Reassessment of the prediction model for the spread of the Eurasian beaver (*Castor fiber* L.) in Flanders

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English Abstract

The re-establishment of the Eurasian beaver (*Castor fiber*) in Flanders after its reintroduction in the beginning of the 21st century is building up momentum. Conservation and protection efforts in Flanders have enabled beavers to expand and recolonize most of their past ancestral territories. An important difference between the present and the past is that the landscape has drastically changed through anthropogenic modifications. Beaver populations are growing and gradually expanding out of the remaining semi-natural habitats into the more urbanised areas. The ecological advantages associated with the presence of beavers with their role as ecosystem engineer in natural environments are clear, but in areas with high human densities, ecological gain and economical cost should be balanced. Therefore, monitoring their movement is key for a successful co-existence. A habitat suitability index (HSI) model was made in 2014, which determined all the suitable areas for beavers in Flanders. This research focused on the validation of this HSI model, testing for its accuracy of predicting the presence or absence and the number of territories. The HSI model output shows that the colonisation is still far from its maximum capacity as many suitable habitats are not yet occupied and population densities are in general still reasonably low. Beavers are present in areas where they were expected, but not yet everywhere. Time lag and introduction site are probably important variables explaining uncolonised areas with suitable habitat. Areas where beavers are present but were not expected can be explained by missing parameters in the model or new ecological features of beavers in more urbanised areas. In conclusion the HSI model is promising but is currently not making the correct predictions for further colonisation. Both population growth and the subsequent area spread of these individuals take time and have not yet reached their full potential for Flanders.

Abstract Nederlands

Een herintroductie van de Euraziatische Bever (*Castor fiber*) in het begin van de 21ste eeuw heeft de bever weer in Vlaanderen gebracht. Inspanningen omtrent het behoud en de bescherming van de bever hebben ervoor gezorgd dat deze terug in opmars is en al de meeste van zijn oorspronkelijke gebieden weer heeft ingenomen. Bever populaties trekken steeds verder weg van de reeds gekoloniseerde half natuurlijke habitats en meer in de richting van verstedelijkte gebieden. De ecologische voordelen die gekoppeld zijn aan de aanwezigheid van bevers, als ecosysteem ingenieurs, in natuurlijke omgevingen zijn duidelijk, echter in dichtbevolkte gebieden veel minder. Daarom is het opvolgen van hun verspreiding belangrijk voor een succesvolle co-existentie. Om dit op te volgen werd in 2014 een Habitat Geschiktheidsindex (HSI) model samengesteld, dat alle geschikte gebieden voor bevers in Vlaanderen identificeerde. Deze thesis is gericht op de validatie van dat HSI-model, namelijk het testen van de juistheid waarin het de aanwezigheid of afwezigheid voorspelt alsook het aantal territoria. De resultaten laten zien dat de kolonisatie nog ver van de maximum kolonisatie capaciteit zit, aangezien er nog zo veel geschikt habitat niet bezet is en de populatiedichtheden over het algemeen nog redelijk laag zijn. Bevers zijn echter wel aanwezig in de meeste gebieden waar ze werden verwacht, maar nog niet overal. Hierbij kunnen de beperkt verstreken tijd sinds de introductie en de introductieplaats zelf mogelijke verklaringen zijn voor de nog overgebleven vrije plaatsen met geschikt habitat. Gebieden waar bevers aanwezig zijn maar niet werden verwacht kunnen worden toegekend aan ontbrekende parameters in het model of nieuwe ecologische aanpassingen van bevers in verstedelijkt gebied. Als besluit kan worden gezegd dat het HSI-model een zekere trend vertoont, maar geen zekerheid geeft in de voorspellingen. De groei van een populatie na een herintroductie kost tijd, alsook de verspreiding ervan over heel Vlaanderen.

Summary

In the past beavers were heavily persecuted by humans and were almost completely exterminated by the beginning of the 20th century. Reintroductions, protection and conservation efforts, at the beginning of the 21st century, led to the reestablishment of the species in Flanders. Beavers are well known for being able to cut down trees and create dams. This makes the beaver an important species in nature as it enhances the species richness of its surroundings by modifying the landscape. The expansion in Flanders is going beyond the remaining semi-natural habitats into the more densely populated urbanised areas. Here human–beaver conflicts can arise and for this reason it is important to follow and predict the future spread of the beaver. This thesis will try to validate a model, made for the region of Flanders, on its efficacy on predicting the presence of beavers and number of territories. At this point, the results still show high discrepancy between the predictions and the observations that were done in the field. On the one hand, beavers are present in areas where they were expected by the model, but not yet everywhere. Time lag and the site of introduction are possible explanations for currently uncolonised areas, considering the time interval between the introductions and the current spread is just 18 years. On the other hand, there are beavers in areas where the model did not predict their presence. Which could be explained by details missing in the model or the possibility that beavers are less choosy in their habitat selection when near urbanised areas. In conclusion the model is promising, but currently not yet capable of making the correct predictions for further colonisation. Both population growth and the following area spread of these individuals takes time, having not yet reached their full potential for Flanders.

