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Reflects chemical communication of Eurasian beaver's density-dependence?

Diploma Thesis

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ZADÁNÍ DIPLOMOVÉ PRÁCE

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Ochrana přírody

Název práce

Je teritoriální chemická komunikace odrazem populačních parametrů?

Název anglicky

Reflects chemical communication of Eurasian beavers density-dependence?

Cíle práce

Chemická komunikace bobra evropského se odehrává za pomoci uvolňování sektretu anaálních žláz obsahujících olfaktorické informace; způsoby komunikace jsou jednak šířením informací vodními toky anebo umisťováním sekretu na pachové stoličky na břehy osídlené bobrem. Je dosti již známo o tom, že k intenzivnímu značení dochází nejčastěji na jaře (Svendsen 1980), a co je v principu obsahem sdělení (Rosell et al. 2002). Částečná je znalost důvodů prostorové distribuce uvnitř teritorií (Rosell et al. 1998), zároveň se dosti ví o vztahu mezi uspořádáním a velikostí rodiny a množství pachových známek (Rosell & Nolet 1997).
Intenzita a distribuce chemické komunikace tak pravděpodobně může odrážet míru a riziko kompetice mezi rodinami.
Cílem práce bude vyhodnocení vztahu distribuce a intenzity komunikace ve vazbě na hustotní charakteristiky populace. Základní hypotéza bude znít: pachová komunikace není závislá na vzdálenostech sousedících teritorií bobrů.

Metodika

Práce bude probíhat dle následujícího schematu:

1. shromáždění základního balíku hrubých vstupních dat (ze sbírek katedry ekologie FŽP) a nastavení základního prostorového rámce

2. formulace vyhodnocovaných faktorů (vztahů), parametrizace vech faktorů

3. prostorová analýza sebraných dat

4. statistická analýza prostorově populačních vztahů

Doporučený rozsah práce

40-60

Klíčová slova

bobr evropský, chemická komunikace

Doporučené zdroje informací

Aleksiuk M., 1968: Scent-mound communication, territoriality, and population regulation in beaver (Castor Canadensis Kuhl). Journal of Mammalogy 49(4): 759–762.

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Děkan

V Praze dne 11. 04. 2016

Declaration

I hereby declare, that this Diploma Thesis was elaborated independently under the guidance of Aleš Vorel, and that I quoted all the literary sources used.

In Prague, April 19 ....

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Abstract

Reflects chemical communication of the Eurasian beaver's density-dependence?

Almost all studies about population density describe certain dependency: with higher population density increased intensity of chemical communication. This is provided by many authors on different animal species. However this study showed that chemical communication does not reflects density-dependence of the Eurasian beaver. Explained variability of final model was $r^2 = 0.02586101$, but with no significance for both variables. However some relationships were tested. Correlation between biomass (amount of consumed woody resources) and number of shelters (beaver nests) was not significant, but correlation between number of shelters and distance was positively significant. This lead to test the alternative special model (mc) where dependency of number of lodges and its changing distance was tested. This model was significant ($p = 0.007182$) and was discovered new relationship in population parameters of beaver populations: with increasing distance increased number of shelters.

Main focus of thesis was to study how the distribution and intensity of the chemical communication is related to parameters of population density. The result was: with increasing distance the intensity of chemical communication doesn't increase.

Keywords: European beaver, chemical communication, population density

Abstrakt

Je teritoriální chemická komunikace bobra evropského odrazem populačních parametrů?

Téměř všechny studie, zabývající se populační denzitou, popisují jistou závislost: s rostoucí populační denzitou roste intenzita chemické komunikace. Tento vztah podporuje celá řada autorů na studích mnoha druhů zvířat. Nicméně předkládaná studie ukázala, že chemická komunikace neodráží hustotně-populační vztahy bobra evropského. Vysvětlená variabilita výsledného modela byla r^2 = 0.02586101, ale výsledek testu nebyl pro obě proměné signifikantní. Nicméně jisté vztahy byly otestovány. Korelace mezi biomasou (množství zkonzumované hmoty-kůra, lýko a větvičky) a počtem obydlí (bobří hrady) nebyla signifikantní, ale korelace mezi počtem obydlí a vzdáleností ano. Následovalo testování speciálního model (mc), kde byla testována závislost počtu hradů na jejich měnící se vzdálenosti. Tento model vyšel signifikantně (p = 0.007182) a byl zjištěn nový vztah mezi populačními parametry u bobra evropského: s rostoucí vzdáleností roste i počet hradů.

Hlavním cílem této práce bylo zjistit, jak distribuce a intenzita chemické komunikace odráží parametry populační denzity. Výsledkem bylo: s rostoucí vzdáleností neroste intenzita chemické komunikace.

klíčová slova: bobr evropský, chemická komunikace, populační densita

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1 Introduction

The new beginning of the Eurasian beaver (*Castor fiber*) in the Czech Republic has become from the 70 th of the 20 th century. Due to the actual environmental conditions of the cultural landscape, beaver can spread almost without restraints. Beaver is still spreading to new regions and while the older populations are close to saturation point. Beaver's spread is quite limited by the quality of habitat, migration abilities of the species, natality-potential production of new migrants, but the crucial factor of settlement is distribution of preferred woody plants (VOREL et al. 2012). Establishing of long-term populations in the Czech Republic is conditioned with substitution of woody plants willow (*Salix spp.*) and poplar (*Populus spp.*) (VOREL et al. 2012).

Beavers defend their territories by using chemical signals by placing of so called scent-marks. These scent-marks are not exposed neither spatially nor temporally random but there is a different pattern in intensity during the year and occupied space. This study considers and describes basic territorial behaviour of the beavers in West Bohemian Region of the Czech Republic.

Chemical communication of the Eurasian beaver is accomplished by secretions of anal glands containing bulk of olfactory information; these are spread by watercourses or placed on scent-mounds on banks of water system where established beaver territories are.

It's well-known that beavers mark mostly during spring (SVENDSEN 1980), also is clear what chemical compounds and data marks contain (ROSELL et al. 2002). However, knowledge partly lacks known about spatial proximities of the scent-marks within the territories (ROSELL et al. 1998); on the other hand there is a lot of studies about relationships among organization and size of the beaver family and the number of the scent marks (ROSELL & NOLET 1997).

Frequency and distribution of chemical communication may probably reflect the rate and the risk of competition between the families; and the problem become more important with increasing population density of the populations.

2 Backgroung research

2.1 Mammal scent communication and importance of scent marks in territoriality

Scent communication

Specific groups of animals, especially terrestrial (or semiaquatic) species of mammals, communicate by using of scent communication. The usual way is using scent marks or specific places that animals mark by their scent, using for instances faeces, urine or the secretions of the specialized skin or anal glands. And these marks may contain a lot of information, but the main meaning is its role in territorial advertising or defence. The behaviour helps to maintain territories (i.e., rights to its holding).

Chemical communication is very difficult to study, because of man's limited smell abilities (TARASOV 1960). However, there are a several studies of scent communication in the wolf (*Canis lupus*-FULLER & NOVAKOWSKI 1955), the rabbit (*Oryctolagus cuniculus*-LYNE et al. 1964) and the pika (*Ochotona princeps*-HARVEY & ROSENBERG 1960) etc. that confirm important role of the scent communication during establishing or maintaining of spatial and temporal population structure.

The role of scent marks in olfactory communication: (1) warning for intruders, (2) sex attractant or stimulant, (3) signing the brief of the territory, (4) an information about individual (JOHNSON 1973), (5) an indicator of abundance (WYNNE-EDWARDS 1962) and (6) orientation of young or dispersing individuals (ROSENBLATT et al. 1969, GREGORY & PFAFF 1971).

Importance of scent marks in territoriality

Some of the mammal species use marking behaviour to maintain their territories. As JOHNSON (1973) mentions marking behaviour plays a role in territorial defence. ALLEN et al. (1999) in their study supported a strong relationship between scent-marking and territoriality in coyotes.

We can find important changes in scent marking during the mating season (RICHARDSON 1985). It's a special case, because scent marking behaviour is stable, except of the mating season when aggressive territorial scent marking occur

(RICHARDSON 1985, 1987a). On the other side it is clear that animals try to avoid fighting whenever possible (PARKER 1974, MAYNARD SMITH & PARKER 1976).

The size of the territory influences rates of scent marking, because in smaller territories scent marking occur at significantly higher rates (especially in males). The bigger size of territory the lower rates of scent marking occur. While there is a certain size of the territory when the intensity of scent marks no longer decreases, because there exists a minimum amount of scent marks that is still effective (RICHARDSON 1991). The reason why the lower rates of scent marking in bigger territories has economical and energetic perspective (KRUUK 1978, BARETTE & MESSIER 1980, MACDONALD 1985, STAMPS et al. 1987). KRUUK (1978) mentions Eurasian badger (*Meles meles*).

According to RICHARDSON (1991) there are several patterns of scent marking in aardwolves (*Proteles cristata*). He found a higher rate of scent marks at borders and so related more intense territorial behaviour. ALLEN et al. (1999) show a preponderance of scent marks found in the periphery of territories; where scent-marking seems to be strongly associated with the establishment and maintenance of these boundaries between packs of coyotes competing for the same resources in a limited space. LINDEMANN (1955) reported that European lynx (*Lynx lynx*) placed scent marks near the borders. Contrary MILLS et al. (1980) found an absolutely different pattern in Brown hyena (*Hyaena brunnea*), the highest densities of scent marks near to the centre of the territory and decrease towards the borders.

One of the patterns of scent marking was that scent marking rates were related to presence of neighbouring territories (MOORCROFT et al. 1999). If the territories had not common border, both sexes of aardwolf marked significantly fewer (RICHARDSON 1991). PETERS & MECH (1975) also found the higher density of scent marks in border zone and GORMAN & MILLS (1984) supply that this certain pattern of scent marking is dependent on territory size.

2.2 Territoriality of the Eurasian beaver (*Castor fiber*)

For definition of territoriality as well as for base lines and role of chemical communication of beavers we can use results of research of the North American beaver (*Castor canadensis*) as well as information about the Eurasian beaver (*Castor fiber*). There exist in scientific literature often overlays among both species, which are ecologically and biologically very close similar.

