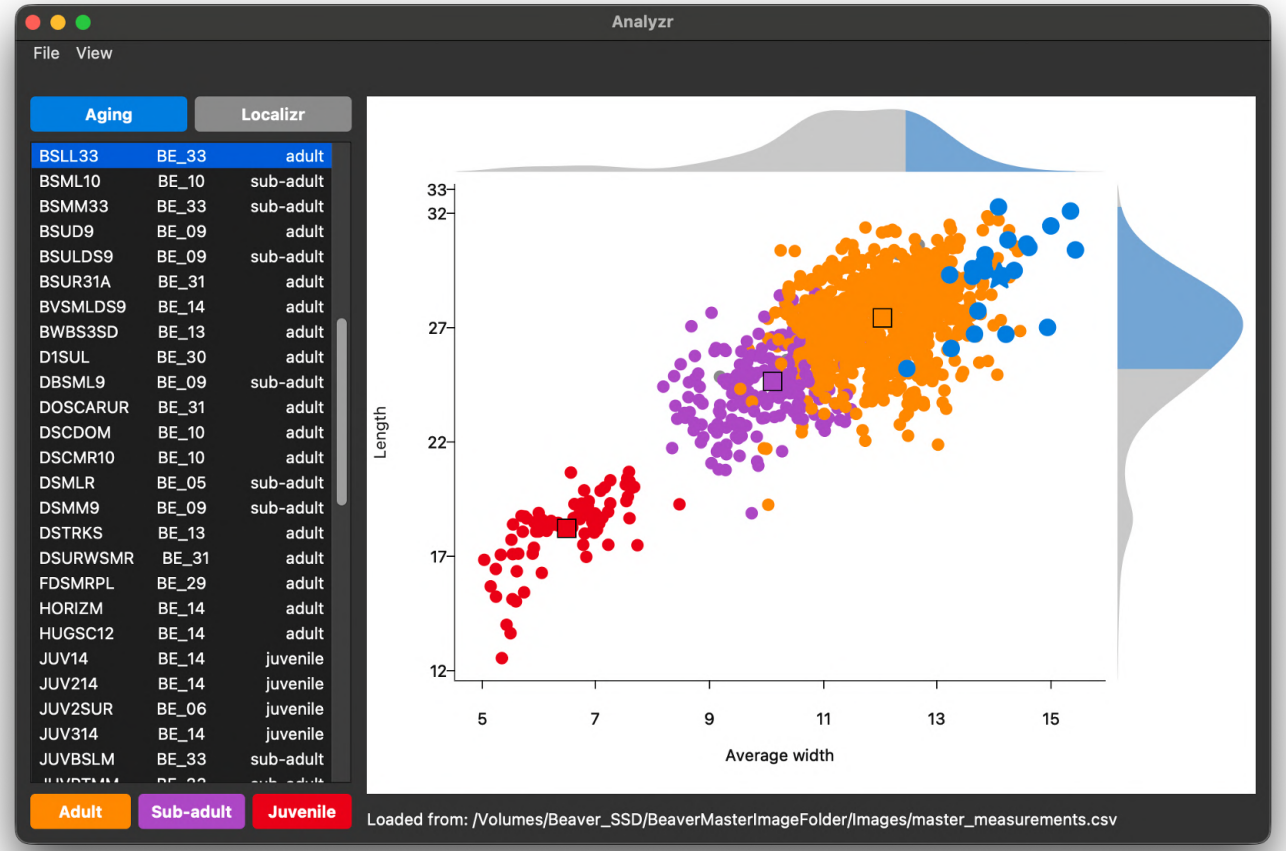

Figure 12: Besides territory assignment, Analyzr was also used to classify each individual by age class. *The squares display the average measurement per age class, while the points represent all measurements in the database.*

2.4. Analyzing the data

To analyze family size, age structure, and movement patterns, we used the capture histories and tail measurements of each individual. All analysis was done inside BeaverFindr running on Python 3.9.20 (Van Rossum & Drake, 2009), starting with general activity patterns at our camera traps and the accumulation rate of newly detected individuals over time. By determining family sizes, we were then able to calculate population density at a finer scale, allowing us to evaluate movement patterns as well as territory interactions in more detail.

Activity and temperature

To test the efficacy of our camera trap setup to capture mainly beavers, we first summed all camera trap events by species over all 90 camera trap locations. Besides the absolute number of camera trap events, we also included the number of camera trap locations at which the species was seen.

To follow the general activity of beavers across the study period we summed the camera trap events of beavers across each night. As it was always 10 territories that were followed in parallel, the camera trap events were summed across the 30 active camera traps. Since beavers are active throughout the night, we aggregated the events by nights. We defined a night as starting at 12:00 and ending 24 hours later the next morning at 11:59.

The beaver's activity patterns were expected to vary due to several factors, including weather conditions (Bartra Cabré et al., 2020). To test the relationship of beaver activity with temperature we used a linear regression. We obtained daily mean temperature from the weather station in Bern / Zollikofen, which is 10 km northwest to the study area. The daily mean temperature is measured from 00:00 to 23:59 and is thus offset by 12 hours relative to the beaver activity period.

Individual discovery

To assess whether the chosen duration of 24 days was appropriate to capture all individuals in a territory, we calculated the rate of discovery of new individuals. For each territory, the number of individuals captured on at least one of the three cameras was counted for each day. If an individual had already been captured on a previous day, it remained in the count for the following days. The resulting curves were then averaged across all 30 territories, ultimately allowing us to evaluate the study duration and whether we could likely capture all individuals. Additionally, the number of camera trap events per individual was counted across the whole data set.

Tail dimension

In order to quantify the distinctiveness of the three age classes, we used the mean measurements of each individual and calculated the 95% confidence ellipse of each age class. The ellipses were calculated on the basis of the 2x2 covariance matrix using the length and average width measurements. The covariance matrix was then decomposed into the respective eigenvalues and eigenvectors from which the orientation and scaling of the ellipse could be extracted. The 95% confidence ellipses were then used to calculate the overlap between different age classes indicating how distinct the measurements of each age class were.

Family size and density

Family size and age structure were determined using the territory and age class assignments. To evaluate the potential error in family size arising from assignment of individuals captured in different territories (see Section 2.3 above), we calculated the minimum and maximum family size by manipulating our territory assignments. To get the lower error, individuals that had sightings in other territories were removed, representing the smallest possible family size. In contrast, the higher error was calculated by assigning all individuals to this territory, that were captured at any of the three camera traps.

The assigned number of individuals was then used to calculate the population density in the study area. The density - specified by the number of individuals per 1 km^2 - was calculated using gaussian kernel density estimation with a bandwidth of 500 m at a grid size of 50 x 50 m. To calculate the density, all individuals of a given family were set to the coordinates of the territory center at the lodge. For each individual, the density at its territory center was then stored for further analysis.

Movement and territoriality

To assess the movement and territoriality, we used the trapping history of each individual. Here we primarily focused on the number of unique camera trap locations where an individual was captured. We then further classified the individual's movement by the number of unique territories in which it was captured, not considering whether it was just one camera trap location or all three in the territory.

We tested the relationship between the number of visited territories and the population density at the individual's territory center using a linear regression. This was tested both across all individuals and within each age class. Finally, we also examined inter-territorial interactions across the study area. Interactions were defined as a capture of an individual from a specific territory in another territory. All captures of extra-territorial movements were thus defined as interactions and the relative frequencies were used to illustrate strength of interaction between two territories. Additionally, the ratio of resident to visiting individuals was calculated for each territory.

3. Results

3.1. Activity and individual discovery rate

Over the course of 79 days, camera traps recorded a total of 33,562 events with approximately 630,000 images. Of a total of 14,848 events that could be assigned to a species, 60% were triggered by micromammals such as mice and rats (Figure 13). Beavers were the second most frequently captured species with a total of 4,223 camera trap events, representing around 28% of all events that could be assigned to a species.

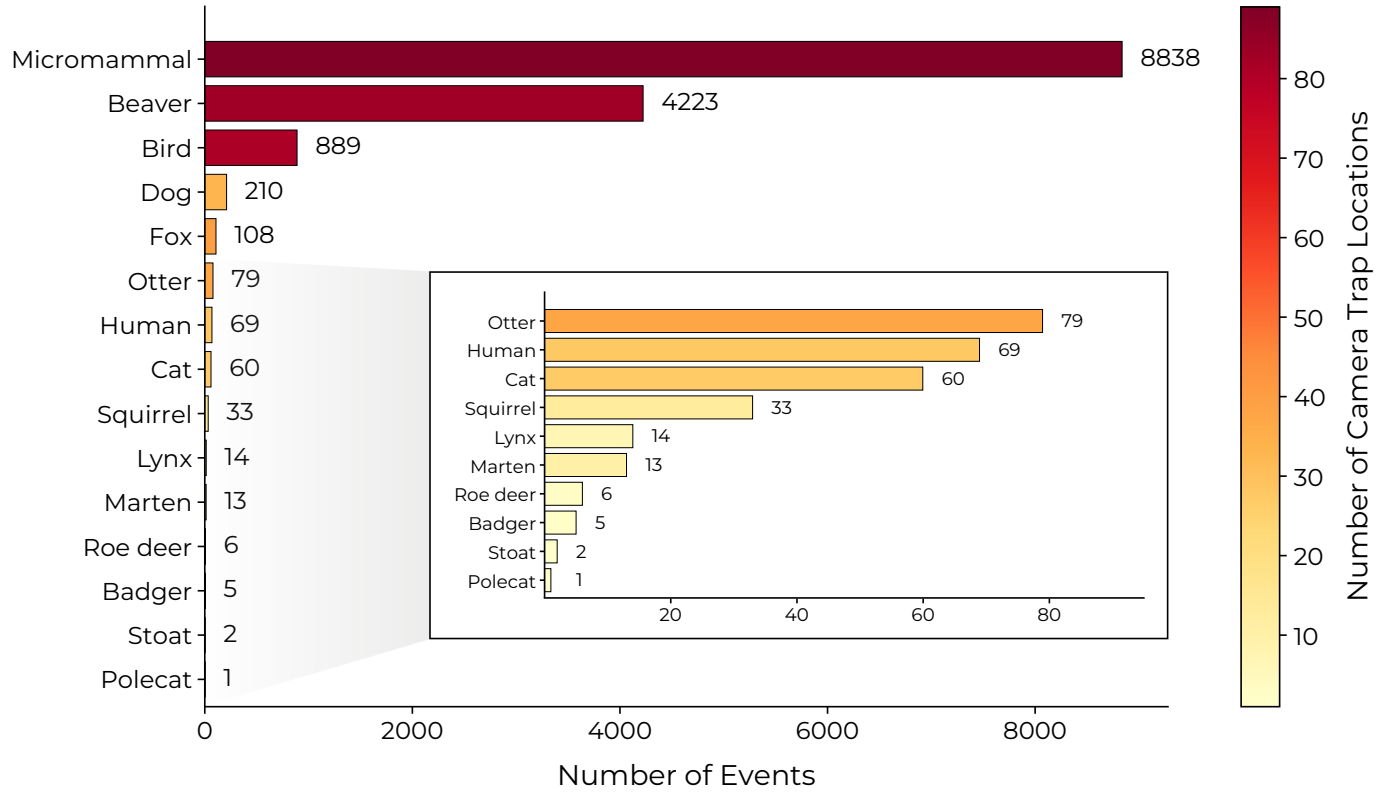

Figure 13: The number of camera trap events by species. *Micromammals were by far the most abundant with beavers as second most common animal on the camera traps. The colour gradient represents the number of camera traps where the animal was captured. Each of the 30 camera traps was placed at 3 locations allowing for 90 different camera trap locations. Darker colours indicate that the species was seen at more camera trap locations.*