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1 Introduction

1.1 Beaver Ecology and Biology

The European beaver belongs to the Rodentia order and the Castoridae family that includes only two extant species: the North American beaver, *Castor canadensis*, indigenous to North America and the European beaver, *Castor fiber* Linnaeus, 1758, indigenous to Eurasia (Belova 2012). The focus in this study is only on the native Eurasian beaver. Beavers are crepuscular, herbivorous, semi-aquatic and the largest rodents in Europe (Nolet and Rosell 1998, Campbell-Palmer and Rosell 2015). A fully-grown beaver has an average body mass of 20 kg but can reach up to 35 kg. The head-body length amounts to an average length of 1,2 m, including the tail (Müller-Schwarze 2011, RVO 2014). In beavers, there are no external differences between the sexes except for visible nipples in lactating females (Wilsson 1971), and only a minor difference in weight with an adult female being on average 1 – 1,5 kg heavier (Campbell-Palmer and Rosell 2010, RVO 2014). These large rodents have an average life span of 7 – 8 years but sometimes live for up to 20 years, mostly in captivity (Svendsen 1989, Campbell et al. 2005, Rosell and Thomsen 2006). Beavers are choosy, generalist herbivores and energy maximizing central-place foragers, feeding on the bark, shoots and leaves of woody plants, terrestrial herbs and forbs, ferns and aquatic vegetation (Haarberg and Rosell 2006, Belova 2012). As central-place foragers, beavers move out from the water to select and cut trees and vegetation, then transport it back to the water to eat immediately, or to the lodge to feed dependent offspring or to store for later use (Jenkins 1980, Fryxell and Doucet 1991). They prefer aquatic environments that are surrounded by woodland, but they can also be found in habitats that are influenced by human presence, like agricultural land and urbanized areas (Halley and Rosell 2002). During the winter, beavers can be dependent on woody plants, especially the bark (Nolet et al. 1994), because they mainly forage on softwood riparian forests and agricultural crops are just temporary, the proximity of such softwood riparian forest habitat is essential for their survival (Van Looy et al. 2012). The availability of woody plants is therefore one of the most important factors in determining beaver range and distribution (Wilsson 1971, Rosell and Parker 1995).

Beavers are known as landscape architects or being ecosystem engineers, hereby creating habitat for many other species (Belova 2012). These animals have a unique ability to modify their environment by actively building dams, creating ponds, and building lodges. No other mammal has such a broad range of construction behaviour (Żurowski 1992, Rosell et al. 2005). In the pre-industrial period, beavers were dominant ecosystem engineers in many European running water ecosystems (Belova 2012) and are most famous for their ability to build dams. The dams are mostly built in smaller streams and here more slow-running parts are preferred. Due to the very intensive stream regulation (straightening, concrete banks, …) that has been done in the past century, beaver activity plays a crucial role in the survival and conservation of flora and fauna of small streams. The dams are built of beaver cut sticks and logs tightly meshed together with mud and other debris. The dams help to create a constant water level that extends their area of foraging, making it easier to transport twigs and branches, and serves as a protection against predators (Wilsson 1971, Belova 2012). The excavation of burrows and canals will have localised effects on site characteristics, but it is through their dam building activities that beavers exert their greatest influence on freshwater ecosystems. Regulation of river flow by beavers formed a big amount of stagnant water bodies and new shallow waters. Thus, diversity of habitats in the river valleys increased. Previously unsuitable for breeding, streams became suitable for many different species (Belova 2012). Also, water regulation which is a major contribution to the conservation of aquatic and wetland ecosystems, for example the use of beaver impoundments or beaver ponds. These beaver beaver ponds slow stream velocity allowing sediment suspended in the water column to settle, aggrading incised stream systems, and reconnecting streams with their floodplains. The increase in surface water promotes groundwater recharge, storage, and supplementation during base flows (Dittbrenner et al. 2018). By retaining water in the lakes there is a reduction in the risk of lakes and rivers drying (Belova 2012). The positive effects beavers have on everything from water storage to groundwater recharge and drought mitigation reveal a species that can transform environments into biodiversity hotspots. As long as beavers are active, the positive effects remain for several years. Compared to man-made pond habitats, slowly degrading through silting up, ongoing beaver activities provide permanent areas of different succession stages next to each other (Belova 2012). The strong effects beavers have on the environment, however, may also impact human activities in that environment, causing conflicts.

1.2 Species history

During the last century, humans have transformed a large portion of the planet's natural landscapes because of agricultural purposes or expanding urban areas to feed and house a growing global population. These human land-use activities have caused the degradation, fragmentation or even loss of many natural habitats (Foley et al. 2005). Human-induced global change is increasingly affecting life on our planet, including living conditions for humans themselves as well as the resources we depend on. As a result, species diversity is strongly declining (Bakker and Svenning 2018). The Eurasian beaver (*Castor fiber*), is known from the Pleistocene in Europe, although there are references to the presence of the genus Castor since the Miocene, ca. 10 Ma (Cuenca-Bescós et al. 2017). The once widespread beaver population across Europe and Asia suffered great losses and was reduced to an estimated 1200 individuals by the beginning of the 20th century (figure 1), considered critically endangered, primarily through over-hunting for fur, meat and castoreum (Nolet and Rosell 1998, Halley et al. 2012, Campbell-Palmer et al. 2015, Mai et al. 2018).