2.2.1 Family structure

Beaver families are typically composed of the adult pair, more generations of subadults born previous year or the year before last and kits (juveniles born this year) (WILSON 1971). The number of animals can vary between 3 to 8 individuals per family, but maximum can be even higher, actually almost 15 individuals (HAMŠÍKOVÁ et al. 2009). For example HAY (1958) mentions 6,3 and NOVAK (1977) 7,53 family members.

Family of beavers usually lives in lodge-construction of mud and branches with several chambers and several underwater entrances (MÜLLER-SCHWARZE & HECKMAN 1980).

2.2.2 Territories

MÜLLER-SCHWARZE & HECKMAN (1980) describe territory as region of highest beaver activity in vicinity of lodge.

The number of individuals in territory is mostly dependent on the habitat quality (HAMŠÍKOVÁ et al. 2009).

2.2.3 Population

Beaver population density can vary spatially and temporally. Some of factors that influence population density are: trapping, habitat and water quality, space for possible expanding, diseases, local predation and territoriality (BAKER & HILL 2003).

2.2.4 What territory means for beaver

Defending area-territory means important and exclusive access to food resources (DAVIES & HOUSTON 1984). BROWN (1964) describes territory as an "economically" defendable area.

2.2.5 Scent communication

Beavers use chemical communication of obvious causes. One of them is well developed smell. While they are primarily nocturnal species, they can't communicate for long distances also they can't rely on sight eye vision (TANG et al. 1993). The only long distance communication (acoustic) of beavers is tail-slapping (ROSELL et al. 1998). The quality of smell plays role as well.

The way how beavers use of chemical communication is scent marking with use of fluid of beaver glands or urine (ROSELL & NOLET 1997). The fluid is called castoreum (ROSELL & SUNDSDAL 2001).

The marks are probably non-randomly distributed within settled sites, in part are placed inside the territories but also outside of them.

Communication by scent marks has a high persistence for a quite long period of time and for beavers is not necessary every day presence of the animal at marked position (WYNNE-EDWARDS 1962).

2.2.6 Beaver glands, functions of castoreum, scent marks

Beaver glands

The beaver has a two pairs of glands: anal glands and castor glands (castor sacs). Castor sacs are located between the kidneys and urine bladder and contain a fluid called castoreum. Anal glands (oil glands) contain anal gland secretions. The odor of castoreum can vary in dependence to diet, but anal gland secretions are specific for each individual (SUN & MÜLLER-SCHWARZE 1998).

Castoreum contains many compounds, up to now 45 of them have been identified (LEDERER 1950). One of the most interesting is castoramine (LEDERER 1950, MAURER & OHLOFF 1976).

There is no difference in compounds of castoreum between sexes (ROSELL & SUNDSAL 2001, SUN & MÜLLER-SCHWARZE 1999).

Functions of castoreum

JOHNSTON et al. (1993) have demonstrated that castoreum can carry different information and, thus have different functions. ALEKSIUK (1968) describes that function of scent marks is a warning for intruding or neighbouring beavers. However WILSSON (1971) have suggested that the castoreum does not keep trespassers away from the territory, its function is mainly advertising about the ownership of the territory. On the other hand ALEKSIUK (1968) showed that beavers in neighbouring territories avoided areas already occupied. This statement may interest; because WILSSON (1971) studied Eurasian (*Castor fiber*) beavers and Aleksiuk studied the North American beaver (*Castor canadensis*).

One of the functions of castoreum is likely role in pair formations (WILSSON 1971). And it‘s possible that castoreum influences the territorial behaviour of the group members (WILSSON 1971). Castoreum can also contain information that helps distinguish family members from non-members and neighbours from a complete stranger (SCHULTE 1998).

Furthermore signals in castoreum may synchronize sexual activity of adult beavers (HOULIHAN 1989).

Scent marks

Beavers of different ages place their scent and so make scent marks. WILSSON (1971) describes scent marking behaviour even for females less than two months old, but in their castor sacs there’s no castoreum yet. The marking intensity increases with age and the most of the scent marks are placed by males (HODGDON & LANCIA 1983). Beavers make scent marks mostly in spring with peak in April (HODGDON 1978, SVENDSEN 1980). SVENDSEN & FABEL (1977) observed the biggest activity of scent marking in May and June in Ohio.

For placing the castoreum beaver builds scent mounds or sign heaps. On these constructions of mud or other bank a material beaver noisily depose castoreum. These piles of mud can vary in size (MÜLLER-SCHWARZE 2011), but it is interesting when compared sizes of mud piles in the North American and Eurasian beavers.

There are other differences between these two species that are in constructing of the piles of mud. ALLRED (1986) describes the North American beavers usually carrying mud in their front paws while walking bipedal to construct a scent mound, while WILSSON (1971) have never observed this behaviour in the Eurasian beavers (they only scratch mud or earth together and make a pile).

To build these constructions beaver uses specific movements (scratching and shovelling). However for beavers is possible to deposit the castoreum on felled tree trunks and other natural hills (WILSSON 1971) or they often use a twisted bunch of grass (MÜLLER-SCHWARZE 2011).

According to MÜLLER-SCHWARZE (2011) there are plenty of reasons why the beavers first build a mound before they spray it with castoreum.

2.2.7 Spatial pattern and frequency of scent marks

How intense and where to place scent marks? This problem must be solved by any territorial scent marking animal, because there is question of energy and effectiveness of such behaviour dependently to size of the territory.

With respect to energy and effectiveness beaver's scent marks should be placed in territorial borders (GOSLING 1982, SVENDSEN 1980). And GOSLING (1982) supplies the pay-off to the owner is the reduced costs of competition. According to BROWN (1964) this kind of maintaining the territory could be called as the „economically defendable“ area.

HAY (1958) had already noticed that clusters of scent mounds were concentrated in certain places, in this case around inhabited beaver nests (lodges). The scent mounds are usually located at predictable strategic locations-lodges, trail or dams (MÜLLER-SCHWARZE & HECKMAN 1980). In contrary SVENDSEN (1980) showed that scent mounds were not concentrated in the vicinity of lodges, dams or feeding sites. What support ROSELL & NOLET (1997), claiming that these different placed marks may also play a role in defence of the territory. ALEKSIUK (1968) adds another pattern of scent marking; he found the most of the marks at the edge of the territory but also some of them near the lodge. RICHARD (1967) support scent marking border pattern and adds occurrence of scent marks through the territory. The intended pattern of scent marks near trails may help in orientation of resident beavers (MÜLLER-SCHWARZE & HECKMAN 1980).

According to ROSELL & NOLET (1997) the number of scent mound constructions increased significantly with the number of adjacent territories and decreased with the mean distance to all other territories. MÜLLER-SCHWARZE & HECKMAN (1980) discovered that the shorter the distance to the nearest active lodge of its neighbour colony was the more scent mounds were found at a particular occupied lodge.

Location of the river has influence on amount of scent marks. In distant streams beavers made relatively few scent marks nevertheless the abundance of beavers was relatively high. It might be explained by smaller urgency of defence of the occupied territories (ULEVIČIUS & BALČIAUSKAS 2000).

MÜLLER-SCHWARZE & SCHULTE (1999) reported that unexploited and exploited populations of beavers did not differ in numbers of scent marks.

2.2.8 The size and composition of the family and number of scent marks in different parts of the year

All members of the beaver family except kits may deposit scent, but the primary maker is male of the breeding pair (HODGDON 1978, SVENDSEN 1980). However, there is no difference in the number of scent marks between breeding and non breeding territories (ROSELL & NOLET 1997).

TOWNSEND (1953) found out that scent mound constructions are mostly made by beavers of all ages in July. According to ALEKSIUK (1968) beavers mostly build scent mounds in spring because of dispersion of the two-years-olds individuals, but SVENDSEN (1980) supplies dependence also on ice melting, and so as MOLINI et al. (1980) adds reason of increasing conflicts between beavers. ROSELL & NOLET (1997) didn't find out significant difference in the number of scent mounds during the season, but they observed a small peak in May. The marking activity is lowest from October to December and marks are mainly located on border lines, because the beavers invest the most of their time and energy to preparation of food supplies for winter (ROSELL et al. 1998). ROSELL & BERGAN (2000) were interested, how beavers mark during the winter and they came with result that beavers marked significantly more during January-March (breeding), than during the rest of the winter (October-December).

2.2.9 Dispersion of two-year-olds and importance of scent marks in territoriality

Dispersion is main mechanism of population expansion (BAKER & HILL 2003). It often situated in spring and it's connected with birth of kits. Beaver can remain in family as subadult for a longer period of time if the habitat quality is good (BAKER & HILL 2003). MÜLLER-SCHWARZE & SCHULTE (1999) reported that in saturated populations had beavers less choices to find a new locality to expand, nevertheless dispersion still proceeds. SUN & MÜLLER-SCHWARZE (1996) measured mean dispersal distance for females 8,876 km and for males 4,013 km. In saturated populations was possible to find even 3-years-old beavers (MÜLLER-SCHWARZE & SCHULTE 1999).

BRADT (1938) and TOWNSEND (1953) stated that beavers probably maintain their territories. Even HAY (1958) wrote that scent mounds have relationship to territoriality.

One of the roles of scent marking system is may be the mechanism of self-regulation in meaning to prevention to further colonisation (ALEKSIUK 1968), because with the higher scent mark density more conflict happens between increasing number of the family members (MÜLLER-SCHWARZE & HECKMAN 1980). NOLET & ROSELL (1994) reported that the degree of scent mounding by the European beaver positively correlated not only to population density but also to resources quality of the territories.

3 Research objectives and research questions

Main focus of thesis is to study how the distribution and intensity of the chemical communication is related to parameters of population density

Main (null) hypothesis:

The intensity and distribution of scent communication is not increasing with higher distances to the nearest neighbouring beaver territories

4 Material and methods

4.1 Study area

The study was conducted on three selected model watersheds (consisting of small sub-mountain watercourses) of Protected Landscape Area (PLA) Český les (in west Bohemia): Hraniční stream (length 16,2 km, watershed area 42,7 km^2), Kateřinský stream (length 20,5 km, watershed area 102,56 km^2) and Nivní stream (length 7,8 km, watershed area 62,9 km^2). All streams belong to Danube basin (VLČEK 1984).

The PLA Český les was established in 2005 and its area is 473 km^2. Kateřinský and Nivní stream (and their tributaries) form Sites of Community Importance (SCI) of Natura 2000.