The capture rate for beavers varied between 5 and 107 camera trap events per night, with an average of 53.4 events per night (Figure 14). Generally, activity, measured in the number of beaver camera trap events, was lower in the first few days after installation of the camera traps but overall, activity was relatively stable throughout the study period and the different camera positions. Although plots showed a notable decrease in activity during the coldest period in January, there was no correlation between beaver activity and temperature (R^2 = 0.006, p = 0.485).

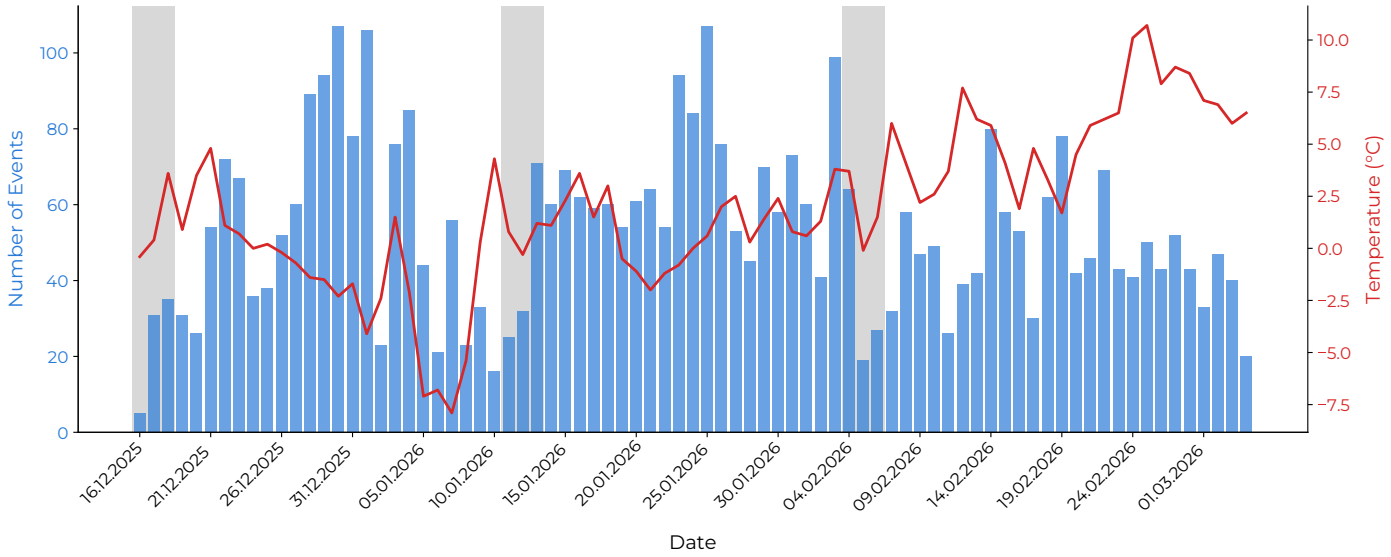

Figure 14: Beaver activity across all 30 territories and locations. *The installation periods are indicated in light grey and the daily mean temperature is indicated in red. The date on the x-axis corresponds to the day of the daily mean temperature while the activity is measured from 12:00 on the corresponding date to the 11:59 on the next day.*

Overall, the camera traps were left for 24-27 days at each location. During this time, we captured an average of 9.5 individuals per territory (Figure 15) with 198 different individuals being observed in total. The number of individuals captured in each territory ranged from 1 to 21 individuals.

The accumulation rate of newly captured individuals also varied across the study area, but more importantly, changed over time. On average, 0.37 individuals were captured for the first time in a territory per night. During the first 10 nights, the rate was higher with 0.71 new individuals per night. From day 10 on, the increase in newly discovered individuals per night slowed down to an average of 0.13. After day 20, there were only 10 territories where the total number of captured individuals still increased and we captured an additional 1.4 individuals per territory added across all nights that followed.

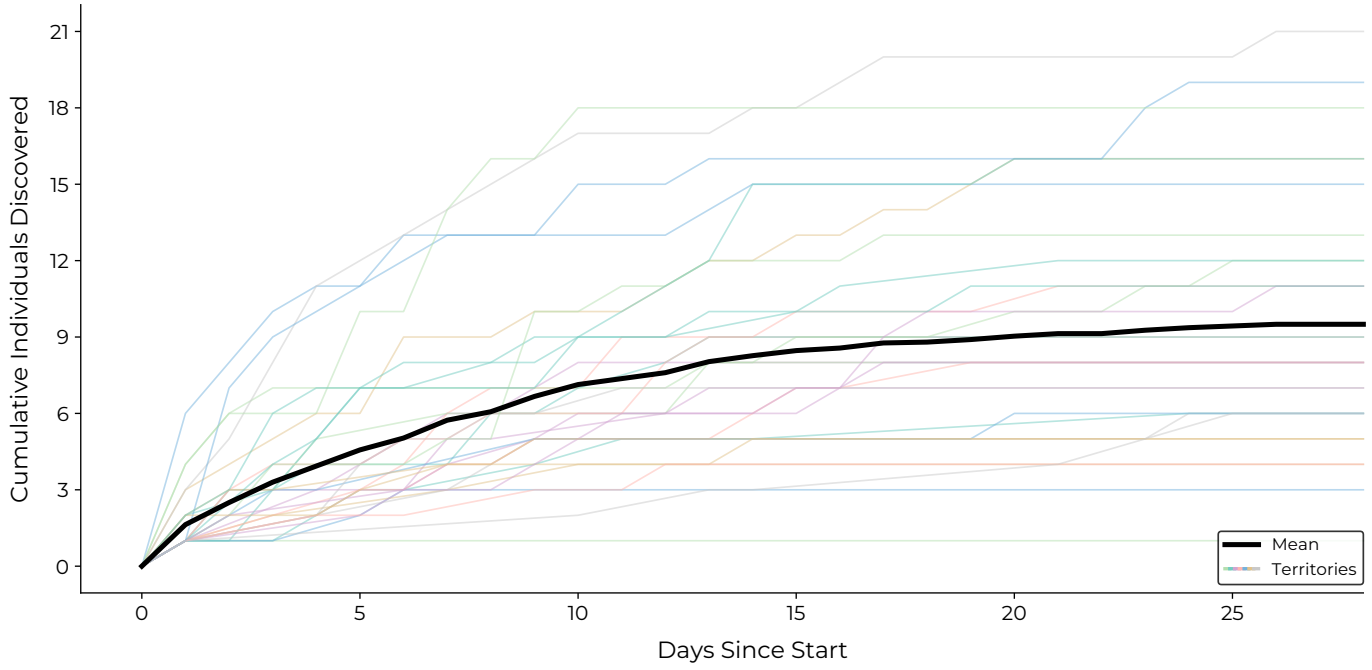

Figure 15: Individual discovery curve in the territories. *Each thin line represents one of the territories with the thick black line representing the average across all territories. Over the course of the 24-27 days, new individuals were mostly discovered in the first 10 days. After this initial period of many new individuals being captured in the territory, the increase rate levelled off at around 25 days.*

Most individuals were captured rarely, and only a few had several recaptures (Figure 16). 85 individuals were captured up to 4 times, while 11 individuals (5.6%) were captured more than 50 times each.

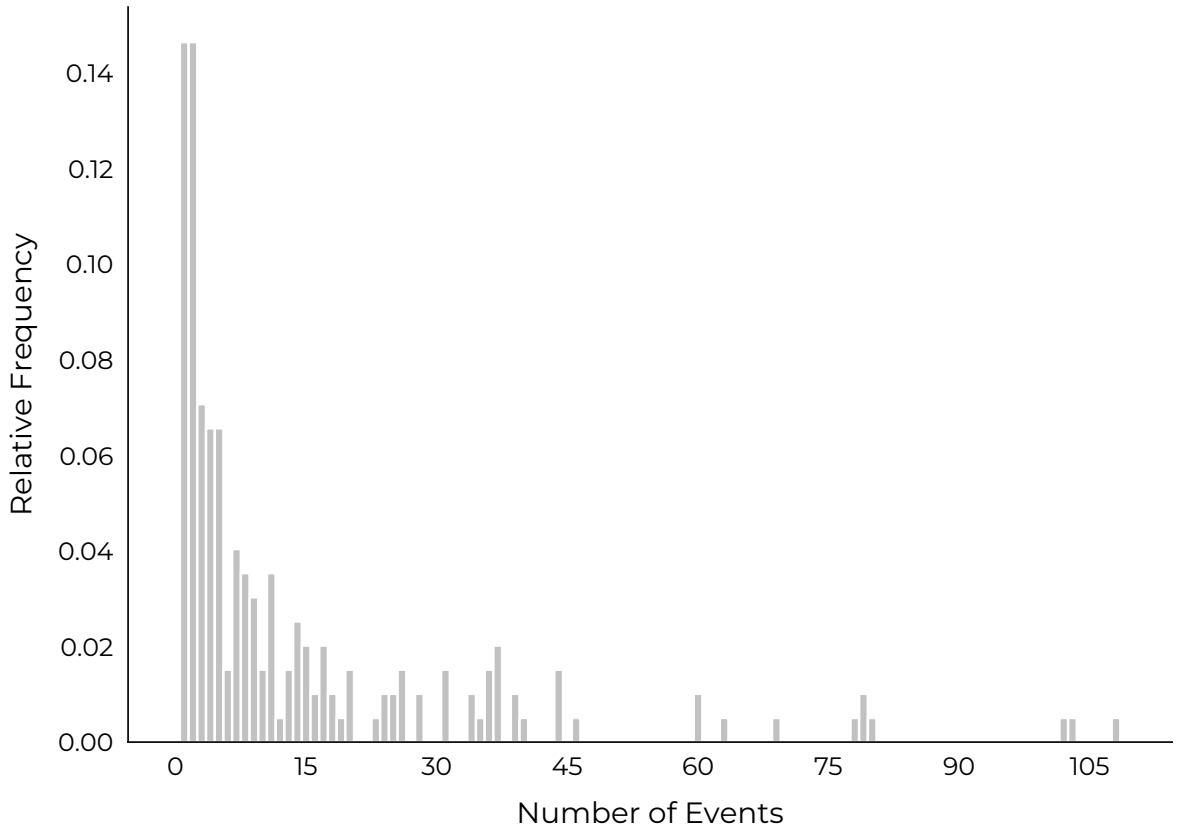

Figure 16: Distribution of the number of camera trap events per individual illustrated by relative frequencies.