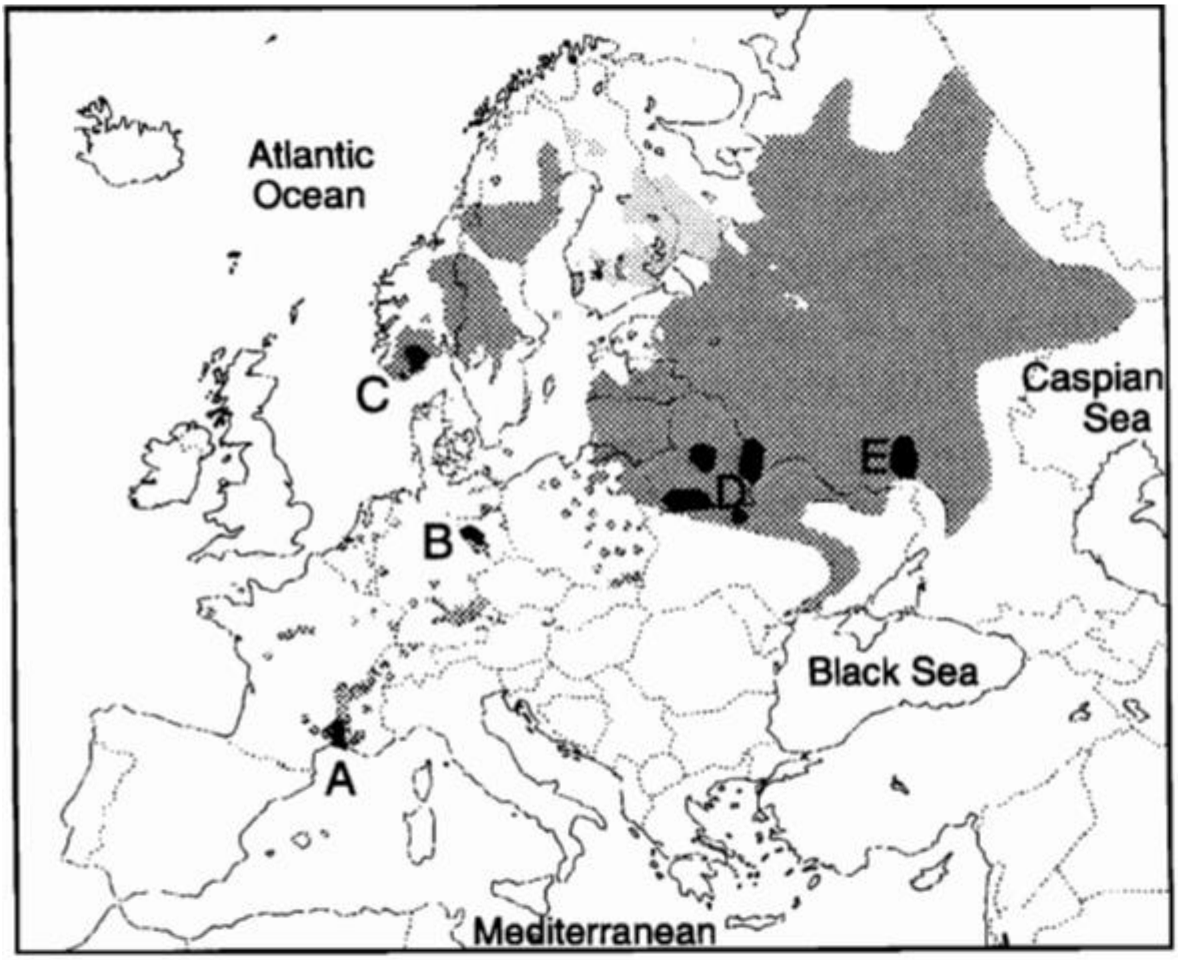


Figure 1: The historic and present (1998) range of beavers in Europe. Black areas show the populations remaining at the beginning of the 20th century, situated (A) along the Rhône, (B) along the Elbe, (C) South Norway, (D) along the Neman and in the Dnepr basin (Beresina, Sosz, Pripjat and Teterev), and (E) along the Don (Voronezh). The present range of Castor fiber *is depicted in dark grey (Nolet and Rosell 1998).*

In Belgium the last beaver was killed in 1848 (Nieuwold 2002). Beavers are part of the native fauna of Europe and, as their demise was caused directly by human actions, many argue that we have an ethical responsibility to conserve this species and restore it to its natural range (Campbell-Palmer and Rosell 2010). Later in the 20th century, many countries had progressively adopted protection and management measures, which allowed remnant populations to survive and recover (Halley and Rosell 2002). The Eurasian beaver (*Castor fiber*) became a legally protected species in most European countries under the Convention for the Conservation of European Wildlife and habitats and the Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora (Annexes II and V) (Strzelec et al. 2018). For Flanders this implied strict protection of the beaver and the areas where it is present. Furthermore, since the decree of the Flemish government of 13 July 2001 the beaver is added to the list of completely protected native species for Flanders. This implies that in Flanders it is at all times prohibited to deliberately kill, hunt, transport, trade, capture or incarcerate beavers, to destruct residences and hiding places, or to significantly disturb beavers nor their residences (Overmars 1999).

The recolonization by beavers in Europe is relatively well documented, as the species disperses and occupies habitat along watercourses, leaving visible marks of their occupancy, such as lodges, dams, or freshly cut trees (Zwolicki et al. 2019). The first beaver observed in Belgium since the species' extinction in 1848 was found in the Rur river system in 1990 (Huijser and Nolet 1991), and probably originated from the Eifel region in Germany (Dewas et al. 2012). Starting in 1998, beaver presence was detected at various sites in Belgium. Beavers were thought to originate from illegal introductions (Michaux J. 2012). In Wallonia, signs of beavers appeared on tributaries of the oriental Ourthe, the upper Meuse, then on the middle Ourthe, the Dyle and the Semois river systems. During the official investigation into this illegal reintroduction, it turned out that between 1998 and 2000, at least 101 beavers had been released (four beavers from the Elbe River and 97 from Bavaria) (Schwab 2002). Conservation efforts have seen populations restored through natural range expansion, translocations and reintroductions across much of its former native range (Campbell-Palmer et al. 2015). Many reintroductions and translocations involved animals of varied geographical origins, resulting in genetically mixed populations (Halley and Rosell 2002). Concerning the Eurasian beavers (*Castor fiber*), the analyses confirmed the presence of at least three different subspecies (*Castor fiber galliae*, *Castor fiber albicus*, *Castor fiber fiber)* in Belgium, Luxembourg and Western Germany. The presence of different subspecies is the result of different reintroductions performed from different European regions (Belova 2012, Michaux J. 2012). If introduced populations are formed by mixing subspecies their morphological characters deviate from the source forms. Morphological forms present in populations with different frequencies may have certain adaptive values especially in connection with jaw apparatus and other functional significant structures of cranium (Belova 2012). These widespread reintroductions, followed by rapid natural population expansion, allowed the settlement of a large beaver population over large parts of Wallonia. During the winter of 2000 – 2001, a regional survey estimated a minimal population size of 100 – 120 beavers (47 sites). During the latest census (2009), the population was estimated at 800 – 1000 animals, occupying at least 220 sites. Currently, geographic expansion continues, especially in secondary drainages. In Flanders (northern part of the country with a higher population density/more urbanized area), in 2003, 22 individuals originating from Bavaria were released in the Flemish part of the Dijle (Dyle) river system (Verbeylen 2003) and 21 more in the Meuse valley (Swinnen 2015) without knowledge of the authorities (Belova 2012). Moreover, beavers reintroduced in the south of the Netherlands, in the province of Limburg close to the north eastern Belgian border, in 2002 / 2004 (origin: Elbe) started to disperse into Flanders via the Belgian Meuse and tributaries (Kurtjens 2009, Belova 2012). Considering that the Bavarian population itself is composed of beavers from different origins, Belgian beaver populations probably contain both the Eastern and Western geographical forms (Durka et al. 2005). Initially, there was no systematic follow-up by the public authorities or a scientific institution (Belova 2012). Eurasian beaver populations worldwide have been steadily increasing in most parts of its reclaimed area during the past years, already reaching the size of around 1 million individuals, including some populations of introduced North American beavers (Halley et al. 2012). According to the same authors, after a powerful recovery Eurasian beavers can be found throughout Europe, comparing the total population of beavers in 2012 (+ 1 million) with 2002 (± 600 thousand). This means that their population has almost doubled in numbers during a time interval of just one decade (Halley and Rosell 2002, Halley et al. 2012), and it is still rapidly expanding in many European countries.