The centre of presence of beavers in west Bohemia is just in PLA Český les in watershed of the Kateřinský stream. The core of the population is especially between Rozvadov, Svatá Kateřina and Železná villages.

Fig. 1 Study area – model watersheds

4.1.1 Climate characteristics

Area of the PLA Český les belongs to the mild climate zone and area above 700 to 800 m.a.s.l. belong to the cold climate zone. Summer is cold, short and mild humid (HOSTÝNEK et TOLAZS 2005). The mean annual temperatures rates from 8°C to 4,5-5°C, thermal maximum is in July with mean monthly temperature 14-18°C and thermal minimum is in January with mean monthly temperature from -2 to -4°C (Český les PLA 2016). The annual precipitation is 696 mm, the poorest are February and March and the richest are June and July. Snow cover persists for long period of winter (HOSTÝNEK et TOLAZS 2005).

4.1.2 Vegetation characteristics

The habitat description is deciduous riparian forests within spacious spruce monoculture with dominant woody vegetation *Salix*, *Alnus*, *Betula*, *Populus*, *Acer*, *Picea* (VOREL et al. 2015).

PLA Český les consists of forests (81%), mosaic of meadows and grasslands. North part of PLA are characteristics by raised peat bogs with Swiss mountain pine and southern part with relict beech forests and low bog or peaty meadows, dry or damp cut meadows and meadow springs (Český les PLA 2016).

4.1.3 Land use

Until 1990 the most of the area was in the border zone, so PLA Český les is relatively untouched by human activities. However PLA is divided in half by highway D5.

Nowadays, this area is poorly settled in comparsion to ages up to the Second World War when the human settlement was much denser. Farms use no forest land mainly for grasslands often situated in vicinity of beavers; hence there is an expectation of subsequent conflicts with beavers: especially of building activity of the beavers when by dams are grasslands-flooded.

4.1.4 Population development and distribution of the Eurasian beavers in Český les

Beavers colonised the area from Bavaria during early 90's of the 20 th century. These animals originate from the Bavarian reintroduction programme (1967-1991) (ZAHNER 1997).

The first settlement occurred in 1985 in Radbuza River (ČERVENÝ et al. 2000) and then in 1990 in Kateřinský stream, Hraniční stream and Nivní stream (KŮS 1999.)

ŠIMŮNKOVÁ & VOREL (2015) noticed that rapid population growth in Kateřinský stream has already started in 1995. VOREL et al. (2012) confirmed presence of saturated population in both parts of Český les.

VOREL et al. (2010) compared results of monitoring in years 2008, 2009, 2010 and got to these counts: 32 territories in 2008, 33 territories in 2009 and 36 territories in 2010, whereas in 2010 was the size of the population estimated at 160-230 individuals and population density at 0,23 territories per km of watercourse. The count of grazing in 2010 was doubled compared to year 2009 (VOREL et al. 2010).

According to TEMPÍROVÁ-KOTRLÁ (2011) beavers were in the first phase of accelerated growth. This phase is characteristic within the highest amount of juvenile individuals. TEMPÍROVÁ-KOTRLÁ (2011) also found, that mortality of one-year-old individuals was high, which means dramatically lower numbers of subadult beavers than juvenile ones. This finding may predict approaching point of saturation and possible dispersion of population to the more food-productive localities (TEMPÍROVÁ-KOTRLÁ 2011). Eventually also ŠIMŮNKOVÁ & VOREL (2015) showed, that population growth of beavers in Kateřinský stream reached saturation point.

4.2 Data collection

4.2.1 Collection of data and basic spatial frame

Scent marks were localised by field survey: during terrestrial (by foot) and water (by boat) trips were recorded GPS coordinates of each active scent mark (distinguishable by human smell). Data were collected during spring 2008 as in the BUTLER & BUTLER (1979) study, which confirming, that this part of the year is the best for observation of scent communication within continental populations of Eurasian beaver.

Early, in winter (from the beginning of January to beginning of March), were collected activity monitoring data (primary data) including: grazing (complete and incomplete), shelters (lodges, semi-lodges, burrows-active and inactive; food caches), also scent marks (active and inactive) and other signs of beaver activity (feeding stations, paths, slides, dams, canals, etc.). Grazed trees were counted in radius max. 5 m and divided into 8 categories via diameter of tree and into species. The locations of all beaver activity were also recorded as a point into GPS device as unique spatial coordinates and scored in special paper forms (VOREL et al. 2010).

Collection of the primary data is time-consuming, thus requires team work. Also field work requires certain knowledge of the technique of the collecting. During the field work is necessary participation of all members of the team. I have been part of Aleš Vorel research team since 2013 and from my perspective, experiences, practise and expertness of each member save a lot of time in the field and therefore it lead to the higher efficiency of the work.

I received the data from Department of Ecology, FES, CULS. I only used selection of the study area and the active primary data of winter 2008-lodges, semi-lodges, burrows, food caches (always active), grazing (active and inactive) and further again active scent mark data collected in spring of even year.

My task was to choose required data pack, proceed point analysis and answer to aimed questions, i.e. my role was only analytical and theoretical.

4.3 Data processing-formulation of the score factors (relationships), parameterization of factors

4.3.1 Transformation of the data into GIS

Coordinates of each points of scent marks (SM), shelters (LODGES) and grazing (OK) were transposed in ESRI ArcGIS 9.3 software (ESRI, Redlands, California, USA) (VOREL et al. 2015). The coordinate system of WGS was transferred into S-JTSK Krovak East North. Then the point shapefiles were created.

After that data from paper forms were connected with point layer (shapefile) and these points became marked points (marked spatial data). All data were categorically multiplied to balance the weight of the spatial points of beaver activity (Vorel et al. 2010).

4.3.2 Estimation of territory delimitation

All marked points were outspread on line of watercourse. Territories were projected in ESRI ArcGIS 9.3 software (ESRI, Redlands, California, USA) by using KernSmooth package (Wand & Ripley 2013), that allowed creation of kernel density estimation (KDE) on presented data (Vorel et al. 2015).

Territory was detected on location, where KDE clustered marked points around an active shelter. The borders of the territory were specified as locations with zero point density or place where densities of points of neighbouring territories started increased. The result of KDE was a polygon layer TERRITORY (Vorel et al. 2015).

4.3.3 Creation of centre of the territory

The centre of the territory was calculated with help of KDE that counted the mean value of the point density and placed point. The result was a point layer named CT.

4.3.4 Data selection for studied area

I restricted the data using selection by attributes for the studied area and each watershed in ESRI ArcMap 10.2.2 software (ESRI, Redlands, California, USA). Then I created point layers (SM, CT, LODGES, OK) and polygon layers (TERRITORY, WATERCOURSE) for each of three watersheds.

4.3.5 Creation of the layer (central) line and reaching all marked points to this layer

I created point layer of point distance 5m (due to accuracy of GPS in the field) on template layer of STREAM. Consequently, I match each of marked point

(SM, CT, LODGE) with the closest point of line layer with the help of coordinates (Spatial Join).

I created three point layers (one for each watercourse) with coordinates of 5m point layer and attributes of input layers (SM, CT, LODGE).

I visualized watersheds by layouts (created in ArcMap 10.2.2) (Supplement 1, 3, 5) and made graphs (created in Microsoft Excel) (Supplement 2, 4, 6, 7) of distribution of the marked points (SM, LODGES, CT). I herewith added ranges of territories into the graphs.

4.4 Data analysis

4.4.1 Spatial analysis of the collected data

I did all of spatial analysis in ESRI ArcMap 10.2.2 software (ESRI, Redlands, California, USA).

I labelled each CT (TERRITORY) with unique code, for watershed of Hraniční stream: H1-H5; for watershed of Nivní stream: N1-N7; for watershed of Kateřinský stream: K1-K8, M1-M3, V1-V3, L1, Z1, J1, R1, P1.

Consequently, I measured to each centre of territory distances to all nearest neighbouring centres. For measurements it was helpful „5m point layer“, where I easily identified the distance – i.e., distances were measured only alongside the water systems. In some cases location of the CTs offered more than one combination, which means more neighbouring territories.

I counted number of scent marks (SM), grazing (OK) and shelters (LODGES) in the „5m point layer“. I counted SM only between the CTs, while OK and LODGES in whole territories.

Grazing was transformed to biomass measure with use of coefficients (Fig. 2). Here biomass reflected amount of palatable and potentially consumed bark, bast and twigs (-in grams).

Fig. 2 Conversion of felled trees to biomass (VOREL et al. 2015)

Number of category	Category of diameter of felled trees	Coefficient of diameter category
1	0 - 2,5	0,000276
2	2,6 - 6,0	0,002297
3	6,1 - 12,0	0,012843
4	12,1 - 20,0	0,051188
5	20,1 - 30,0	0,136096
6	30,1 - 40,0	0,36126
7	40,1 - 50,0	0,617665
8	more than 50,1	1,000000

The results of spatial analysis of each watershed are mentioned in Fig. 4, 5, 6. The overall results counted of particular watershed data (Chapter 5.2) are represent in Fig. 3.

4.4.2 Statistical analysis of spatial-population relationships

Data were analysed with R software (R Development Core Team 2009). As depending variable was selected number of scent marks (SM) for each inter-territorial distance between two territory centres and as independent variables were selected distances between two territory centres, amount of biomass and numbers of shelters (lodges and food caches).

Each obtained value of scent marks (SM) was divided into three categories (Fig. 3) and each category was used in test as separate variable: sm_s (total sum of scent marks), sm_i (numbers of scent marks within defined boundaries of territories), sm_o (number of scent marks outside territories).

Two categories of shelters (lodges) were included in analysis: lodges (numbers of lodges, burrows and food caches), lodges2 (numbers of lodges and burrows).

The process of analysis was chosen in this manner:

1. Some of assumed correlation were tested (more closely below this list) with Spearman correlation coefficient
2. testing by LM (Simple Linear Regression)
3. analysis of residuals of the LM model (diagnostic plots)
4. in case of insufficient results use of GLM (Generalized Linear Model) with Poisson distribution of errors
5. eventually use GLMMs (Generalized Linear Mixed Model)
6. (comparing of GLM (Poisson) and GLMMs)
7. for analyse of models was further used ANOVA and normal distribution of residuals was tested by Shapiro-Wilk test

These final models were tested:

```
m1<-lm(sm_s~lodges2+distance)
m2<-lm(sm_s~distance)
m3<-glm(sm_s~lodges2+distance,family=poisson)
m4<-glm(sm_s~lodges2+distance,family=quasipoisson)
m5<-glm.nb(sm_s~lodges2+distance)
```

These correlations were tested:

```
cor.test(biomass,lodges,method="spearman")
cor.test(biomass,lodges2,method="spearman")
cor.test(lodges,distance,method="spearman")
cor.test(lodges2,distance,method="spearman")
```

5 Results

5.1 Overall data description

All founded values of spatial analysis from ArcMap 10.2.2 were recorded to the table (Fig. 3).