3.2. Tail dimension

We obtained tail measurements from 2,098 images of 174 individuals (Table 5). On average, we thus had 12.3 measurements per individual. Per individual, the standard error for the length measurement was 0.52 cm and 0.18 cm for the average width measurement. Based on an individual's measurements, it was then assigned to one of three age classes.

Seven individuals with a total of 93 measurements were classified as juveniles, 34 individuals with 329 measurements as sub-adults, and 133 individuals with 1,676 measurements as adults (Figure 17). Calculating a 95% confidence ellipse for each age class, we found about 2.0% of overlap between juveniles and sub-adults. The overlap between subadults and adults was greater, with 8.7% of overlap between the confidence ellipses of their respective age classes.

Table 5: Tail measurements for each age-class.

	Juveniles	**Sub-adults**	**Adults**
Individuals (count)	7	34	133
Measurements (count)	93	329	1676
Mean length (cm)	18.3	23.7	27.4
SD length	1.7	2.1	1.9
Mean width (cm)	7.2	10.3	12.9
SD width	1.0	1.2	1.0

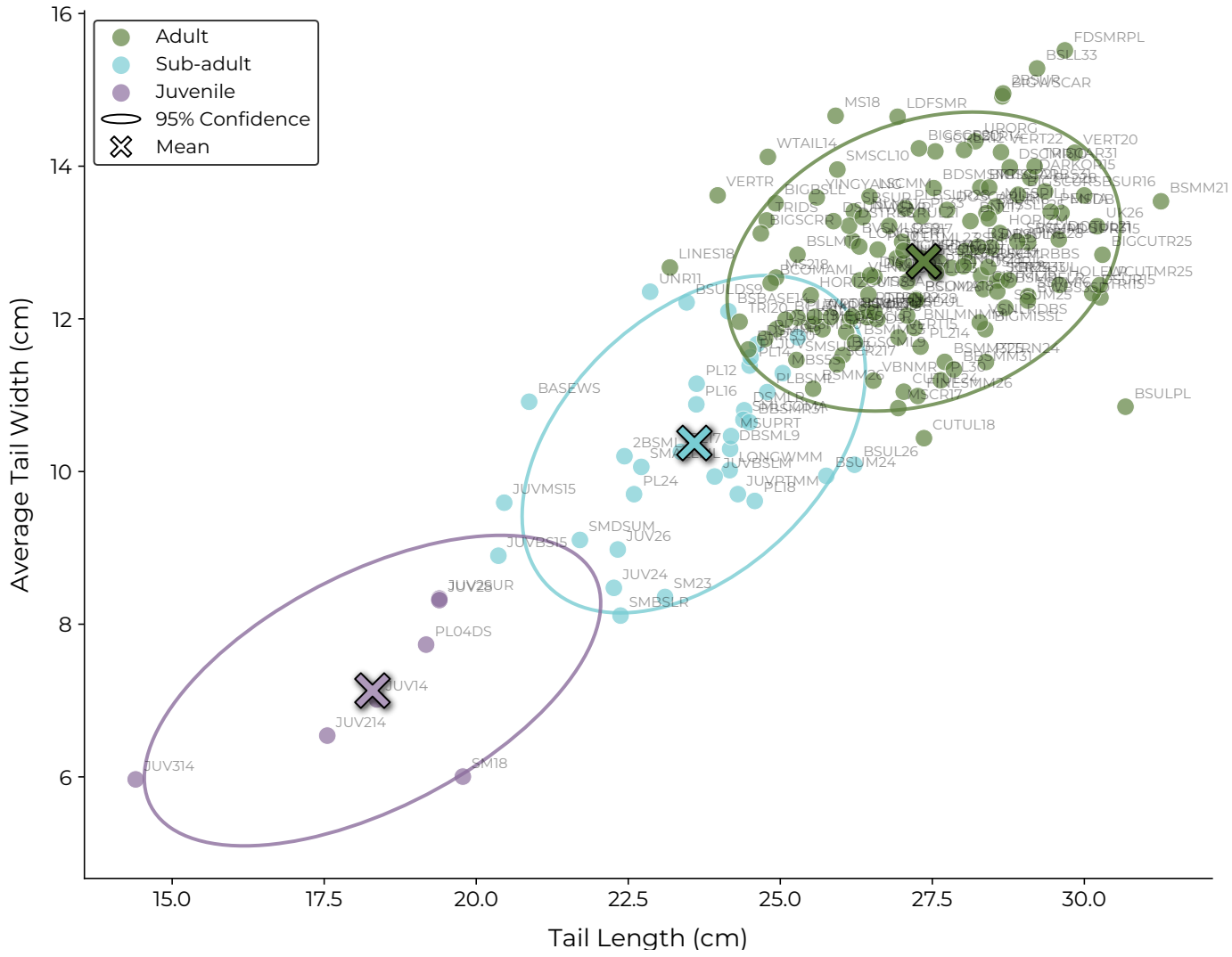

Figure 17: The tail dimensions (length and the average width) for each individual and age class. *If multiple measurements for an individual were available, the average across all of them was used. The large circles represent the 95% confidence ellipse of the mean which was also used to calculate the overlap between age classes.*

3.3. Family size & Age structure

Based on the locations of each recorded event, the individuals were then assigned to a certain territory (Figure 18). Across the 30 territories, we observed an average of 6.6 individuals with family sizes ranging from 1 to 16 individuals. The uncertainty calculations showed that accounting for misassignment, 73% of families would be within +/- 5 individuals.

Generally, family sizes of 3-5 individuals were the most common but families with 10 or more individuals were also observed eight times (Figure 19). Per family, we observed an average of 4.3 ± 2.8 (mean ±s.d.) adults per family with 1.1 ± 1.0 subadults and 0.2 ± 0.6 juveniles (Figure 20). The number of adults in a family ranged from 0 to 10 individuals whereas the number of sub-adults and juveniles varied between 0 and 3.

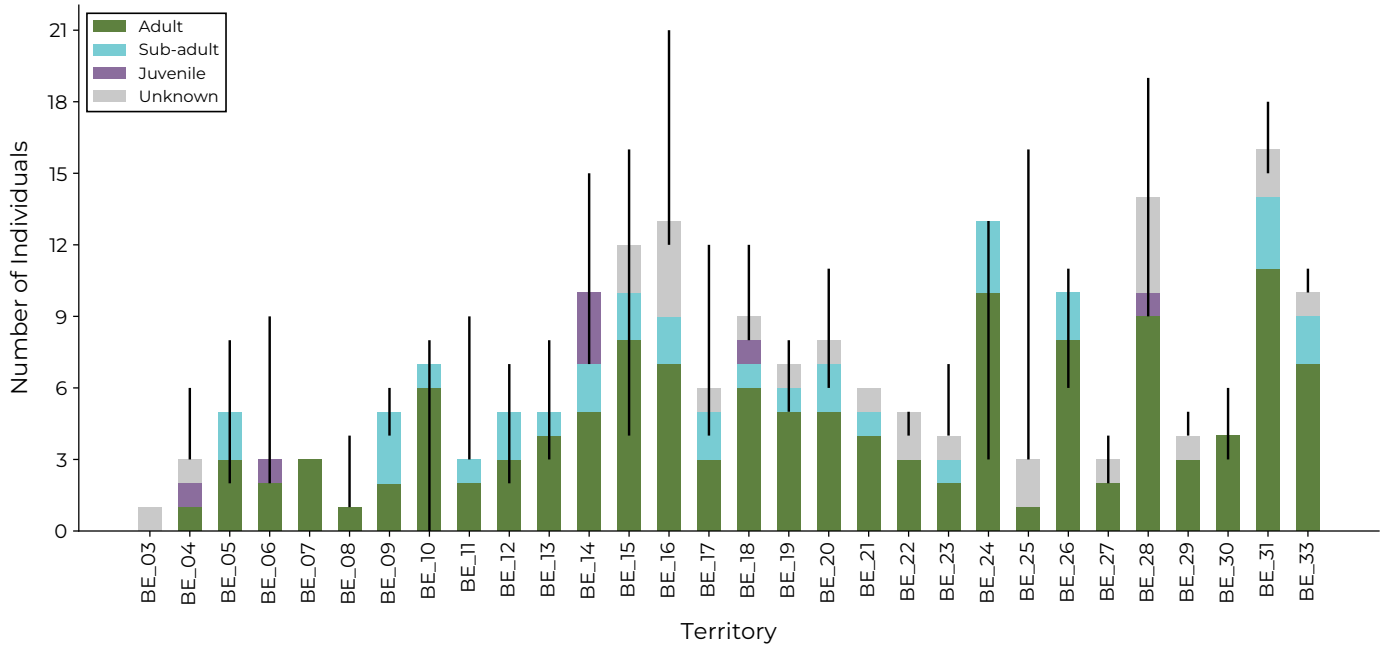

***Figure 18: Family size per territory**. The bars represent the number of individuals of a given age class that were assigned to the particular territory. Individuals that were clearly identified but could never be measured are indicated by grey bars. The thin black line represents the maximum and minimum error in territory assignment. The maximum represents the case where all individuals that were seen in the territory were actually assigned to this territory, ignoring sightings in other territories. The minimum represents the case where only the individuals were assigned to the territory that had only been seen in this particular territory.*