The Eurasian beaver appears on the International Union for Conservation of Nature Red List of threatened species. From a conservation perspective the species is now considered to be secure, categorised as 'Least Concern', but conservation efforts are recommended to ensure this species does not become threatened again (Campbell-Palmer and Rosell 2010). Knowledge about the beaver's past population trends and present distribution is critical to its effective management.

The threat of an alien species (*Castor canadensis*)

In Belgium we have two species of beavers, the North American beaver (*Castor canadensis*) and the Eurasian beaver (*Castor fiber*). In 2009 the presence of allochthonous North American beaver, *Castor canadensis,* was demonstrated in Rhineland-Palatinate (Germany), in Wallonia (Belgium) and in Luxembourg. This gave rise to a risk of possible erosion of the native Eurasian beaver population in this region of Europe (Belova 2012). Until now, there are no indications of the North American beaver in Flanders (Northern part of Belgium) (Swinnen et al. 2017), only in Wallonia (Southern part of Belgium) (Belova 2012, Dewas et al. 2012, Michaux J. 2012). Both species are superficially similar in appearance and require close and expert examination to allow the distinguishing features to be determined (Gaywood 2008).

According to Gause's competitive exclusion principle, two species with identical niches cannot coexist indefinitely. The imminent question is whether coexistence or competitive exclusion will ultimately result, with the possible regional extirpation or eventual extinction of *Castor fiber* (Belova 2012). Body size is similar and with just minor differences in life history, ecology and behaviour that were found, suggesting nearly complete niche overlap (Belova 2012). Two important differences between the species are that the North American beaver matures earlier and has larger litters than the Eurasian beaver. An overall mean value was calculated for colony size of 3.8 for the Eurasian beaver and 5.2 for the North America beaver (Rosell and Parker 1995, Pollock et al. 2003). However, research found out that age of dispersal, and eventual reproduction, were influenced by population densities (Hartman 1997). His results suggest that at low densities the differences between the species would be less important, i.e., both species could exhibit yearling dispersal and early attainment of sexual maturity. Though competitive exclusion resulting in the extinction of a native mammal by an alien congener at the continental landscape scale has been rare, the process may be difficult to detect due to potential time lags of centuries. Thus, there is a distinct risk that *Castor canadensis* may eventually competitively exclude *Castor fiber* at all landscape scales (Belova 2012).

1.3 Colonisation and spread

Beavers are highly social and territorial animals which normally live as a family unit, also called a colony. The colony consists of two parental adults or the dominant breeding pair, the yearlings born the previous year, and the young of the year, also called kits (Wilsson 1971, Campbell et al. 2005). The beaver is a typical obligate monogamous species (Rosell and Thomsen 2006), with the breeding pair being mates for life. The mean size of a beaver family is around four individuals (Zahner 2005). The young are born in May-June and generally, the two-year olds when they have reached sexual maturity, and occasionally one-year olds, leave the parental colony and move to new areas just before this time. Second year animals determine the territorial dispersal of the local population and are at the same time the most vulnerable group in the population (Belova 2012). If these dispersing sub-adults fail to establish territories they may return to the parental colony (Wilsson 1971, Hartman 1996, Collen and Gibson 2001). In more recent studies a delay in dispersal up to the age of seven is found in saturated populations (Mayer et al. 2017).

Habitat selection plays an important role, especially in long-lived and territorial herbivores, such as beavers for which a settlement decision is crucial, and has long-lasting consequences for the survival and reproduction of a colony (Zwolicki et al. 2019). During selection within the scale of habitat patches, animal costs are linked to a foraging strategy and to time spent moving through suboptimal microhabitat patches, when this time could be used for exploiting the habitat or potentially better ones (Zwolicki et al. 2019). The sizes of the territories that they occupy are usually around 3 km of river bank (Nolet and Rosell 1994, Fustec et al. 2001, Dewas et al. 2012). These sizes can also vary from 0.5 km up to more than 12 km depending on the quality of the habitat and the population density (Gaywood 2008). The study of Nolet and Rosell (1994) could explain rapid colonisation, because beavers are highly territorial animals and information about territories that are not colonised yet reach nearby beavers rapidly.

This territory occupancy is advertised by chemical cues, called scent-marking (Rosell and Nolet 1997, Rosell and Bergan 1998). Dominant territory holders build scent mounds: small piles of mud and debris that are mainly positioned at territory borders, but also within the territory (Rosell et al. 1998). Subordinate beavers occasionally over mark scent mounds of conspecifics (Rosell and Thomsen 2006, Tinnesand et al. 2013), suggesting that they could assist in territorial defence (Rosell et al. 2000). Intruders are treated aggressively and territorial combat can result in serious or even fatal injuries (Crawford et al. 2015).