A total of 528 scent marks (SM) were recorded within 31 territories within three model watersheds during spring 2008, 29 distances were measured, minimum of scent marks was 0 and maximum was 61, average number of neighbouring territories was1,8. These results include calculations with excluded sections H2-H3 and K7-K8 (Fig. 3).

Fig. 3 Result table

year	id	distance	sm_i	sm_o	sm_s	watershed	biomass	lodges	lodges2
2008	h1-h2	1965	5	0	5	Hranicni	106,22	4	2
2008	h2-h3	6500	11	50	61	Hranicni	57,27	0	0
2008	h3-h4	1645	19	1	20	Hranicni	102,71	3	2
2008	h4-h5	1960	47	4	51	Hranicni	98,79	3	2
2008	n1-n2	2775	0	0	0	Nivni	50,52	8	4
2008	n3-n4	1950	6	0	6	Nivni	33,13	3	3
2008	n4-n7	4240	8	9	17	Nivni	29,68	1	1
2008	n5-n6	1030	14	0	14	Nivni	77,03	2	2
2008	n6-n7	1770	17	14	31	Nivni	84,55	2	2
2008	k1-k2	1685	27	4	31	Katerinsky	106,96	3	3
2008	k2-k3	1450	21	10	31	Katerinsky	147,81	3	2
2008	k3-k4	1415	17	10	27	Katerinsky	63,80	2	1
2008	k4-k5	685	6	0	6	Katerinsky	13,62	1	1
2008	k5-k6	960	18	0	18	Katerinsky	20,72	1	1
2008	k6-k7	1255	20	0	20	Katerinsky	103,59	1	1
2008	k7-k8	6575	14	25	39	Katerinsky	132,75	2	2
2008	m1-m2	775	7	8	15	Katerinsky	142,65	3	2
2008	m2-m3	805	1	4	5	Katerinsky	39,78	3	2
2008	v1-v2	3545	18	8	26	Katerinsky	45,85	5	4
2008	v2-v3	1645	7	0	7	Katerinsky	46,32	3	2
2008	l1-z1	2865	0	0	0	Katerinsky	71,02	3	2
2008	l1-k1	3940	4	0	4	Katerinsky	71,37	3	3
2008	z1-k1	2915	4	0	4	Katerinsky	37,31	4	3
2008	m3-k3	1675	11	2	13	Katerinsky	69,49	3	2
2008	m3-k4	1780	16	8	24	Katerinsky	13,93	1	1
2008	j1-k4	1195	29	3	32	Katerinsky	7,89	1	1
2008	r1-k4	1090	1	0	1	Katerinsky	31,12	2	1
2008	v3-k5	755	17	0	17	Katerinsky	20,26	1	1
2008	p1-k6	2930	3	0	3	Katerinsky	43,97	3	2

explanatory notes:

id-labelling of couple of the territory centres

distance- distance in metres between two territory centres

sm_i-number of scent marks inside territories

sm_o-number of scent marks outside territories

sm_s-sum of the number of scent marks between two territory centres

watershed-name of the model watershed

biomass-amount of biomass in kilograms

lodges-number of shelters (lodges, semi-lodges, burrows and food caches)

lodges2- number of shelters (lodges, semi-lodges, burrows)

The data were rearranged by deletion of strange values (due to incomparably large measured distances without valid dependent values). The first serious case appeared in Hraniční watercourse between CTs H2 and H3. This section was distinguished by very long distance (6500m), high number of scent marks (61) and no created territory. The second case appeared in Kateřinský stream between CTs K7 and K8. This section was also distinguished by very long distance (6575m), high number of scent marks (39) and no created territory. Reasons of both excluding are explained in Discussion section.

5.2 Particular watershed data

5.2.1 Watershed of Hraniční stream

The total length of Hraniční stream is 16,2 km, whereas analysed sector had 12,07 km (74,5%). The total number of CTs (territories) was 5 (Supplement 1, 2).

Fig. 4 Extremes, average and number of events in Watershed of Hraniční stream

	max	min	average	N
distance (m)	1965,00	1645,00	1856,67	3
sm_s	51,00	5,00	25,33	3
sm_i	47,00	5,00	23,67	3
sm_o	4,00	0,00	1,67	3
biomass (kg)	106,22	98,79	102,57	3
lodges	4,00	2,00	3,33	3
biomass (kg) per TER	78,48	25,61	46,91	5
lodges per TER	4,00	0,00	1,40	5

explanation of terms-Fig.3

biomass (kg) per TER-amount of biomass in territory

lodges per TER-number of lodgs in territory

5.2.2 Watershed of Nivní stream

The total length is 7,8 km whereas analysed sector had 4,86 km (62,3%). The total number of CTs (territories) was 7.

Fig. 5 Extremes, average and number of events in Watershed of Nivní stream

	max	min	average	N
distance (m)	4240,00	1030,00	2353,00	5
sm_s	31,00	0,00	13,60	5
sm_i	17,00	0,00	9,00	5
sm_o	14,00	0,00	4,60	5
biomass (kg)	84,55	29,68	54,98	5
lodges	8,00	1,00	3,20	5
biomass (kg) per TER	75,09	1,94	24,31	7
lodges per TER	5,00	0,00	1,86	7

explanation of terms-Fig.3

biomass (kg) per TER-amount of biomass in territory

lodges per TER-number of lodgs in territory

5.2.3 Watershed of Kateřinský stream

The total length is 20,5 km whereas analysed sector had 14,03 km (68,4%).The total number of CTs (territories) was 19. The territory with the most number of neighbours (5) was K4 and this was accepted for entire study.

Fig. 6 Extremes, average and number of events in Watershed of Nivní stream

	max	min	average	N
distance (m)	3940,00	685,00	1756,05	19
sm_s	32,00	0,00	14,95	19
sm_i	29,00	0,00	11,95	19
sm_o	10,00	0,00	3,00	19
biomass (kg)	147,81	7,89	57,76	19
lodges	5,00	1,00	2,42	19
biomass (kg) per TER	112,67	3,77	35,15	20
lodges per TER	3,00	0,00	1,37	19

explanation of terms-Fig.3

biomass (kg) per TER-amount of biomass in territory

lodges per TER-number of lodgs in territory

5.3 Correlations of biomass with lodges and lodges with distance

Biomass and lodges

First I tested correlation between estimated biomass and lodges (Fig. 3). For analyse were used two cases of lodges data, *lodges* (food caches included) and *lodges2* (without food caches). There was a correlation between *biomass* and *lodges* (r_s = 0.4569441, p = 0.01657) and also between *biomass* and *lodges2* (r_s = 0.4182452, p = 0.02993). In both cases were correlations significant and positive, but very untight.

Lodges and distance

Second I tested correlation between number of *lodges* and *distance* of territorial centres (Fig. 3). For analyse were used both lodges data: *lodges* (food caches included) and *lodges2* (without food caches). There was a correlation between *lodges* and *distance* (r_s = 0.5122821, p = 0.006297) and also between *lodges2* and *distance* (r_s = 0.5398801, p = 0.003653). Relationship in both cases was significantly positive: with increasing *distance* increased number of *lodges*.

5.4 Models

For models was chosen variable *lodges2*, due to tighter correlation with *distance* (r_s = 0.5398801, p = 0.003653).

In the first model (m1) I tested dependency of *sm_s* to *lodges2* and *distance*. This model was not significant neither for *lodges2* (ANOVA: $F_{1,24}$ = 0.6817, p = 0.4171) nor *distance* (ANOVA: $F_{2,24}$ = 0.2219, p = 0.6419).

In the second model (m2) I tested dependency of *sm_s* only to *distance*. This model was not significant (ANOVA: $F_{1,25}$ = 0.7002, p = 0.4107).

Because of insufficient analysis of residuals of both LM models (overdispersed data), was next step use of GLM with Poisson distribution of errors. In the third model (m3) it was tested variables same as in the first model (*sm_s*, *lodges2*, *distance*). But even this dependence did not appear as significant neither for *lodges2* (df = 24, p = 0.117) nor *distance* (df = 24, p = 0.123).

The fourth model (m4) was same as the third model (m3) except of distribution of errors. For this case was chosen quasipoisson distribution of errors.

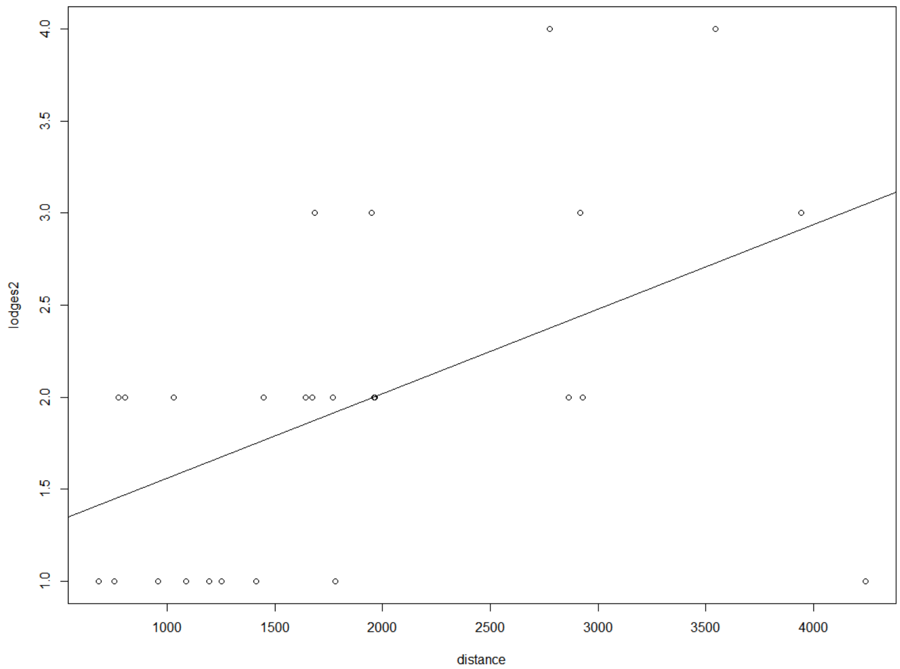
But model was not significant neither for *lodges2* (*df* = 24, *p* = 0.643) nor *distance* (*df* = 24, *p* = 0.649). Shapiro-Wilk test of residuals has *p* = 0.4651.