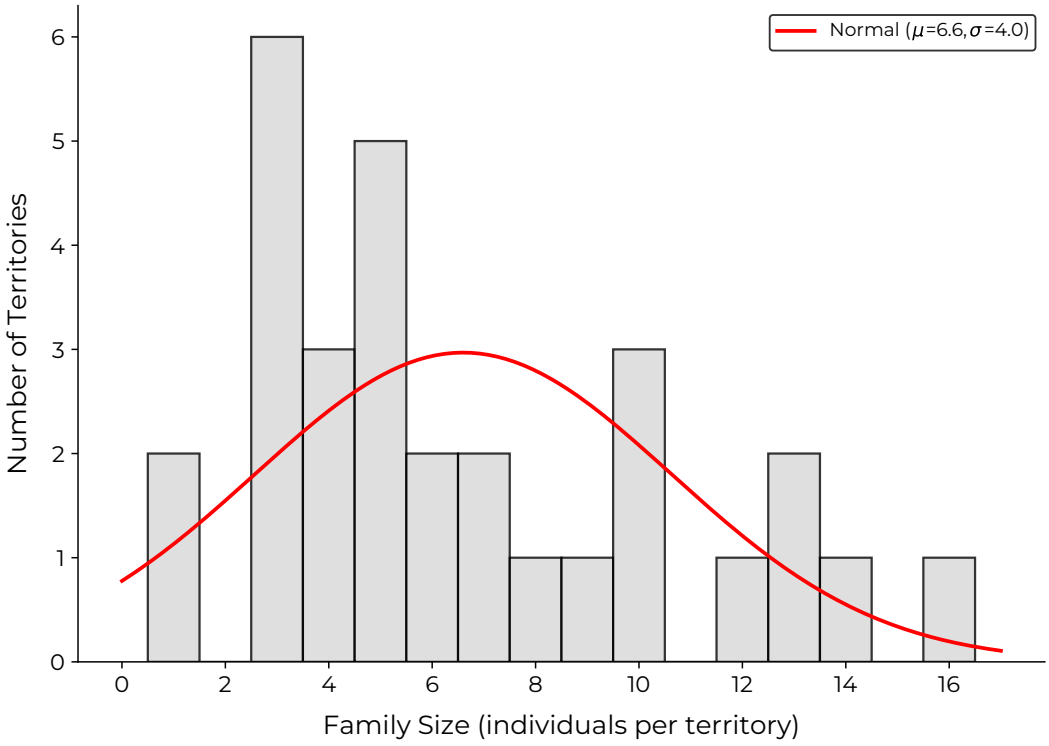

***Figure 19: Distribution of family sizes.** Observed family sizes are indicated by grey bars while the approximated normal distribution is indicated by a red line.*

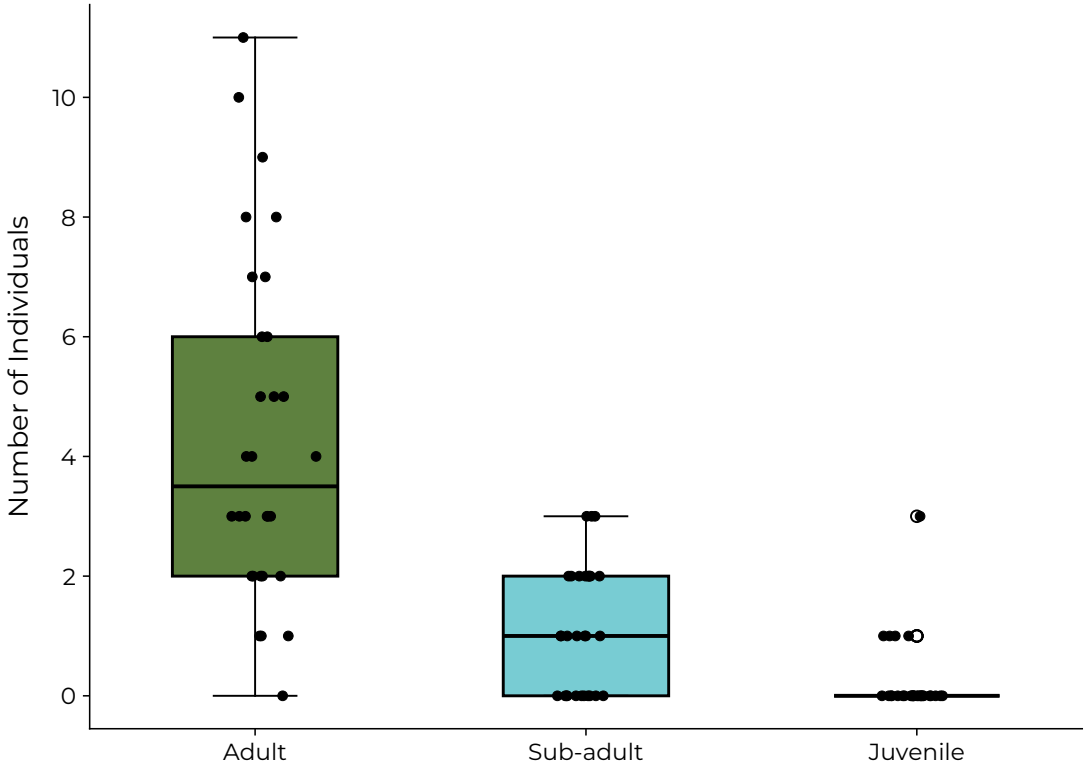

***Figure 20: Age structure across families**. The boxplots indicate the number of individuals of a given age-class in each of the territories (N = 30). The actual data is shown with small black points jittered to improve visibility of each data point. Hollow points represent outliers.*

3.4. Movement and territoriality

On average, the 198 individuals were captured 14.2 times though the actual captures ranged from 1 to 108. The captures per individual were recorded across one to seven different camera traps spread across up to five territories.

Juveniles were captured at one or two different locations. Sub-adults were captured at an average of 2.0 different locations however, one specific sub-adult individual was captured at five different camera trap locations, of which only two were in the same territory, leading to a total of four different territories where this individual was captured.

Adult individuals were captured on average at 2.3 different camera trap locations. Two individuals were captured at seven different camera trap locations placed in five different territories. An additional individual was captured at six different camera trap locations which were located in five different territories.

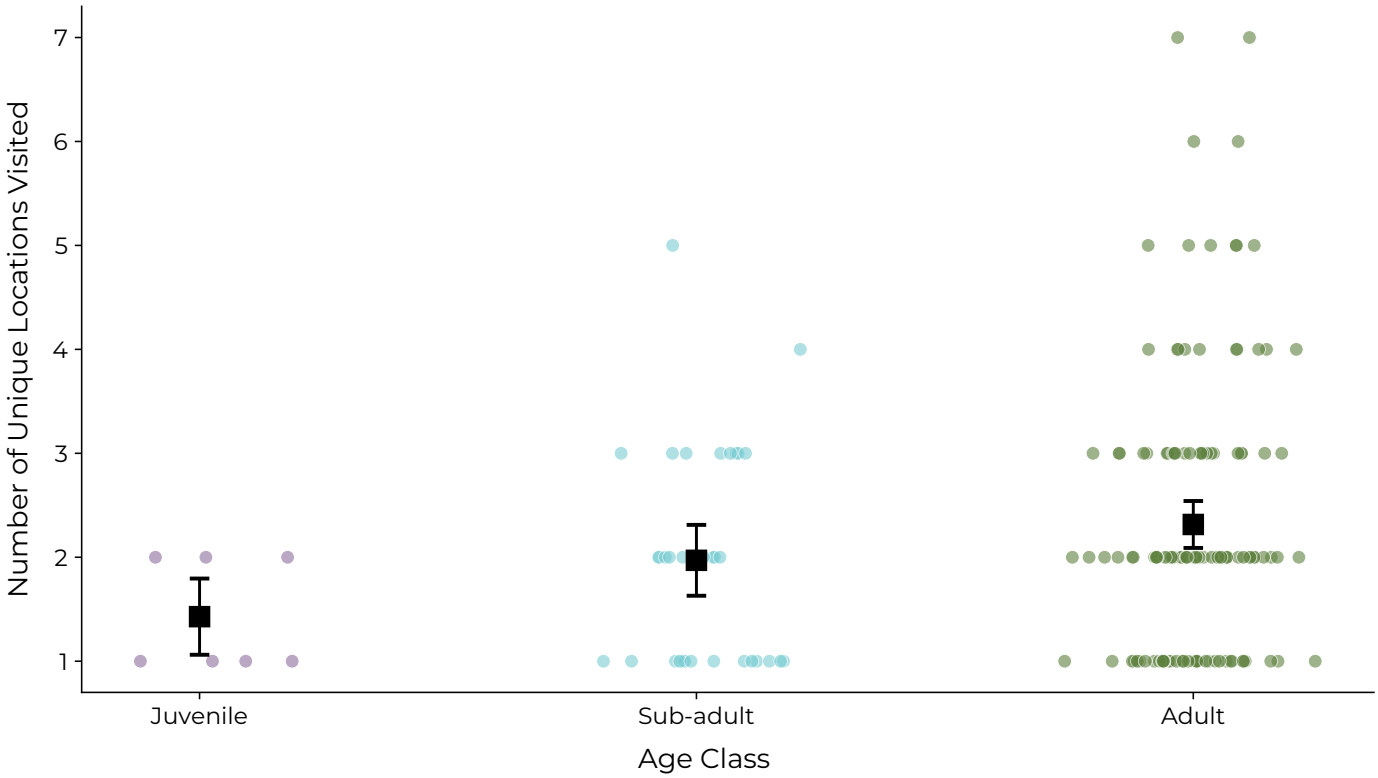

***Figure 21: Movement between locations by age-class**. Here, the number of unique locations where each individual was captured was used as a proxy for movement. The black square indicates the mean for each age class with the 95% confidence interval of the mean displayed by error bars.*

Combining the capture history of an individual with the population density at the individual's territory (Figure 26 in the appendix), there was a statistically significant but weak correlation between the number of territories visited with population density when we aggregated all age-classes (R^2 = 0.022, p = 0.038). The correlation was similar for adults (R^2 = 0.049, p = 0.040), but it was not significant for sub-adults and juveniles.