1.4 Human - beaver impacts

A major challenge for conservation biology is facilitation of co-existence between humans and wildlife. The beaver’s return to the ecosystems from where it was absent for a century or more, will have significant changes on vegetation communities and even on landscape elements (Belova 2012). With Flanders being one of the most densely populated areas in Europe and having such small nature area remaining, the recolonization of the beaver will undoubtedly cause conflicts. Beaver populations will continue to grow and few, effective population reducing, predators exist for beavers in Flanders, in this list are the wolf (*Canis lupus*), brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*), pine marten (*Martes martes*) and otter (*Lutra lutra*) (Tyurnin 1983, Kile et al. 1996, Rosell and Hovde 1998, Nowak et al. 2011). Of all these predators, the wolf appears to be the only species that regularly preys on beaver (Rosell 1996). In parts of America the wolf may be able to regulate local populations of North American beavers (Shelton and Peterson 1983). However, this is unlikely to happen in Europe as the wolf and other potential predators are rare (Rosell 1996). Besides predators the only disease known to potentially decimate beaver populations is tularemia (Bloomquist and Nielsen 2010). The main cause of death is mainly due to anthropogenic influences. A study in Serbia identified humans (43.7 %), diseases (31.2 %), predators (3.1 %) and unknown (21.9 %) as the different causes of mortality. The anthropogenic influences include traffic accidents, poisoning, … as well as (illegal) net fishing and (illegal) hunting. In regard to the age structure, the greatest mortality was recorded in sub adults (46.6 %), followed by adults (36,6 %) while the lowest mortality was recorded in juvenile beavers (16.6 %) (Belova 2012) The higher mortality in sub adults is because they are more prone to migrate and therefore encounter human interaction/conflicts.

Human-beaver interactions have increased as human populations live or expanded into previously prime beaver habitat. The risk of human-wildlife conflicts will thereby rise, as it is just a matter of time before beavers occupy all remaining preferred habitat and are forced to seek less optimal habitat in undesired conflict areas (Belova 2012). This can then over time cause for habituation of beavers to people. Habituation of wildlife to humans often results from wildlife seeking food, shelter, or nesting sites in close proximity to people (Jonker et al. 2009, Campbell-Palmer and Rosell 2015).

Human–wildlife conflicts arise when wildlife activities or presence negatively impacts upon humans (Treves et al. 2006). As a result, beaver dam building activity can cause flooding of roads and human property and are perceived as a nuisance (Belova 2012). An increase in the population of beavers in a given area is accompanied by a greater number of reports of damage caused by their activity (Tajchman et al. 2018). The most frequent problems include flooding of fields, grassland, and forest crops, felling and chewing trees in forests, tree stands, and fruit orchards, damage to pond banks, flood embankments, or road and railway embankments, and destruction of agricultural crops, e.g. maize, carrots and beets. The greatest damage is noted in the initial period of a beaver family settling down, when building material is needed for lodge and sometimes dam building. Its extent declines with stabilisation of the population (Tajchman et al. 2018), as maintenance of lodges and dams require less wood. Besides the physical damage they cause, there is also a possible public health risk involved (Gaywood 2008). The most common public-health issue raised in relation to beavers is Giardiasis or often called, ‘beaver fever’. *Giardia* and other potential pathogens, such as *Cryptosporidinium*, which can both be found in untreated water, previously already occurred in the natural environment and human populations (Gaywood 2008). These are more often linked because of their coexistence, than of the real threat that beavers will cause in spreading these diseases.

It is important to acknowledge that there can be problems caused by beavers in certain places and at certain times, but the level of damage at a national scale is not reported as significant. This has to be balanced with the wider benefits that beavers may bring (Gaywood 2008).

1.5 Modelling colonisation

The patterns of how species spread are of great interest in both spatial ecology and conservation practice. Future scenarios regarding the spread of species, in this case dispersal to former inhabited areas, may be predicted based on either simulations of mechanistic models or extrapolations from previously observed patterns (Šimůnková and Vorel 2015). Therefore, the descriptions of general dispersal mechanisms in various environments (especially in human-made landscapes) have become increasingly important in spatial ecology (Šimůnková and Vorel 2015).

Beavers have rapidly colonized their historical distribution (Halley et al. 2012), making them a useful model species for characterizing the process of habitat selection in different stages of population development (Zwolicki et al. 2019). Both extant beaver species (*Castor fiber* and *Castor canadensis*) are examples of semi-aquatic mammals which mainly require the use of a linear platform for spreading (i.e., most often dispersal trips follow the waterlines), but also documented trips along catchment basins (Hartman 1994, Halley et al. 2012). Increasing conflicts among beaver conservation and human-made landscape utilisation raise interest in the detailed patterns of beavers' expansion and increases the necessity to acquire and predict future spreading scenarios (Šimůnková and Vorel 2015). Hartman published a general model for the spread of beavers by describing the rapidity of the colonisation front and the development of the population density during decades of population establishment (Hartman 1994, Hartman 1995). The adequacy of a particular model can only be evaluated relevant to the purposes at hand, and to particular scales of investigation (Hartman 1995). Several models take specific factors affecting the process into consideration, such as topographic irregularities, finite velocity and non-random movement, Allee-effects, and density-dependent movements (Hartman 1995).

This thesis is based on a former doctoral research that used a Habitat Suitability Index model (HSI), that examined the potential habitat suitability for beavers of the yet uncolonised parts of Flanders (Swinnen 2015). Analysis of the habitat characteristics, of the locations where beavers were present during the study of Swinnen et al (2015), were used to examine the rest of Flanders for similar environmental conditions. Then these locations were identified as sites that are suitable or unsuitable based on the situation of the inspected area at the time of the study conducted by Swinnen et al (2015). This was done by using species distribution models. Not surprisingly, distance to water, willow stands, wetland vegetation and poplars were the main explanatory variables. In conclusion he estimated that within Flanders there is sufficient habitat to support 924 beaver territories (Swinnen 2015).

1.6 Thesis outline

As the central question in this study we investigate the hypothesis, that the HSI model (Swinnen 2015) is accurate in estimating the presence and number of beaver territories in Flanders. The results will be discussed based on background knowledge of beaver ecology. Following aspects will be included in the discussion:

(i) A prediction model based on suitable habitat for beavers used for colonisation predictions;

(ii) Natural and anthropogenic factors impacting beaver population development in Flanders;

(iii) The link between beavers and their favourite class of vegetation in proximity of a waterbody;

(iv) Amount of suitable habitat still available to beavers in Flanders;

(v) Human – beaver conflict situations in Flanders.

As Flanders is one of the most densely populated areas in Europe this study will help to understand how their future colonisation will take place in a more suboptimal environment. In essence we want to know how we can contribute and foster the coexistence between man and beaver in a densely populated area such as Flanders and maybe even act as a possible model or example for other Western European countries.