Because of the too high dispersion parameter (because of the persisting overdispersion-Dispersion parameter = 11.14839) as the last model (m5) was chosen GLM with negative binomial distribution-MASS package (VENABLES & REPLAY 2002). This model was not significant – *lodges2* (*df* = 24, *p* = 0.682), *distance* (*df* = 24, *p* = 0.583). Dispersion parameter was 1.2772. Shapiro-Wilk test of residuals has *p* = 0.5745. Pseudo r^2 = 0.02586101.

The first case of special model was model m. This model addressed question: how variability would look like, if it was cleaned of *lodges*. But even in this case distance was not significant (*p* = 0.493).

The second case of special model was model mc. The result of correlation between *lodges2* and *distance* (*lodges* and *distance*) lead to test the question: if it is here the dependence of number of *lodges2* to combinations of *distance*. And the result was, that with increasing *distance* increases number of *lodges* (*df* = 25, *p* = 0.007182).

Fig. 7 Dependence of lodges2 to distance



The analyses of all models were processed with *sm_i* and *sm_o* variables (in replace of *sm_s*). None of the models with these variables were significant (Fig. 8 and Fig. 9).

Fig. 8 Analysis of sm_i

model	**p value**
m1<-lm(sm_i~lodges2+distance)	lodges2 = 0.4052 distance = 0.4354
m2<-lm(sm_i~distance)	distance = 0.2679
m3<-glm(sm_i~lodges2+distance,family=poisson)	lodges2 = 0.336 distance = 0.016
m4<-glm(sm_i~lodges2+distance,family=quasipoisson)	lodges2 = 0.760 distance = 0.446
m5<-glm.nb(sm_i~lodges2+distance)	lodges2 = 0.846 distance = 0.290

Fig. 9 Analysis of sm_o

model	**p value**
m1<-lm(sm_o~lodges2+distance)	lodges2 = 0.7340 distance = 0.5671
m2<-lm(sm_o~distance)	distance = 0.7431
m3<-glm(sm_o~lodges2+distance,family=poisson)	lodges2 = 0.168 distance = 0.163
m4<-glm(sm_o~lodges2+distance,family=quasipoisson)	lodges2 = 0.581 distance = 0.577
m5<-glm.nb(sm_o~lodges2+distance)	lodges2 = 0.774 distance = 0.794

6 Discussion

The base of this thesis was to study how is the distribution and intensity of the chemical communication of Eurasian beavers related to parameters of population density. Beaver's chemical communication is sustained and maintained through the system of chemical marks-scent marks. To capture most of the information about chemical communication of beavers is spring the best part of a year (ROSELL et al. 1998). Therefore collection of the scent mark data in my study was performed in spring, in April. The other data (primary), consisting of locations of grazing, shelters and other beaver activity, were collected in winter (January-March) the same year. This is the most productive period of beaver activity in whole year. The scent mark data I received were quite rare, because in most cases SM data are part of primary data. This situation was advantageous, because estimation of the territories (centres of territories) was not based on scent mark data (as usually does) and therefore was allowed to study the information of different data layers (primary data from winter and scent marks from spring).

The result of this study did not prove dependency of distance of nearest neighbouring beaver territories to intensity of beaver chemical communication. Changing distance between CTs had not influence number of active (fresh) scent marks between each couple of CTs, respectively number of scent marks inside territories, number of scent marks outside territories and sum of both categories, respectively.

Furthermore was proved, however, positive correlation between number of shelters and its distance (distance among neighbouring territory centres): with increasing distance increased number of shelters (Chapter 5.4). Previous finding was tested in model (mc) (Chapter 5.4), it was tested dependence of number of shelters to distance. Model was significant and the result was: with increasing distance increased number of shelters (Fig. 7).

6.1 Density-dependence effects

It was expected tight relationship between distance and number of scent marks or dependency. The one of hypothesis was that with increasing distance decreases number of scent marks. That seems logic and in harmony with theory of effectiveness of time and energy spent on scent marking. The alternative explanatory hypothesis should be opposite: with decreasing distance (or with increasing number of neighbours) increases number of scent marks (MÜLLER-SCHWARZE & HECKMAN 1980, DAVIS et al. 1994). It should be expected that with decreasing distance increases possibility of conflict among resident and transient or neighbouring beavers and therefore more intensive scent marking behaviour should occur. MÜLLER-SCHWARZE & SCHULTE (1999) reported that in denser populations may occur higher events of competition between beavers, fight that may end with tail scars.

However, results of this study did not indicate any tendency of intense marking due high proximity of competing beavers (i.e., high population density). So why beavers were not forced to defend their territories, if they had many near territories? In other words, why they did not make higher number of scent marks, if neighbouring territories were close enough?

The result was that varying distance of CTs had not any influence to intensity of scent marking behaviour i.e. number of scent marks. Thus scent marking behaviour of beavers is likely controlled with diverse population aspect then by population density.

On the other hand, surprising was that number of shelters significantly correlated with distance: with increasing distance increased number of shelters. This relationship brought to idea that would be useful to test this relationship (*lodges2* and *distance*) in model. Model mc (lm(*lodges2~distance*)) was significant therefore there was a confirmed dependency of number of shelters to distance among territories: with increasing distance increased number of shelters. The effect might be based on lower stress level when holders of territories are distant to each other. The larger distances provides to individuals lower competition which might be projected in higher reproduction success. Therefore increasing building activity probably correlate to family size, i.e. numbers of individuals within neighbouring families. In sum one might predict, that lower competition presses stress which allows higher reproductive success.

6.2 Data reduction

Data I got from analyses in ArcMap 10.2.2 had to be reduced by some values. I noticed some of meaningful deviations during analyses of residuals. These two cases of strange values appeared in Hraniční watercourse and Kateřinský watercourse.

There was a big gap between territory centres H2 and H3 (see Supplement 1), this means high distance-6500m (Fig. 3). What is especially suspect is fact, that between these two territories were recorded 61 scent marks (Fig. 3) but only one active burrow. There were no points that can enter to KDE analysis, except of the mentioned scent marks, so no territories (and territory centres) could be drawn.

Similar problem appeared between territory centres K7 and K8 (see Supplement 5). The distance between K7 and K8 was evidently the longest in the whole watershed-6575m (Fig. 3). This distance was quite similar to that between H2 and H3; however the number of recorded scent marks-39 (Fig. 3) was lower. There is no satisfactory explanation of why would beavers intensively defend this section of Kateřinský stream. There were no food sources and even no shelters found, so obviously no territory could be drawn.

I considered that these sections were inapplicable and won't participate in statistical analysis. The explanation of this fact could be inexperience of a field worker that collected the data (shelters). But I can't see explanation of such a high number of scent marks on those long distances. I would recommend further analysis of environment around the problematic areas or try to collect the data more precisely and for several years.

6.3 Watersheds

Watershed of Hraniční stream contained 5 territories (Fig. 3) and was the only one with no tributaries. The southern part of the Hraniční stream seemed to be more marked (Supplement 1). Further visualization of distribution of active marks (Supplement 2) showed aggregated structures of scent marks on specific places. Even changing distance of territories showed certain pattern of placing scent marks.

Between H1-H2 was found maximum of lodges-4 (Fig. 3), whereas all lodges were in territory H1. This territory was also characterized by the greatest amount of biomass-78,478 kg (Fig. 4). Unmistakable is no evidence of shelters in territories H2, H3 and H5 (Fig. 4).

Watershed of Nivní stream contained 7 territories (Fig.3). The main stream-Nivní stream had 3 tributaries. What is obvious at first sight is a distribution of scent marks in the watershed (Supplement 3 and 4). The major number of scent marks is placed on Farský stream-the last tributary of Nivní stream, between N6-N7 (Fig. 5), all kinds of scent marks are presented in maximum counts: sm_s-31, sm_i-17 and sm_o-14 (Fig. 5).Visualization of scent marks in the last part of the Nivní stream (Supplement 3), give a suspicion of a near territory. This section was not included into any analysis because of unrelated meaning to studied territories and because of the lack of the data. The visualization of Nivní stream ends, where state border begins, but it was known that beaver activity continued behind the state border.

Watershed of Kateřinský stream had most of tributaries-7 (Supplement 5), therefore the most measured distances (Fig. 3). The same case as in Hraničí stream was necessary to solve. Section between K7 and K8 was questionable long-6575m (Fig.3) and contained great number of scent marks-39 (Fig. 3). This section was excluded because of similar reasons as in Hraniční stream.

The territory with the most number of neighbours-5 (Fig. 3) of the watershed (even of all study) was K4. It lay in the middle of the beaver activity in Kateřinský stream. Interesting was a big number of sections without any outside scent marks (sm_o)-10 (Fig. 6). And lot of sections-6 has only one lodge (Fig. 6).

6.4 Spatial relationships of population parameters

Before any test was started I decided to divide lodges data into two packs. I suspected that it would be more precisely using of lodges without food caches, even if the food caches is the good proof of beaver residence. But I decided that one lodge could have more food caches, so I split the data, but I did analyses for both packs so I could compare results.

The first tested correlation was between estimated biomass and lodges. I asked if it is better to subsequently model number of scent marks against distances. Correlations between biomass and lodges and biomass and lodges2 were significant and positive, but very untight.

However, lodges are less correlated with biomass than lodges2, probably because food caches in lodges make statistical noise this was supported by SWENSON et al. (1983) that found food caches less reliable in estimation of population size. Contrary EASTER-PILCHER (1990) showed contrast. Therefore building behaviour of food caches vary in different composition of ages of beavers (OSMUNDSON & BUSKIRK 1993).

The second tested correlation was between lodges and distance and lodges2 and distance. These both relationships were positively significant: with increasing distance increased number of lodges.