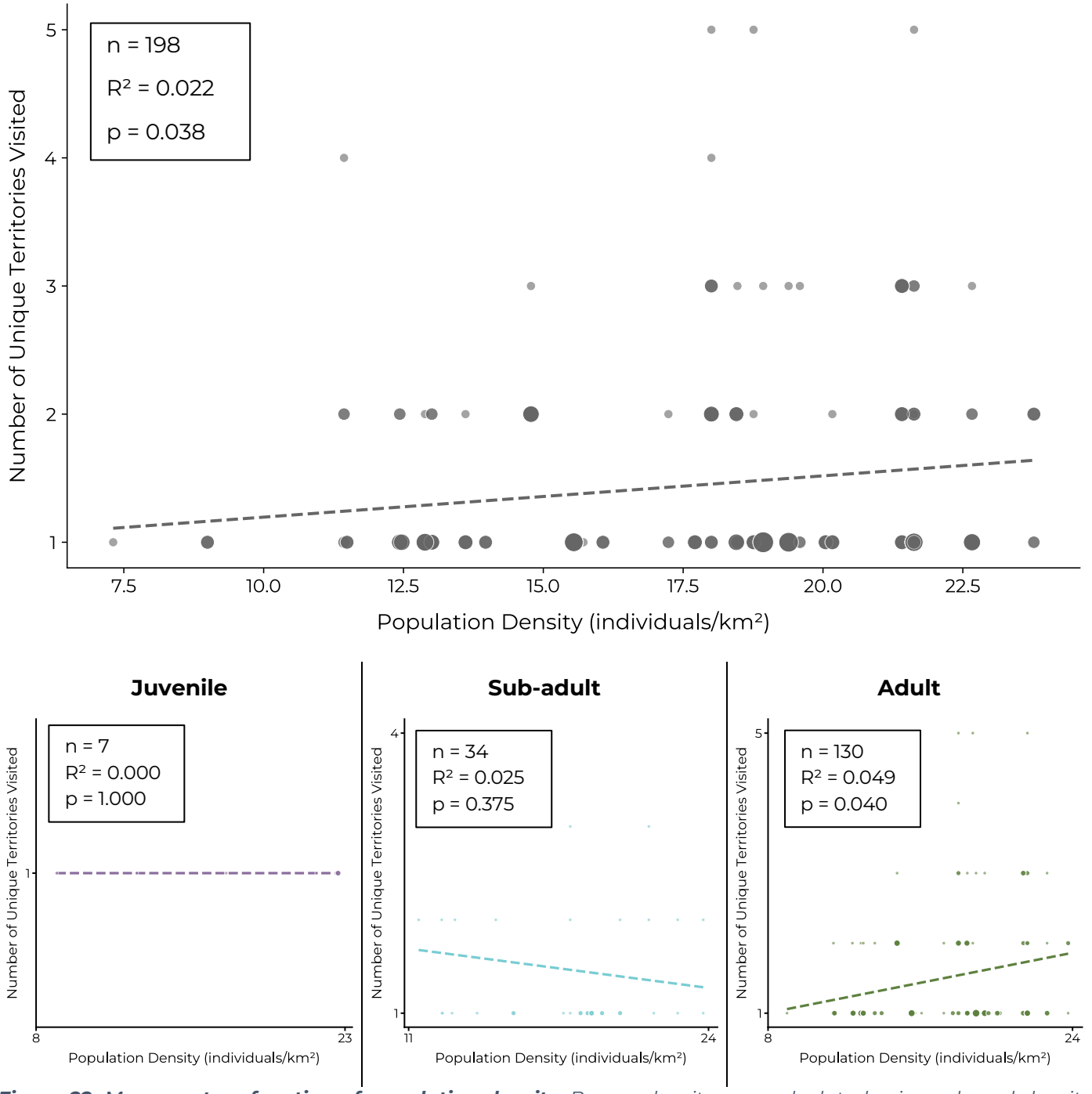

***Figure 22: Movement as function of population density**. Beaver density was calculated using a kernel density estimation at 50 m grid cells across the study area using our family size estimates. For each individual, the population density at the territory center of its assigned territory was used. Points indicate different individuals while larger points indicate multiple individuals of the same values.*

At the scale of territories rather than single individuals, we observed frequent interactions between territories (Figure 23). Interactions were defined as individuals of either territory being captured in the other territory. The most common interactions occurred between territories that were in close proximity to each other, although there were numerous interactions across territories that were also further away from each other (Figure 27 in the appendix). In some territories, the frequency of visiting individuals was very high; for example, in territories BE_08, BE_11 and BE_25, more than 60% of all camera trap events of beavers were of visiting individuals.

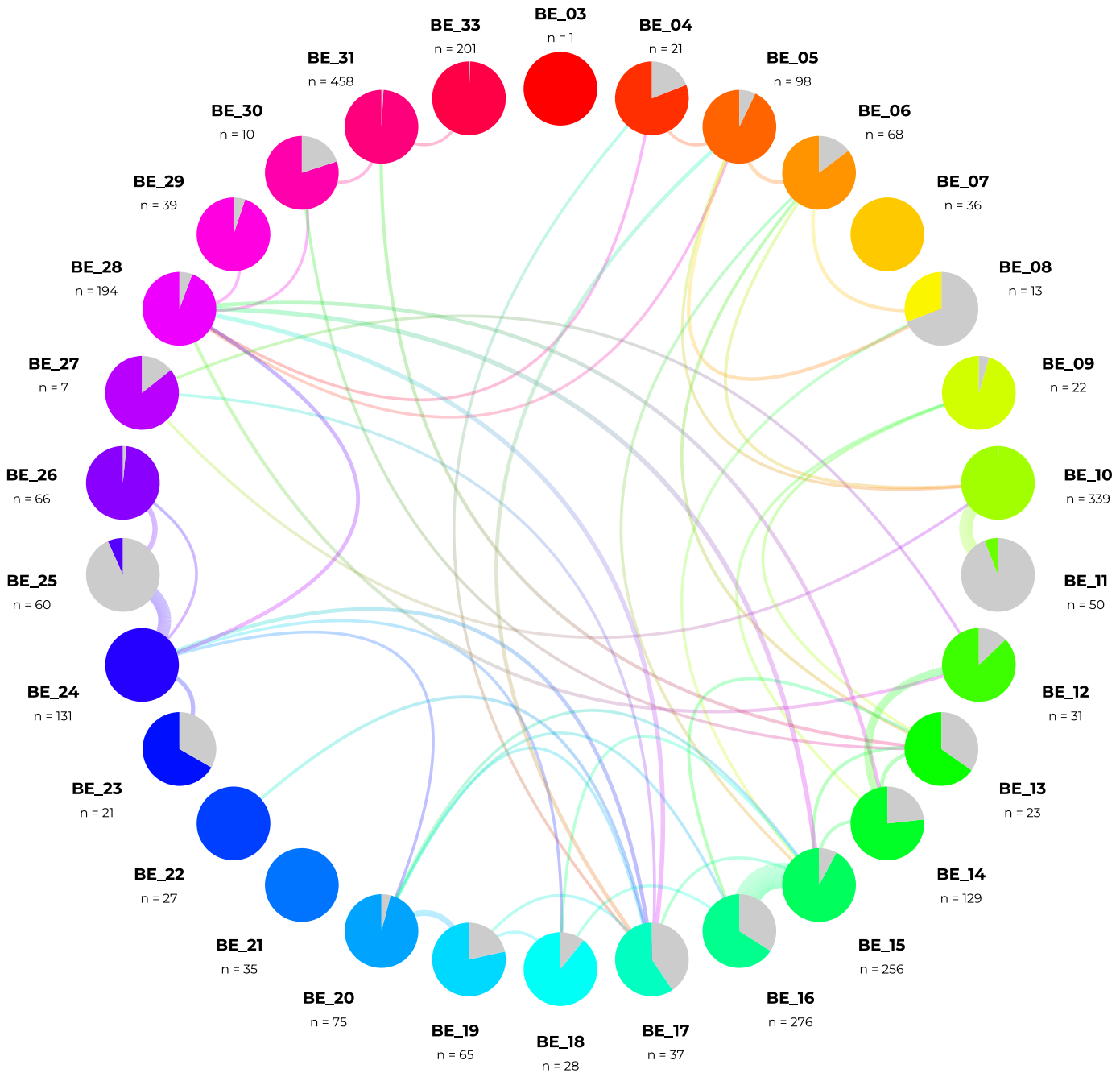

Figure 23: Interactions between the territories. *The coloured area of each pie chart represents the frequency of captures of beavers belonging to the respective territory. In grey, the frequency of visiting beavers is displayed. The total number of camera trap events that could be assigned to an individual is indicated for each territory. Lines connecting two territories represent interactions between the territories, meaning individuals of either territory were captured in the other territory. The thickness of the lines is scaled to the frequency of interactions.*

4. Discussion

Our observations of large family group sizes with a high adult-to-offspring ratio indicate a population at or near carrying capacity in our study area. The larger number of adults per family group is likely linked to the delay of dispersal in the offspring, first reported by Mayer et al. (2017c). Our observations of extra-territorial movements in several individuals support the theory that these individuals remain in the natal territory, to optimize their time of dispersal according to Mayer et al. (2017c). Some individuals might also not directly belong to a family group but live as floaters across a number of territories (Crawford et al., 2008). Altogether, we observed several mechanisms likely all working together to stabilize the population, even at high densities. Our study thus indicates that density-dependence of population growth might arise due to an interplay of several factors and is not just influenced by a single mechanism.

In the remainder of this discussion, we will first address the methodological improvements and limitations before shifting to ecological topics such as family size and age structure.

4.1. Methods

Using the described set up and design of camera traps, we were able to efficiently study family size and movement patterns in a large system of beaver territories. The use of camera traps allowed us to avoid the direct negative effects of more invasive methods, and to capture individuals that might have been missed using classical capture-mark-recapture methods using physical capture (Petit & Valiere, 2006). By optimizing both the camera trap set up as well as the pipeline for the analysis, we were also able to significantly improve the efficiency of gathering data in such manners.