2 Materials and methods

2.1 Study area and overall setup

In an earlier study on beavers in Flanders an HSI model was used to estimate the distribution of beavers across landscapes by correlating species occurrences with spatial environmental information (Swinnen 2015). A series of eight environmental predictors were put together in the HSI model of Swinnen (2015), defining all suitable beaver habitat in Flanders and with a predicted total of 924 territories (figure 2). Visualising Flanders as a raster map and dividing it into 645, 5 x 5 km, Universal Transverse Mercator (UTM) squares that not only predict the presence or absence but also the number of expected territories within a grid cell.

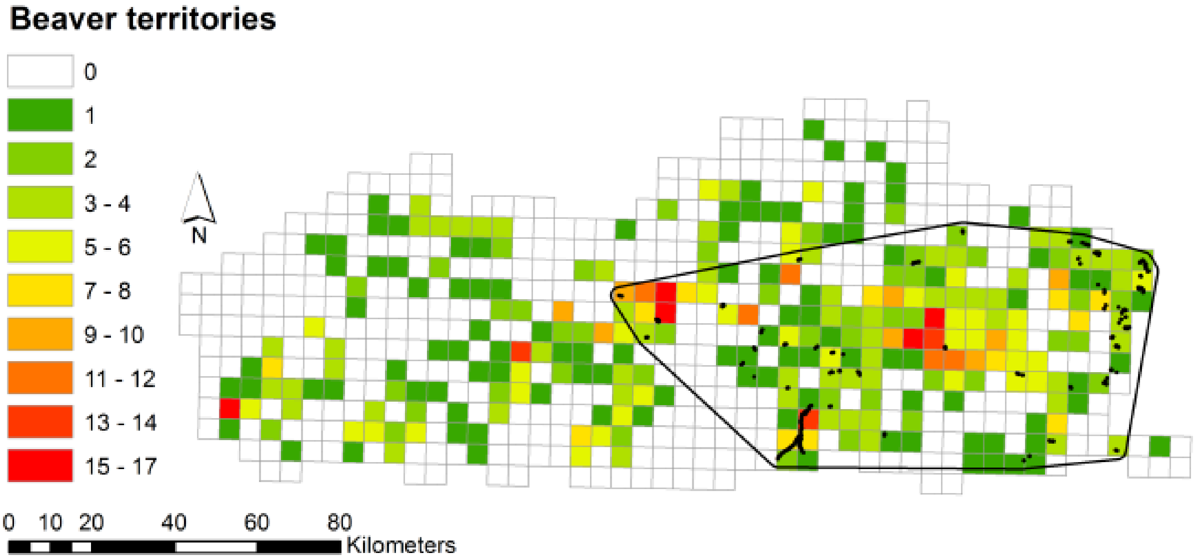


Figure 2: The original HSI model with 645, 5 x 5 km, UTM squares that cover the whole area of Flanders. The black dots and the polygon represent the spread and known beaver territories in the year 2014 (Swinnen 2015).

We investigated, to what extent the current occupancy of beaver territories in each UTM square is in line with the predicted number of potential territories. To check for the presence or absence of beavers in the UTM squares a series of field visits to the squares was necessary. Afterwards the observational data from the field was compared with the predicted data from the model.

In order to select the UTM squares to be visited, we used data made available by Natuurpunt (confirmed sightings in “waarnemingen.be”) or by the Research Institute for Nature and Forest (INBO).

The first of these datasets (2010 – 2017) was shared by Natuurpunt and is based on public sightings (Citizen Science) of beavers and all sorts of beaver activity in the landscape that can be registered online on a portal site (waarnemingen.be). This portal site works with online registration of sightings. There is a series of data such as date, time, species, number of individuals and additional information that can be reported. The second dataset (2017) that was received, is from INBO (the Flemish Research Institute for Nature and Forestry). INBO receives its data from the Agency for Nature and Forests (ANB), reporting it as a presence/absence dataset but actually showing only presence data. INBO is a scientific institution from the Flemish government, which provides insight in nature through qualitative research. INBO does not work on a public basis, data is instead collected by people with a certain expertise. Their data includes only territories of beavers based on lodge locations, which were located and visited by people of Flanders Environment Agency (VMM), ANB and INBO.

The HSI model of Swinnen (2015) includes the whole area of Flanders, but since only 4 years passed starting from 2014, beavers may not yet have had time to reach all parts of Flanders. Indeed, the combined observational datasets from Natuurpunt and INBO did not show any observations yet in areas that are far away from the edge of the distribution in 2014. Therefore, we left out these areas from further study and used two types of restricted areas instead. Restricted area 1, is Flanders without the province of West-Flanders, where beavers so far have not yet been observed. Restricted area 2 includes only the visited UTM squares. This has been done because of the short time interval between the introduction in the beginning of the 21st century and the current colonisation and spread of the beaver across Flanders. Besides the HSI model the two obtained observational datasets were included for determining fieldvisit locations. Important is that these datasets are presence only datasets, i.e. they contain data about confirmed presence of a species in an area, but there are no data about confirmed absence. Still, an assumption can be made that if a conspicuous species like beaver is not reported from an area, it probably does not occur there.

During the selection of the field sites that had to be visited, there was a difference in the reliability of the datasets. These presence only datasets are often publically accessible and hold great numbers of data points, which are afterwards checked or validated for their probability. Knowing that Flanders is a densely populated area and only the presence is noted, areas with no sightings can then be regarded as locations where beavers are absent. Still the selection was done with a certain caution as the dataset of Natuurpunt could have lots of misleading data points, having in mind the fact that an unexperienced observer easily can make mistakes: the sighting of a muskrat (*Ondatra zibethicus*) instead of a beaver, a flood blockage mistaken for a dam or a pile of branches seen as a lodge. For these reasons only reliable data points (close to other data points, in line with the HSI model or confirmed sightings) where picked out and used to select areas to be validated by field visits.

2.2 Field data collection

When starting the investigation, if beavers are present or absent on a certain location, there are several factors that must be taken into account. Beavers are mainly nocturnal or crepuscular so they emerge late in the evening or at night (Swinnen et al. 2015), which makes the observation of beavers themselves quite difficult. The presence of beavers in an area is best shown by their tracks and building or foraging activities. All these can be easily seen during the day from a boat on the water or by walking the banks. The locations where visited by foot, bike or boat depending on the kind of terrain.