The correlation coefficient for lodges and distance was 0.5122821 but for lodges2 and distances was counted ever higher correlation coefficient 0.5398801. This confirms statement, that food caches in lodges probably really made statistical noise. And positive correlation between number of beaver lodges (without, but even with food caches) and rising distance of the centres of the territories was found.

However if we look closer, we can find out, that one value is very distant. It was section N4-N7 with distance 4240m and only 1 lodge (Fig. 3). This distance was allowed for presence of scent marks above N4 and N7 (Supplement 3). It was difficult to who relate these scent marks and it was necessary to explain it. I decided to measure the distance from N4 to the nearest territory centre (besides N3). The choices were N1 and N7. At last N7 had shorter measured distance, so I explained these scent marks with relationship N4-N7.

6.5 Models

Models in most cases were not significant (Chapter 5.4, Fig 8 and Fig. 9). I tested dependence of scent marks to *distance* and *lodges2* and scent marks only to distance. In tested models were used different kinds of variable scent mark-*sm_s*, *sm_i*, *sm_o*. Were used LM, GLM with Poisson distribution of errors, GLM with quasipoisson distribution of errors and GLM with negative binomial distribution of errors.

According to the process of analysis (Chapter 4.4.2), the use of GLMMs was not outright. I did not assume the influence of watershed; therefore it was not necessary to complete the model of random effect. Moreover the set model would not have enough number of degrees of freedom (df) – it would have only 0 degrees of freedom.

The last model (m5) explained the most of the possible variability in the data- Pseudo r^2 = 0.02586101. But variables lodges2 and distance were not significant. This model was not successful because of few amounts of data, therefore the little of explained variability. I suppose that scent marks are influenced by something different.

The only significant model in this study (mc) tested dependence of lodges2 to distance. The result was that with increasing distance increased number of lodges. This is a new finding that has never been published by anyone yet.

I would insist on vigorous collecting of the data (primary and scent mark), however I know how difficult is to find to reliable fieldworkers. Collecting of the data still requires a lot of time and people therefore is very important co-working with experienced people. Further I would recommend collecting scent mark data preferably every year or at least after every winter collection of the primary data.

The measuring territory distance from CT to CT appeared as elegant as simple solution however creation of CT is not always simple. It requires high-quality of primary data. Even drawing of territory boundaries by KDE is elegant and again it depends on quality of primary data. Analysis of point structures in or outside drawn territories is then very simple and fast.

The visualization of intensity and distribution of active marks of beaver activity (Supplement 2, 4, 6, 7) is very helpful, however with increasing number of tributaries the visualization happens to be not well-arranged, so it’s better to represent each tributary separately.

7 Conclusion

The results of this study are contrary to already published studies about relationship between population density and intensity of chemical communication of beavers. There are several possible explanations, however further research is needed. I would recommend to again testing of relationship between chemical communication and population density in different beaver habitat. This thesis was studied on small sub-mountain watercourses, therefore it would be necessary to obtain more robust data to confirm results obtained in this study.

Relationship population density-chemical communication was not significant contrary to other studies. This offers several explanations a further analysis. However number of scent marks was not explained with changing distance or number of shelters of number of lodges. There is need for finding other explanatory variable that would explain more variability.

In this study has been shown relationship between number of shelters and its distance: number of shelters (lodges without food caches) increased with increasing distance. First explanation that appears is that beavers feel save and unexploited with increasing distance of neighbouring territories.

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9 Supplements

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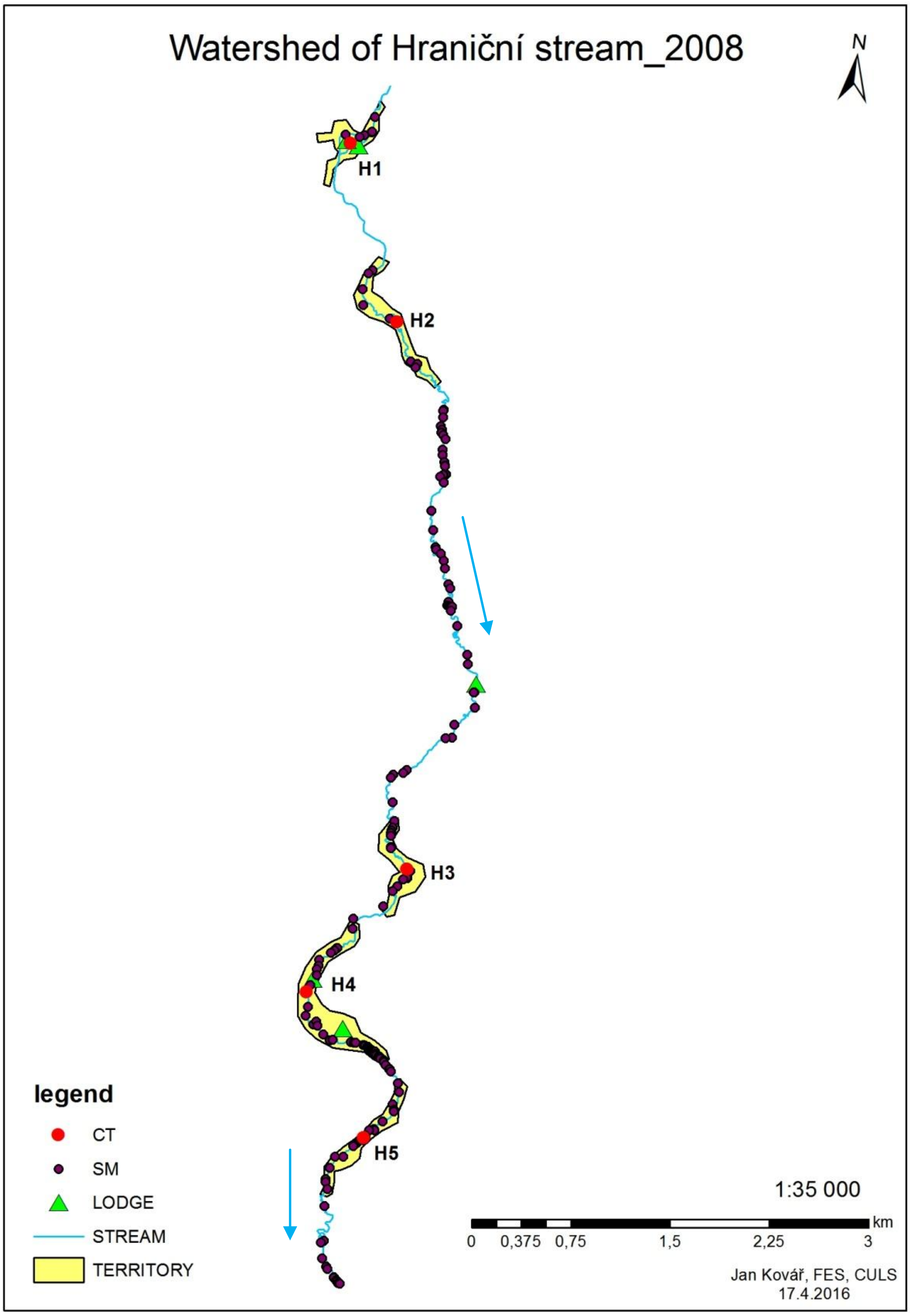
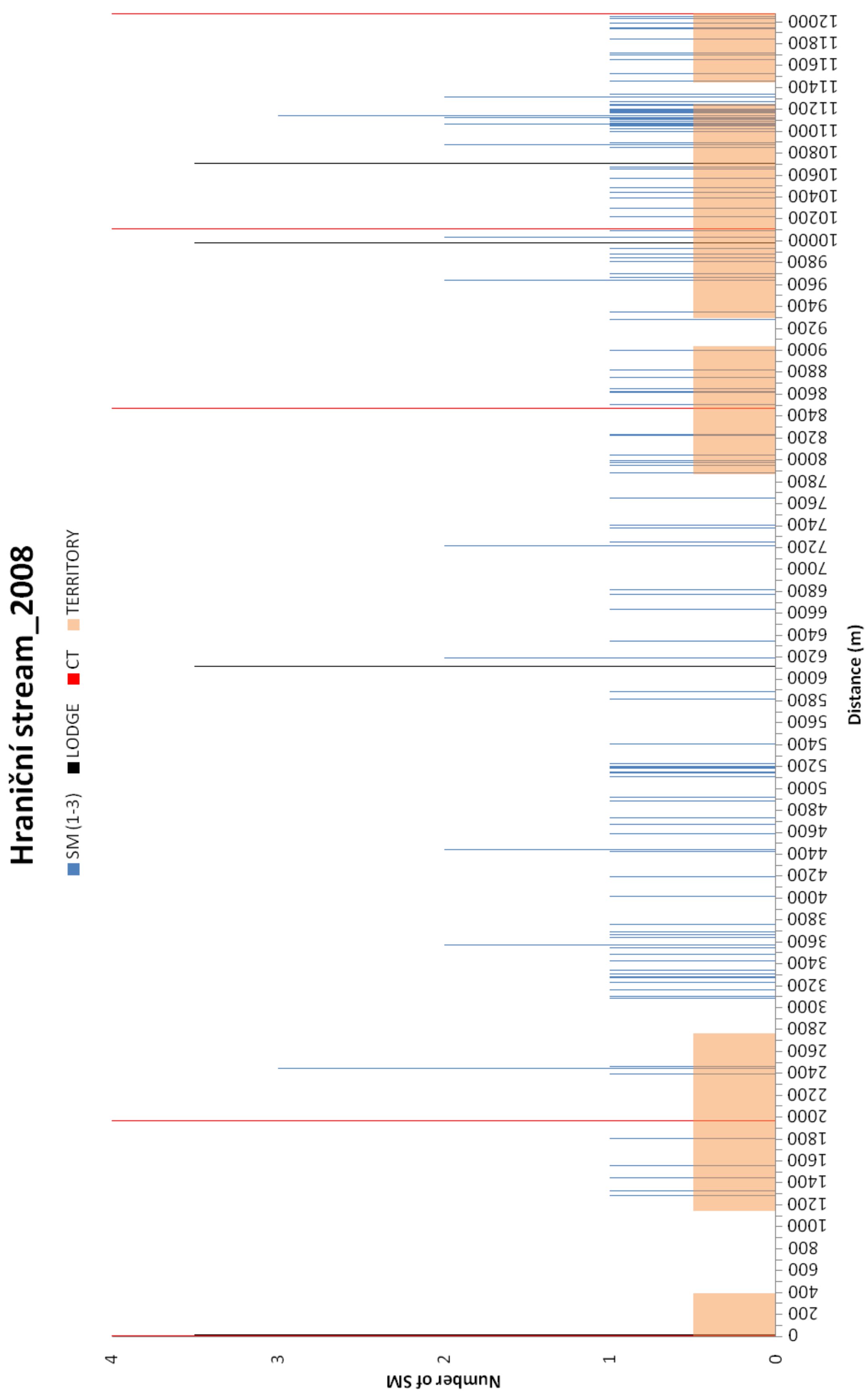
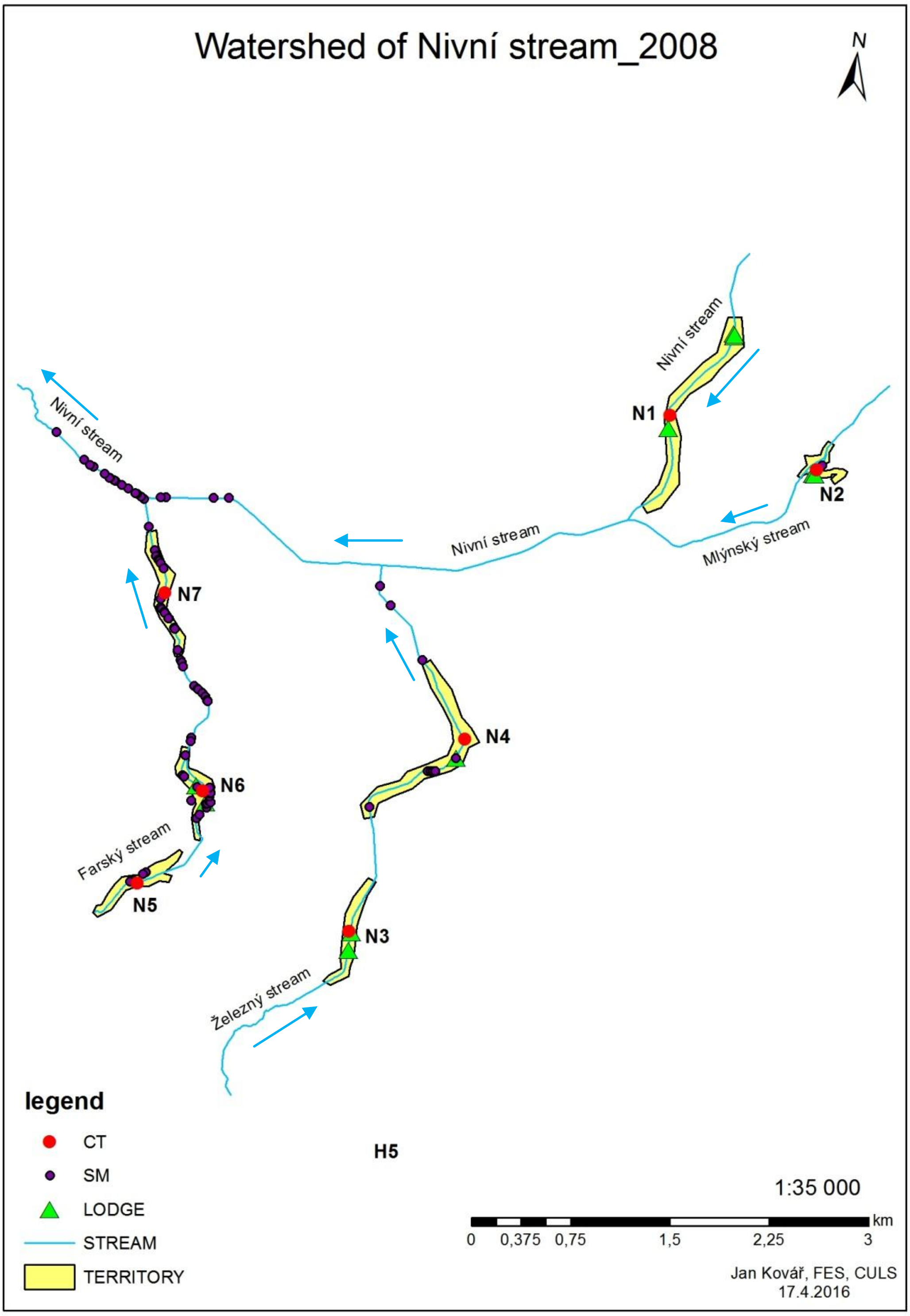
Supplement 1 – Vizualization of Hraniční stream (ArcMap)