Inspired by Dytkowicz et al. (2023), we added a diopter lens in front of the camera trap, allowing us to position the cameras closer to the ground, not only improving sharpness but also resolution on the tail (pixels/ tail area). While the improved quality of the images allowed us to make out even small differences between individuals, some individuals remained difficult to identify. This was mainly the case when the tails had no particular marks. In such cases, we had to rely mainly on the scale pattern itself, which was visible in most cases but only allowed for clear identification under certain lighting conditions. While SIFT-algorithms have been shown to work on scale patterns on the tail, this demonstration was performed under highly controlled lighting conditions, using DSLR cameras and stuffed beaver tails (Hinds et al., 2023). In our case, lighting varied considerably and as tails were wet to different degrees, images often displayed strong reflections. These image artifacts often interfered with the efficacy of the SIFT-algorithm, highlighting the need for a more sophisticated matching algorithm. Although these algorithms were not yet available due to the lack of training data, using the measured tail dimensions to aid in identification as well as an efficient user interface made it possible to confidently identify these difficult beavers in most cases. In the rare case where a tail was not recognizable, it was discarded and thus also had no effect on the results.

Using an improved calibration method to correct perspective skewing, as well as a more advanced algorithm to measure tail dimensions we obtained significant gains in both efficiency and accuracy. Although obtaining accurate measurements of tail length remained difficult, mainly due to the fur as well as the posture of the tail varying between images, this effect could be minimized by taking multiple measurements per individual, achieving a robust age class assignment.

The slowing accumulation rate of capture of new individuals, also suggests that we observed most individuals in each territory. Nonetheless, there were many individuals that have only been captured a few times or even just once. This was also dependent on the camera trap's position and the suitability for camera traps in the territory in the first place. While we consider 24 days to be sufficient to capture all individuals in our territories, longer study periods could enable more detailed findings especially regarding movement and discrimination of different life history strategies.

Conversely, longer study periods require efficient data processing to disentangle the family dynamics at a higher level of detail. Generally, our improvements to the camera trap setup, as well as our software BeaverFindr, made processing the camera trap data significantly more efficient and accurate. While more advanced matching algorithms could further speed up the process, the current pipeline was already a distinct improvement over previous methods, ultimately enabling us to study 30 territories with almost 200 individuals. With this large data set now annotated, it could also open the door for future projects, training more advanced algorithms for projects on a larger spatial or temporal scale.

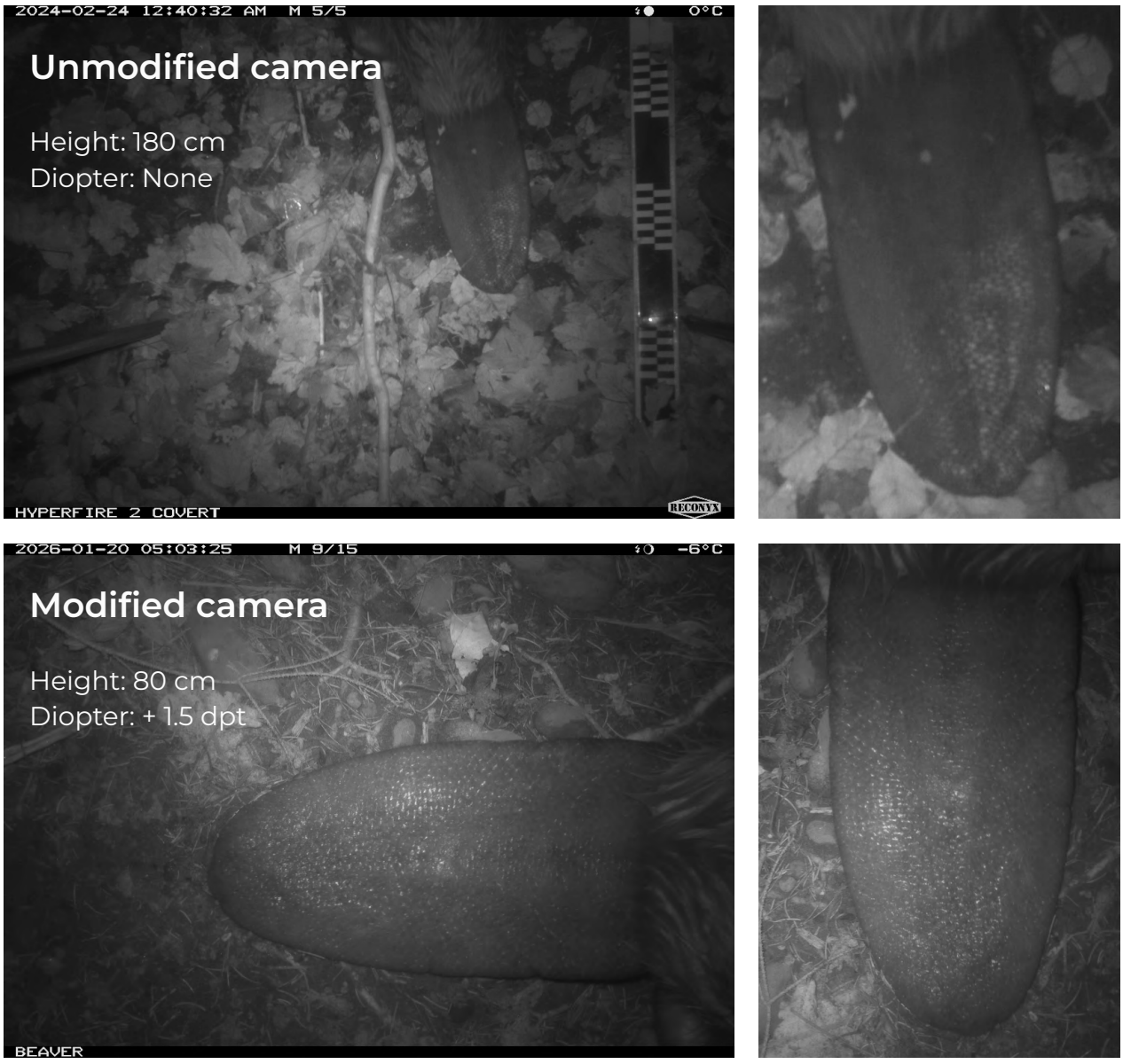

Figure 24: Two images of the individual TSI once using the previous camera trap setup and once using the improved setup. *In the image with the unmodified camera, marks are difficult to identify and distinguish from dirt on the tail and the scale pattern is only slightly visible. Using the improved camera trap setup, marks and scars on the tail are clearly visible as well as the scale pattern. Dirt or foliage can be clearly distinguished from marks on the tail.*

4.2. Family size and age structure

The observation of large family sizes with a high adult-to-offspring ratio suggests several life history adjustments at or close to a saturated population (Payne, 1984a; Rosell & Campbell-Palmer, 2022; Żurowski & Kasperczyk, 1986). In our study, we observed several families that held ten or more individuals, with the largest families reaching up to 16 individuals. A previous review of 13 studies on the Eurasian beaver found a mean range of 2.4 to 5.5 individuals (Rosell & Parker, 1995) with the largest reported family size of 18 individuals found in Russia (Goloduško & Fomenko, 1973). With the observation of these large family sizes while also observing them in close proximity to each other, we are confident in our assumption that the population in the area is close to saturation.

This premise is further strengthened by the low number of observations of juveniles across the study area, which is likely linked to slowing population growth and delayed dispersal. It is a widespread phenomenon that growth rate is negatively correlated with population density (Ceballos et al., 2005) and while for the beaver, this could be due to a variety of factors (Rosell & Campbell-Palmer, 2022), a study in the North American beaver found density-dependence of reproductive rate (Payne, 1984b).

At low population densities, offspring tend to disperse within 1-3 years (Payne, 1984b; Sun et al., 2000). At high population densities in Southern Norway, Mayer et al. (2017c) however found a mean age of dispersal of 3.5 years with certain individuals delaying their dispersal for more than 5 years. We cannot directly infer the age of our individuals as that would require a long-term monitoring project. Nevertheless, the observation of a very high adult-to-offspring ratio, with certain territories holding up to 11 adults, is a strong indication for delayed dispersal. It seems very likely that in such territories, several adults stemmed from previous generations of offspring, having delayed their dispersal for an unknown number of years, as previously reported by Mayer et al. (2017c).

With the high frequency of movement of individuals across territories, it is possible that some individuals have been misassigned. Some lodges were very close to each other and thus, delineating territory borders was not always straightforward. We tried to place the upstream and downstream camera traps in areas of very high density as close as possible to the territory center. However, some of these camera traps might have been accidentally placed in the adjacent territory, which may have led some individuals to be misassigned to the wrong territory.

Generally, territories with close neighbors showed a higher number of interactions and thus it could potentially also be a single territory consisting of two separate and active lodges. In some territories, beavers can build several lodges and move between them based on seasonal preferences (Rosell & Campbell-Palmer, 2022). The simultaneous occupation of two lodges to accommodate larger family groups is, however, less reported (Crawford et al., 2008). We observed frequent interactions between several territories that were closely positioned to each other. In case of territories BE_25 and BE_24, whose lodges were only 280 m apart, we assigned 3 and 13 individuals to the territories based on capture patterns. Depending on the placement of and activity captured by the camera traps, it could also be that some of these individuals were accidentally assigned to the larger BE_24 family group, simply because its camera traps were more effective at capturing beavers. Splitting the total of 16 individuals equally across both lodges would return a more realistic 8 individuals per lodge. Similarly, in territories BE_30 and BE_31, capture rates were low at BE_30 and thus splitting the assigned 4 and 16 individuals would result in 10 individuals each.

The observations of very high family sizes in one of the two territories could therefore originate from our sampling design and the way we assign individuals to a territory. This would then however also imply an underestimation of territory interactions, further fueling the question whether a territory could potentially consist of two (or more) subgroups. Whether these represent two separate families or simply two subgroups of an overall large family remained unknown. In either case, both scenarios are consistent with our general observations of large families due to high population density.

In the case of the territories BE_15 and BE_16 (415 m apart) we also observed strong interactions but had 12 and 13 individuals assigned each. Here, equally distributing the individuals across both territories does not result in lower family sizes, suggesting that these large family sizes are not just an artifact due to misassigning individuals or the sampling design.

While acknowledging the limitations due to sampling design, we are confident that our observations are accurate. Even if select individuals could've been misassigned, the overarching family sizes are still surprisingly large. The observation of a very high adult-to-offspring ratio further strengthens our premise that the population is at or close to saturation, demonstrating significant shifts in life history.

4.3. Movement and territoriality

The evidence for delayed dispersal by offspring would in turn suggest that a large proportion of individuals are waiting to occupy their own territory. Generally, it is hypothesized that beavers are well informed on neighboring territories and population density, as well as the state of their conspecifics (Mayer et al., 2017c). This information is gathered through regular exploratory movements which have been well-documented in the past (Aleksiuk, 1968; Havens, 2006; Van Deelen, 1991). This is in accordance with our observations where several individuals could be captured in various territories. In Norway, a study could track subordinate individuals intruding up to 5 different territories, while dominant adults mostly intruded neighboring territories (Mayer et al., 2017b). In our study, we did not differentiate between dominant and sub-ordinate individuals, but nevertheless we also observed individuals that were observed in up to 4 foreign territories.