The data collection protocol used in this study is based on the methods used in the study of Dewas, Herr et al. in combination with the methods of the species directive report of the Rijksdienst Voor Ondernemend Nederland (RVO). Which relies on the observations of beaver activity signs along prospected water bodies (rivers, lakes, ponds, …). Each type of sign is associated with a level of probability of beaver presence. The frequency and variety of signs found at the same site allow the observer to estimate the degree of beaver presence and settlement. For our study the selection was narrowed down to absent/present, probable was not included in the options.

During the field visits an application was used for the on-site data collection, regarding the presence or absence of beaver activity. The application called ‘Bever Monitoring’ (figures 3 A&B) was developed by INBO for the monitoring of beavers in Flanders and is part of a series for specific species. By using this application in the field, it was possible to easily collect all the data and made it possible to visit many locations, because of not manually having to write down all the data and coordinates. The data collection consisted of coordinates on an online map that registered the location, there was an accuracy of at least ten meters depending on my position. Furthermore, the selection of possible beaver activity signs which could be selected; Burrow/Lodge, Dam, Canals/Slides, Gnawing activity, Others and NULL. Others include beaver sounds, scent markings, beaver droppings, sightings of living or dead beavers and food caches. When in doubt if a sign was of a beaver or not it was also marked as others and accompanied by a comment, description and photograph. The NULL option is chosen when the site did not show recent signs of beaver activity. The confirmation that there are no beavers present or not present anymore is also important to determine the accuracy of the prediction model. This data was then automatically stored in an online data bank (Google Sheet).

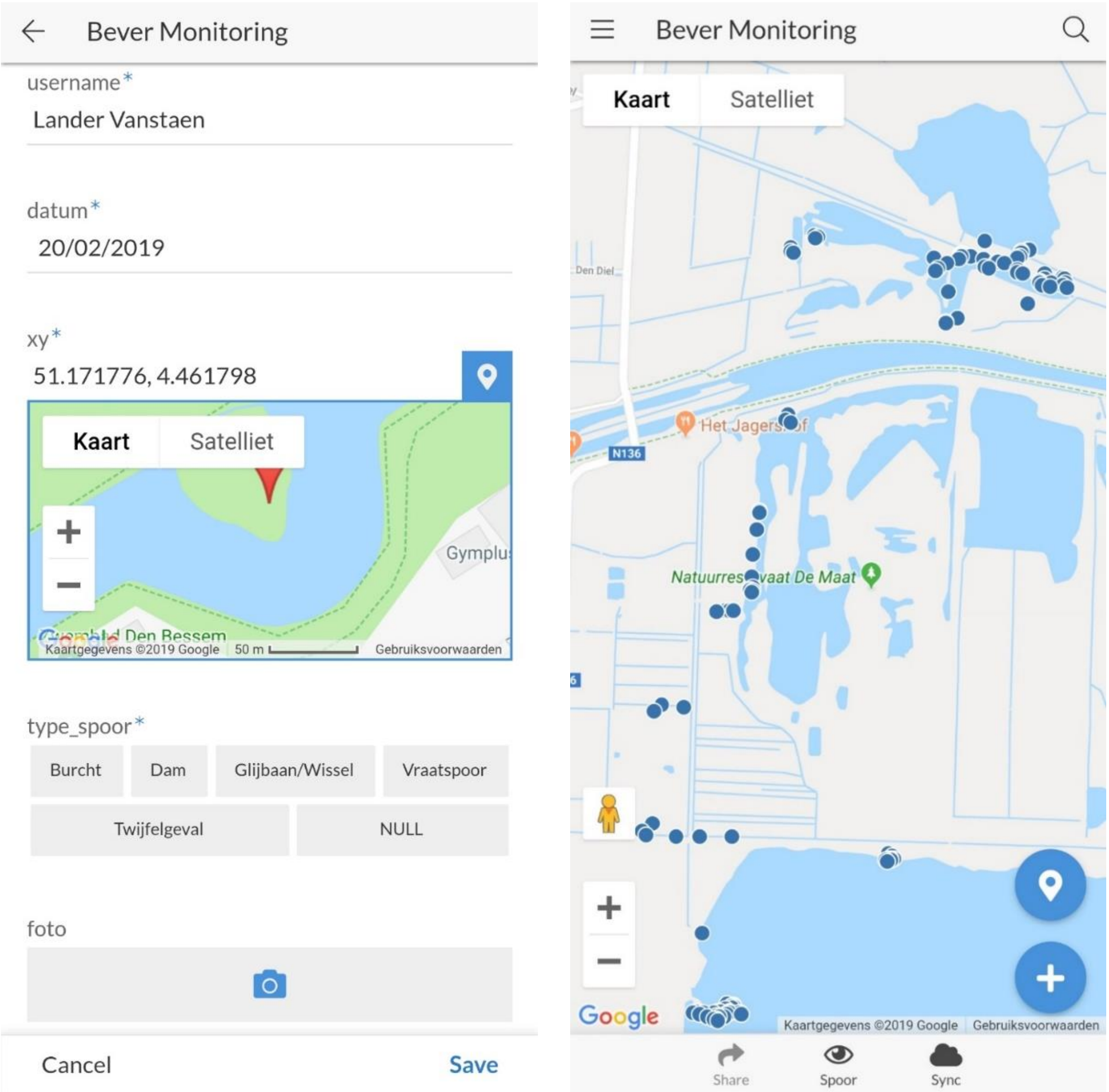


Figure 3: A, visualisation of how a data point is assigned to a certain location in the 'Bever Monitoring' application (INBO). Showing the observer, the date, its specific coordinates, and type of sign sometimes accompanied by a photo for extra information. B, an overview of an investigated area with each individual blue dot representing a data point.