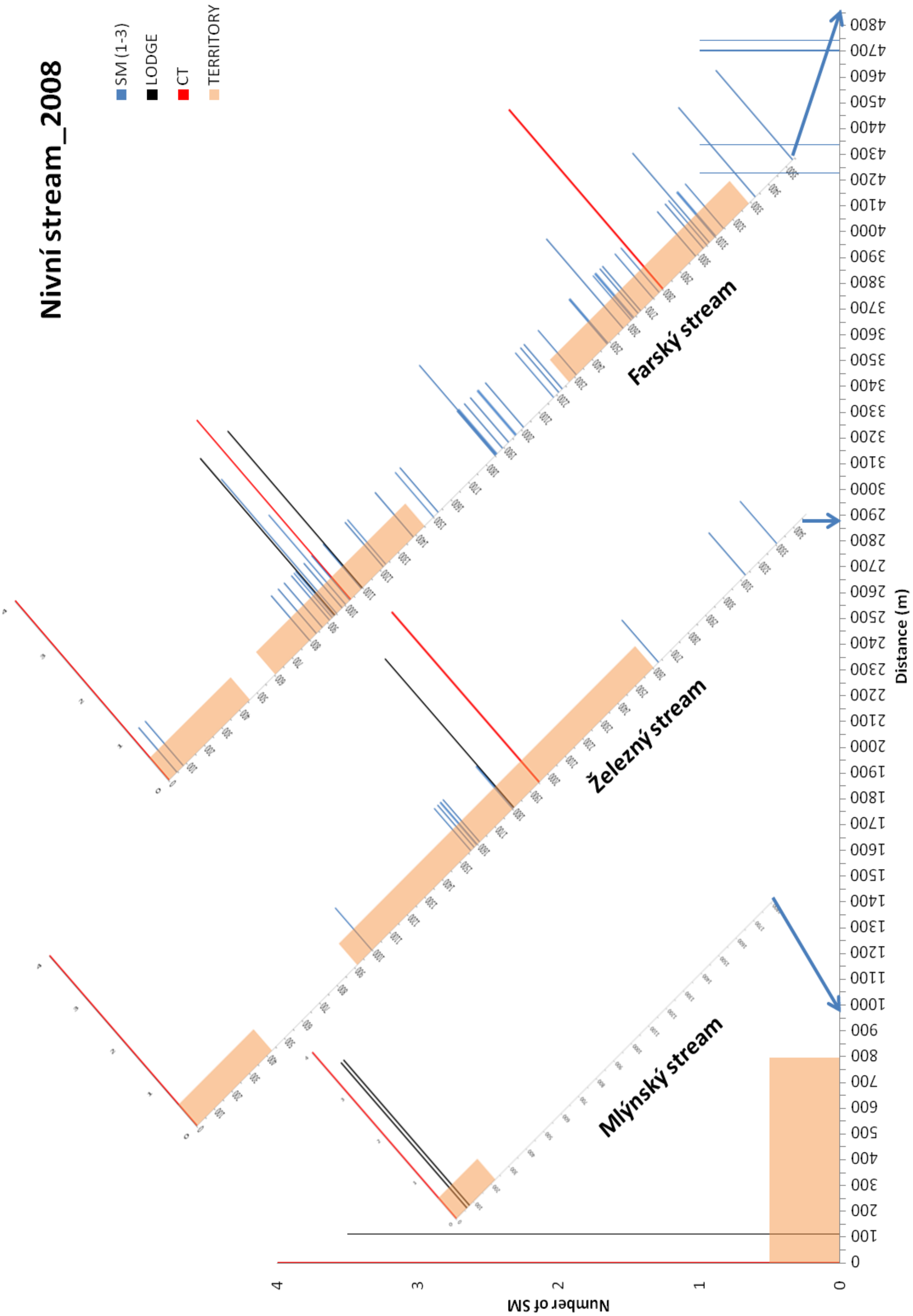
Supplement 2 – Vizualization of Hraniční stream (graph)