However, while we did record many individuals with extra-territorial movements, the captures per individual were usually not numerous. Using GPS-transmitters, Mayer et al. (2017b) could show that individuals outside their home range would spend more time in the water and travel more quickly. While these behaviours most likely seek to avoid detection by dominant individuals, they probably also led to reduced capture rates on the camera traps. We aimed to place upstream and downstream cameras in land spots between two water bodies, where exploring individuals would be forced out of the water and thus be more likely to be captured. However, such locations were not always feasible, meaning extra-territorial movements are likely still underestimated.

In previous studies, extra-territorial movements were documented for 30-60% of the sub-ordinate individuals that were followed (Hartmann, 1997; Havens, 2006; Mayer et al., 2017b). In our case, we captured 32% of all sub-adults and 33% of all adults in 2 or more territories. However, for some individuals the number of captures was rather low and spread fairly homogenously across territories. With no observed center of activity, this could also be due to the so-called floating strategy and not necessarily forays from sub-ordinate individuals.

Floaters are individuals that live temporarily in territories to which they are not related to (Crawford et al., 2008). Contrary to individuals on extra-territorial forays, floaters do not have a territory on their own but move across established territories in the area. While floaters are mentioned in a variety of studies (Crawford et al., 2008; Havens, 2006; Svendsen, 1980), there is little documentation of the life history of floaters and to what extent they contribute to the guest family and to what extent they are tolerated by the dominant pair. Rosell & Bjørkøyli (2002) tested the "dear enemy" hypothesis using scent marking of neighboring or floating conspecifics, whereby dominant individuals appeared to react more aggressively towards non-territorial floaters. Nevertheless, Crawford et al. (2008) suggested that these unrelated individuals can sometimes also be tolerated in a family and potentially even take over the territory, if one of the dominant individuals disappears.

At high population densities, the frequency of floaters among territorial individuals is estimated to reach up to 20% (Molini et al., 1980). Differentiating between floaters that are moving across territories and sub-ordinate individuals, exploring beyond their territory boundaries is however not feasible on the basis of non-invasive imagery of camera traps. Individual genetic information would help trace

individuals to their territory of origin and relatedness, and longer studies would allow following individuals over multiple years. In our case, we assigned each individual to a unique territory, even though the individual might actually be floating across different territories and might actually be unrelated to the family itself. As each individual could be followed across the whole study area, the risk of double counting was minimized, and the family group size (during the study period) was not accidentally inflated.

4.4. Ecological synthesis

Our observations of large family group sizes together with the high adult-to-offspring ratio indicate that the population in our study area is close to - or has reached – carrying capacity (Payne, 1984a; Rosell & Campbell-Palmer, 2022; Żurowski & Kasperczyk, 1986). Under such conditions, only the fittest animals can successfully occupy and defend a territory (Kokko & Ekman, 2002; Mayer et al., 2017a; Sun et al., 2000). To increase their fitness, offspring delays dispersal, as evidenced by high observed ratio of adult individuals. The small number of juveniles across the study site suggests that the reproductive rate decreased and there might be years of no offspring, as documented in other studies (Campbell, 2010; Parker et al., 2017). Therefore, the increased family size potentially arises as a result of a delayed slowing of the reproductive rate. In this case, the increased family size might be only temporary, reverting to a stable state at lower family group sizes. The outcome will most likely also be determined by the sites resource availability (Rosell & Campbell-Palmer, 2022). While the conditions of such a stable state require further research, our study illustrates some of the mechanisms by which this stable state might be achieved.

Besides the large family group size, we observed many individuals exploring beyond their territory borders. While we cannot distinguish between floating strategies and extra-territorial forays of subordinate individuals, both possibilities suggest that there is a larger fraction of individuals that are under the intention of occupying their own territory. A study on the Canadian beaver reported that disappearing territories can be quickly filled by surrounding sub-ordinate individuals (Svendsen, 1980). A similar process could occur in our study area, suggesting extra-territorial movements are an additional factor that benefits the stability of the population.

All our observations indicate that in our study area, the population has reached or is close to a saturated and possibly stable state. Through changes in life history traits, such as family size, age structure and territoriality – factors that also interact with each other – the Eurasian beaver might be able to reach a stable population, without significant predatory or anthropogenic hunting pressure.

As Meier (2023) found smaller family sizes (2.53 individuals in 15 territories) in low-density area and we observed an average of 6.6 individuals per family in a very dense population, we see no immediate need to change the assumption of 5 individuals per family for the national beaver survey (Angst & Auberson, n.d.). Our study could demonstrate however that locally, the actual family size can vary to a surprising extent. As these larger family sizes are linked to the high population densities, the modelling of this density-dependence might unveil larger uncertainties in the estimates of population size than expected. Additionally, the high adult-to-offspring ratio and the observation of extra-territorial movements leads us to believe that in case a dominant individual or pair will disappear, the territory will be quickly occupied again. In light of the new hunting ordinance, this could significantly reduce the effect of selectively culling beavers that are causing considerable amount of damage. If these individuals were to be removed, the re-colonization of the area could happen quickly and increase costs in the long term. Non-lethal measures thus might be more costly at first, but more cost-effective in the long run.

5. Conclusion

At high population density, the Eurasian beaver can alter its life history to maintain a stable population size. In our high-density study area in Switzerland, we observed demographic shifts across the population due to a delay in dispersal and a reduced number of offspring, which ultimately resulted in larger families consisting of adult individuals. As suitable unoccupied territories had become rare, we recorded many individuals on extra-territorial forays, probably collecting information on the surrounding population status. We also gathered strong evidence that part of the population consisted of floating individuals, moving across territories with no clear home range. These observations of floaters alongside delayed dispersal and extra-territorial forays thus indicate that population growth levels off at high density through an interplay of several factors.

With almost 200 individuals across 30 territories, we were able to study life history traits of the beaver at an unprecedented scale, particularly considering the non-invasive techniques that we employed. This was achieved by optimizing our methodology and developing the BeaverFindr software, enabling more efficient data collection and individual identification. Our advancements should therefore also pave the way for subsequent studies, further disentangling key mechanisms in the beaver's life history and understanding its ecological relevance.

The frequent observations of extra-territorial movement and the presence of floating individuals both lead us to believe that disappearing dominant individuals will quickly be replaced by exploring subordinate or floating individuals. Regarding the revised hunting ordinance, this could have severe implications as the removal of individuals through culling could be offset by exploring individuals ready to take over the territory. We captured visiting beavers in numerous territories. It is realistic to assume that some of these individuals would take over the newly unoccupied territory. As such, sustainable management solutions might be more costly upfront but offer greater cost-effectiveness in the long term.

6. Literature

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7. Acknowledgments

This project was only possible thanks to the help of numerous people. I would like to thank Stefano Canessa for his supervision and support throughout my Bachelor and Master thesis. Christof Angst first inspired me to work on this research topic and helped me whenever I had questions regarding the study species. Both of them also helped me immensely while finalizing this thesis by providing generous feedback.

Together with Silvan Minnig, they also provided me a large part of the field materials needed, from camera traps to the mounting frames. I also received additional technical support from Alejandra Morán Ordóñez and Andrin Dürst.

Before placing cameras in the field, I also had very insightful discussions with Kurt Grossenbacher, who knows the study area and the local beaver population inside out. I want to extend my gratitude to the Canton of Bern as well as Lorenz Hirni who granted me permission to access the nature reserves in the study area.

Justin Thinner from Reconyx provided me with the necessary information to improve the camera trap optics with Lisa Moser being involved in providing the diopter lenses for the camera. I also thank Emmanuel Lucchini who 3D-printed the lens holders for the camera traps.

During the whole field season, I could count on many generous and kind helpers. Matilda Angeloni, Valeria Benz, Rémy Desaules, Dominik Epli, Colin Guignet, Adina Hermes, Shaquille Matthys, Céline Partridge, Pascal Pini, Sofia Roque-Avilés, Amélia Rottmeier, Janis Steiner and Michael Wyss all contributed to really enjoyable days in the field, even if the weather didn't always have the best intentions.

Finally, I would like to thank my parents and my grandmother, who supported me from day one in pursuing my dreams. My parents also had to put up with the occasional dirty car after fieldwork, not to mention half a ton of sugar beets in the garden, before we could put them into the field.