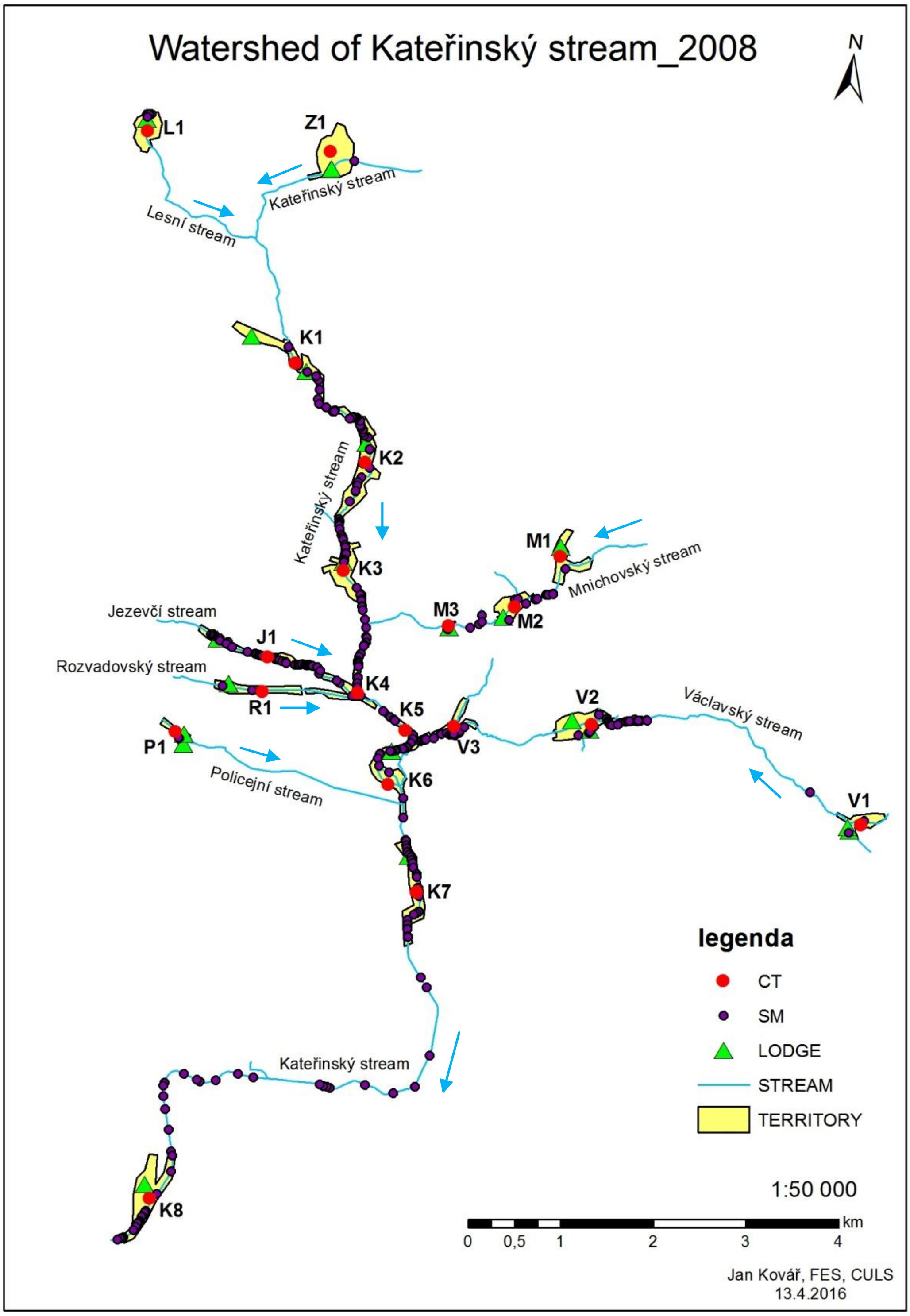
Supplement 3 – Vizualization of Nivní stream (ArcMap)



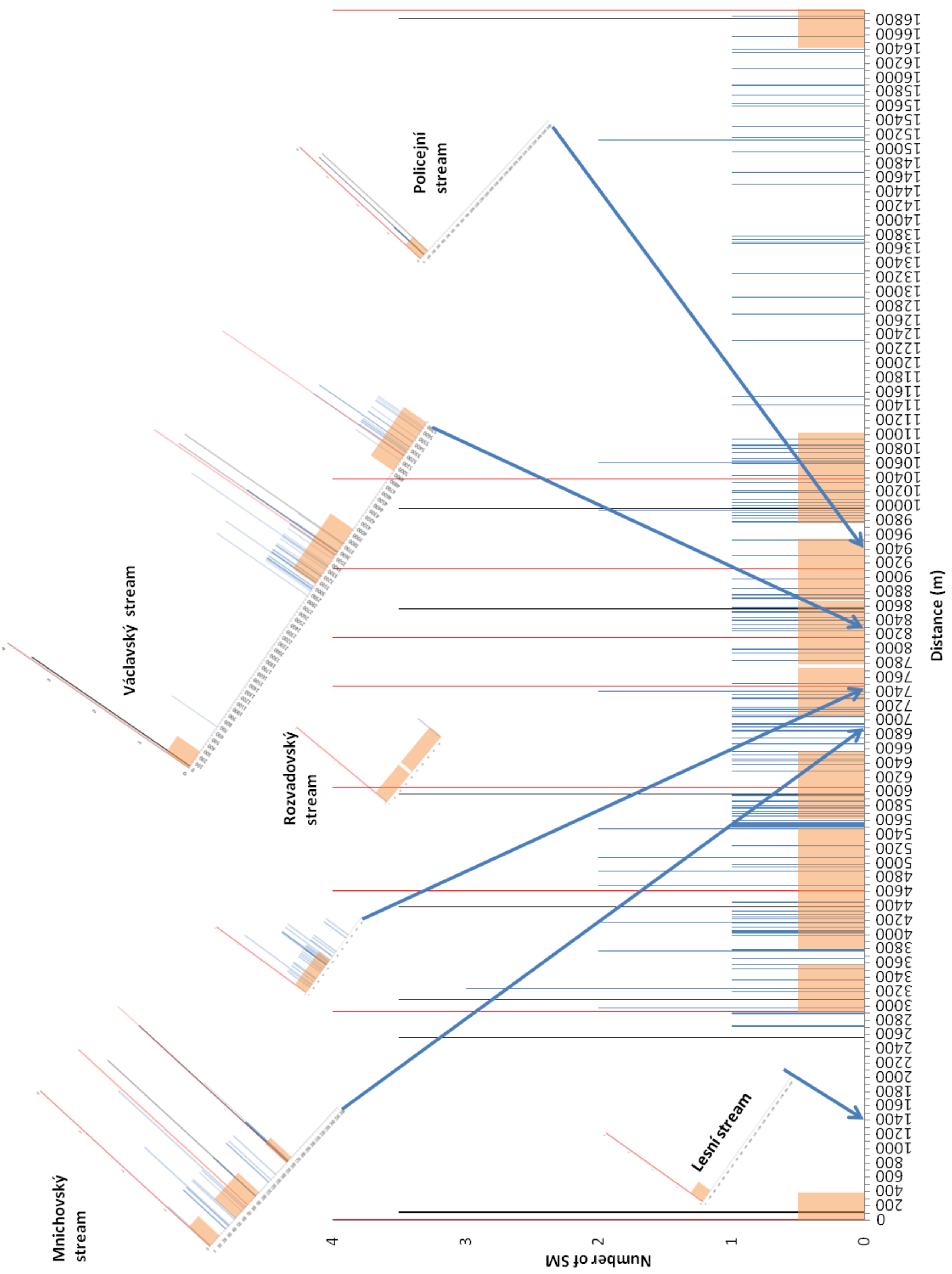
Supplement 4 – Vizualization of Nivní stream (graph)



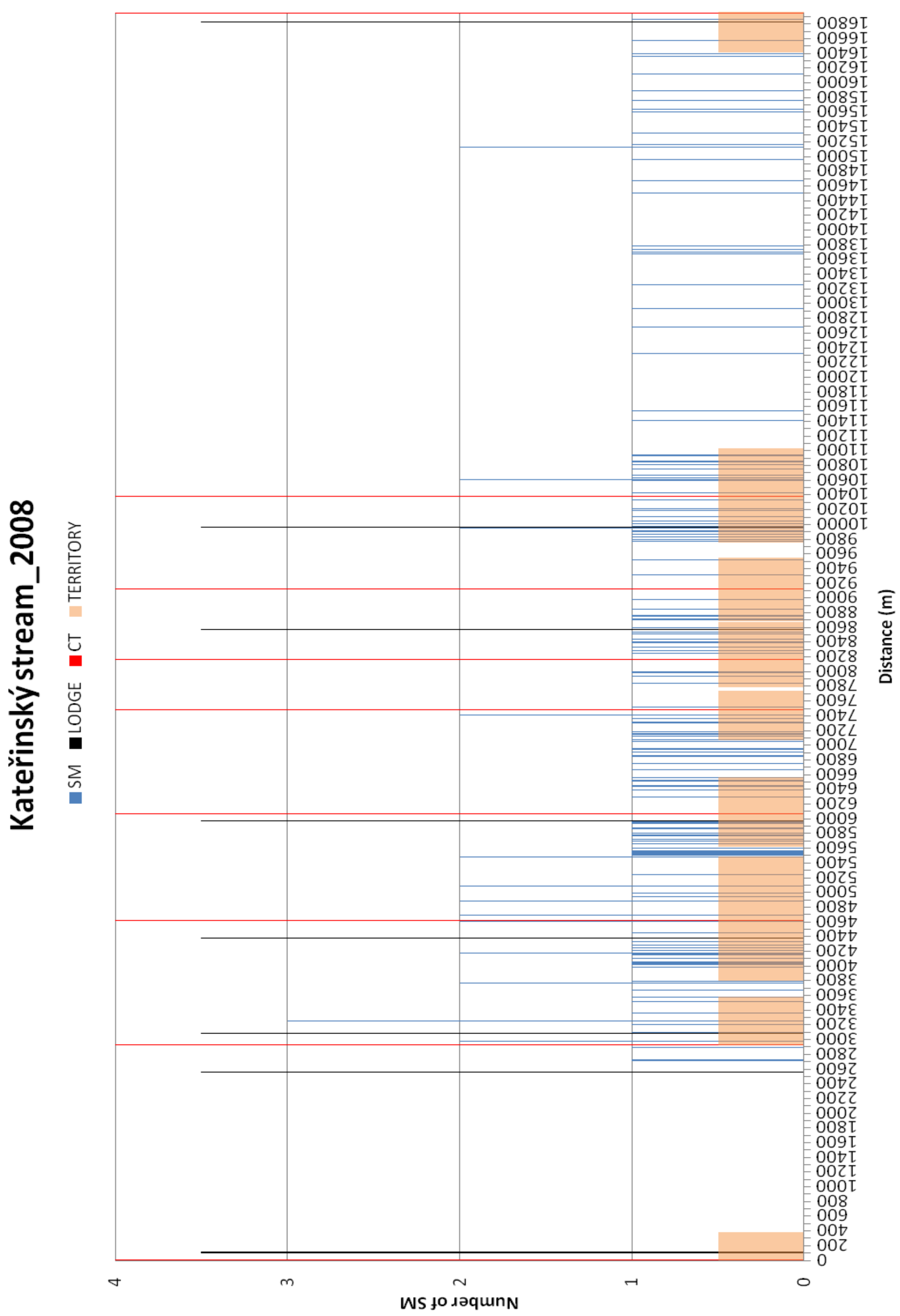
Supplement 5 – Vizualization of Kateřinský stream (ArcMap)



<u>Supplement 6 – Vizualization of Kateřinský stream (graph)</u>



Supplement 7 – Vizualization of Kateřinský stream without tributaries (graph)



Supplement 8 – Scent mound with fresh scent mark made of grass by the Kopanice stream, SCI Soutok-Podluží. Photo by Jan Kovář

Supplement 9 – Scent mound with fresh scent mark made of sand by the Elbe river, near Hřensko. Photo Jan Kovář