8. Appendix

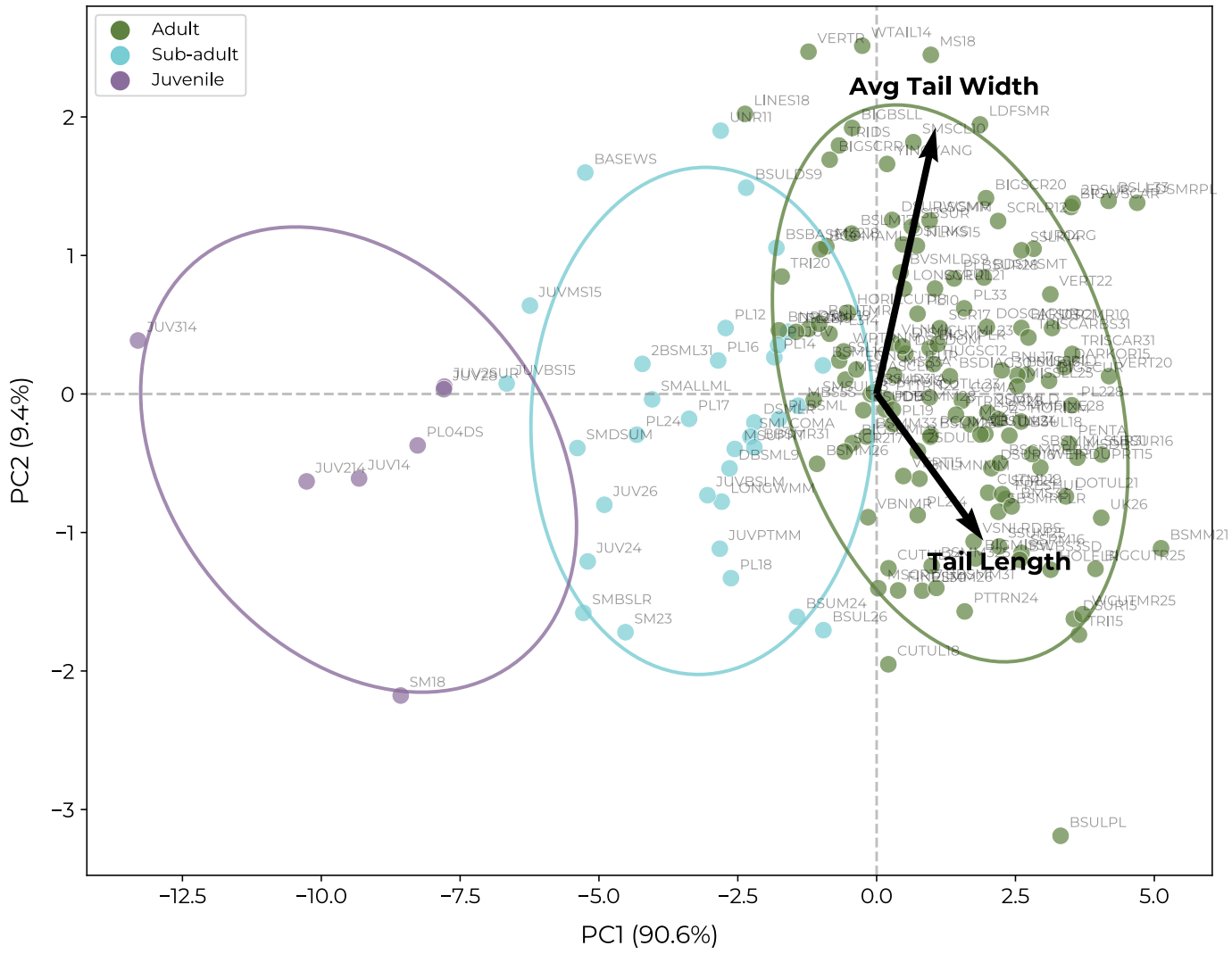

Figure 25: PCA for the tail dimensions. *We used both the tail length and average tail width as components. The proportion of total variance explained is indicated in parentheses for both components. The confidence ellipse for each age class was also used to calculate the difference between each age class.*

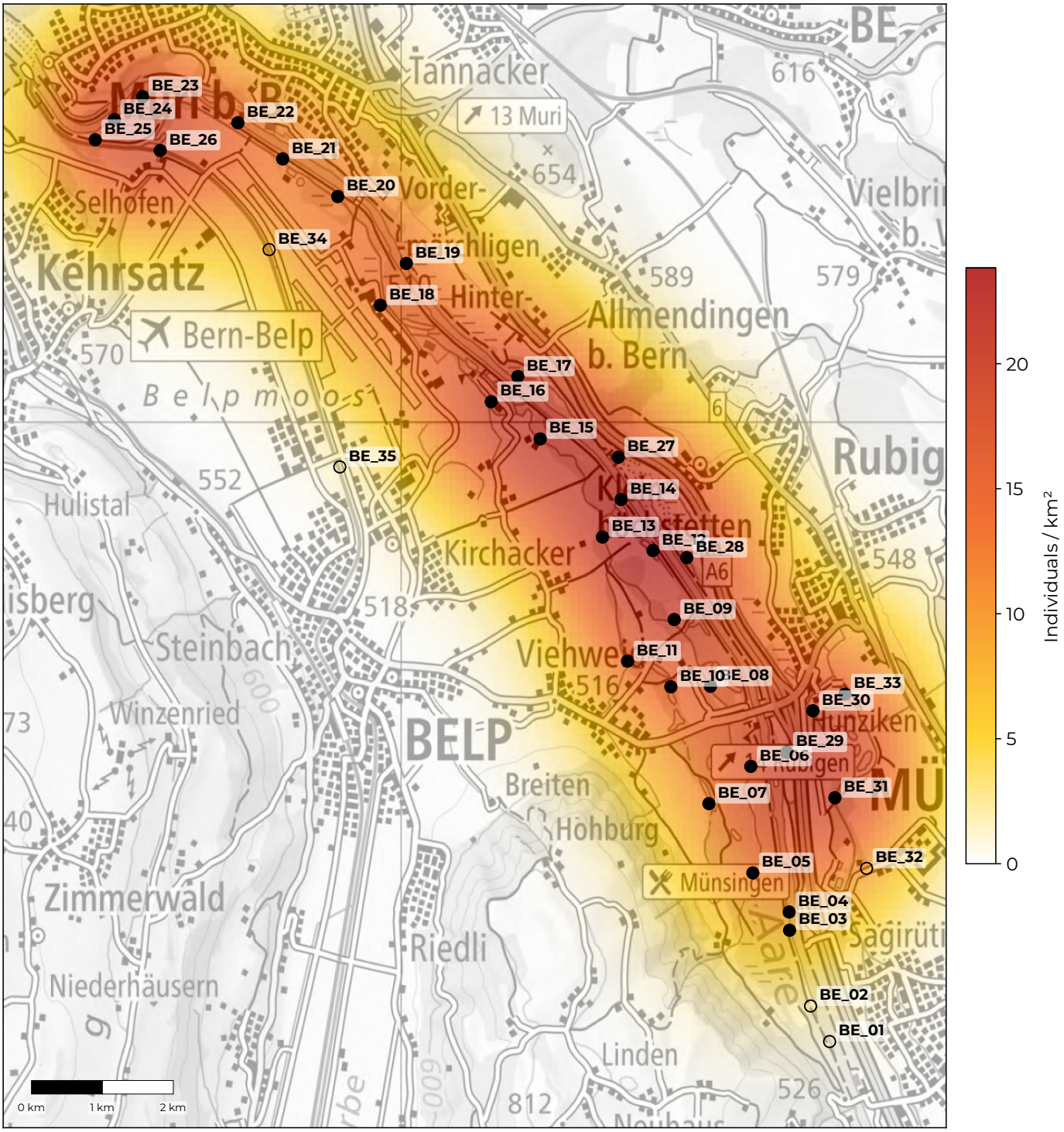

Figure 26: Beaver density across the study area. *The density (represented as individuals per 1 km²) was calculated using kernel density estimation on the basis of the assigned family sizes. We used a bandwidth of 500 m at a grid size of 50 x 50 m.*

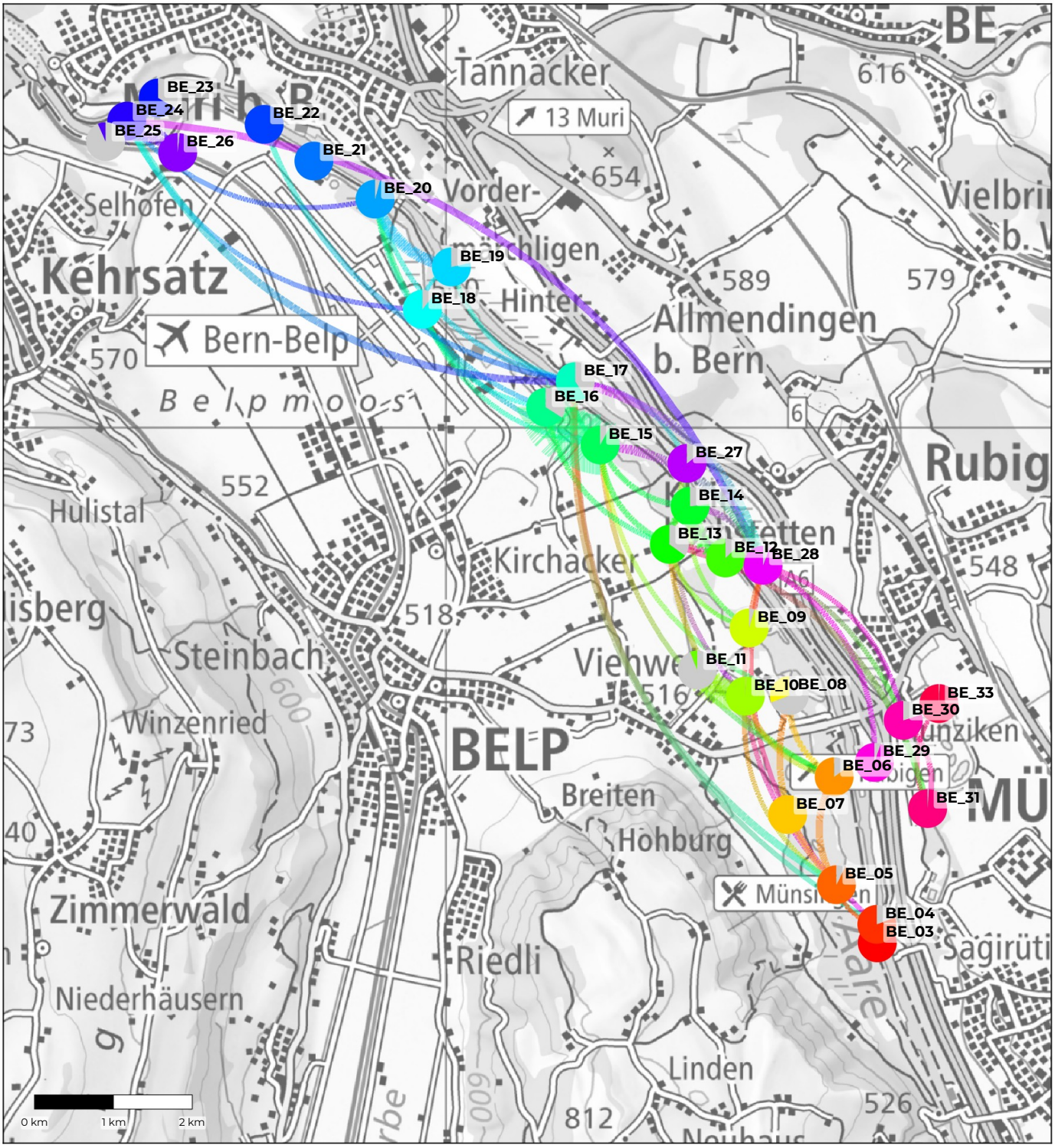

Figure 27: Territory interactions across the study area. *Each pie chart corresponds to one territory. The coloured area of each pie chart represents the proportion of captures of beavers belonging to the respective territory. In grey, the frequency of visiting beavers is displayed. Lines connecting two territories represent interactions between the territories, meaning individuals of either territory were captured in the other territory. The thickness of the lines is scaled to increase with the frequency of interactions.*