2.2.1 Lodges, burrows or bank dens

Lodges are dome-shaped constructions built from branches or even tree trunks, sometimes stripped of their bark, depending on the construction lust of the beaver, combined with grass, slime, mud and sometimes rocks. Depending on the construction resources in the area these lodges can vary in size. Not only because of the resources the size of a lodge will vary but also because of differences in the family size, they can inhabit one large lodge or several smaller in the same territory. Beavers have a preference in choosing the location of their lodge, when building in lakes if possible they will place it on an island, when building in rivers they will choose a spot where the water depth remains more or less constant or in between self-constructed dams. When in conflict with humans, people often break down lodges with the idea that the beaver will move or wander off. Except that the outcome is often the same as for breaking down dams, beavers most of the time rebuild their lodge bigger and stronger on the same location. Majority of beaver lodges persist for more than 10 years, thus being quite permanent structures of the environment (Belova 2012), which makes it more difficult to determine whether it is an active or an old lodge. Accumulation of organic matter on the surface of lodges enables their overgrowing by plants (Belova 2012) and can serve as a form of camouflage to blend in to the landscape.

Beavers are not always able to build large lodges or build a lodge at all on the banks. In more urbanised areas, areas with less building materials or steep banks, beavers will tend to dig holes in the side of the bank. These burrows or bank dens are more elusive and can go unnoticed, because the entry of such burrows is mostly under water and can only be seen in extreme drought periods. This way a beaver can be living in a place without anybody knowing where exactly the burrow is. Beaver burrows are mostly temporary structures that often collapse if it is unused for one or two years (Belova 2012), so when finding large holes in the bank it can be recognised as a left burrow.

2.2.2 Dams

When a dam is found the presence of a beaver is almost certain. Yet even if there is no sighting of a dam, beavers can still be present as beavers do not always build dams. Beaver dams consist of a wall of branches and mud, sometimes even fortified with rocks (Gaywood 2008), standing perpendicular to the flow direction of the water. Dams are always built to the complete width of the water body and when the dam gets overflown the beaver will adjust the dam in width and height to again make a complete blocking of the water flow. With the spread of beavers in more inhabited areas, the use of agricultural crops in dams is more and more observed. These are mostly temporary because they are used as an additional passage way to the agricultural fields until the harvest of the crops, for example the use of maize in the building of dams in drainage ditches. More often conflicts arise between people and beavers, especially in case of dams and farmers as they flood their fields or block entry ways (Gaywood 2008). Most of the time dams are then broken down, but as beavers are “stay-at-home” minded they will rebuild the dam on the same location (Taylor et al. 2017) and most of the time even bigger and stronger.

2.2.3 Canals or gutters and trails or slides

Beavers dig canals, sometimes also called gutters, during periods of drought or in swampy terrain. These with the purpose of having a waterway towards a food source or to a lodge, a beaver will always prefer the waterway instead of being forced to walk on land (Gaywood 2008). When they do have to cross a piece of land it is most often seen as a worn-out pathway or game trail, also called slides. Slides have the main function of connecting useful locations with spending a minimum of time out of the water or on land. Most of the seen slides are mainly found between a water source and a food source, a dam and the building material source or two different water sources. The usage of these paths influences the banks, because beavers move low over the ground they almost drag themselves and by this move a lot of dirt. When using these paths for a long time a beaver can create entire holes in the bank and even sometimes disconnect banks and create new connections between water sources.

2.2.4 Chewing/gnawing activity on vegetation

Nocturnal and semi-aquatic lifestyles make monitoring more difficult. Recording food uptake and fresh feeding signs are important methods (Campbell-Palmer and Rosell 2015). Beavers are strict herbivores well known for cutting down trees and leaving behind ‘pencil stems’. These beaver cuttings are easily recognized by their conical shape, height above the ground and arrangement of tooth marks. Depending on the season their diet consists of aquatic vegetation, terrestrial herbs, bark, leaves and sometimes agricultural crops. Beavers are good swimmers and poor walkers, so they will usually not go much further than 50 m up the bank. Because of this it is easy to narrow down the observation area during a field visit. When coming across a woody bank it is most often only necessary to scan the banks for signs of activity. Gnawing activity in this study was mostly seen as damage to different types of vegetation differentiating from the clearly visible pencil stems and large hourglass shaped notches in trees unto the typical small detached and stripped-down branches (“beaver sticks”). The presence of young beavers can be deduced when the beaver sticks are thinner and smaller and have lots of smaller teeth markings on the wood. For a time estimation it is important to watch the colouration of the gnawing activity on the wood (figures 4 A&B), because these are visible for a long period of time and can be of many years in the past. When there are only old signs or mostly dark coloured gnawing activity (figure 4 A), this can mean that there are no more beavers present, that it was a beaver passing by or that it is visited from time to time as an additional feeding ground. Depending on the sort of data needed or having a time frame in mind, it is important to decide which to include and which to leave out. For example, all stems that had been completely severed from the trunk or were in the process of being severed, were estimated in time by the freshness of the wood chips on the ground (figure 4 B).

Figure 4: A, a tree showing mostly dark colouration of the notch and lack of fresh woodchips around the stem, representing old activity signs observed in the field. B, another tree showing lighter colouration of the notch and many fresh woodchips around the stem, representing recent activity signs.

2.2.5 Other signs of beaver activity

2.2.5.1 Sighting of living or dead animals

Beavers are described as nocturnal or crepuscular (Swinnen et al. 2015) but are from time to time also active during the day (Campbell-Palmer and Rosell 2015). It is best to search for the animals themselves during sunset or sunrise. When swimming swiftly, only the head is held above the water line, showing only the nose, nostrils, eyes, and ears of the beaver. In contrast, the remaining part of the body (back and pelvis) are below the water surface (Zahner 2005). To distinguish a beaver from other animals like otters (*Lutra lutra*), muskrat (*Ondatra zibethicus*) and coypu (*Myocastor coypus*), it is best to watch for the characteristic tail. Beavers have a large, flat tail, covered with leathery scales, although it is hard to spot while swimming as it is submerged. The beaver is also the largest native rodent in Europe, in addition to its tail, the size is also a good criterion to identify a beaver. The head-body length amounts to an average length of 1.2 m, including the tail (Müller-Schwarze 2011, RVO 2014), in beavers, there are no external differences between the sexes.

2.2.5.2 Scent markings

Both sexes possess two anal glands and two castor sacs where retention of urine creates the fluid castoreum (dietary derivatives mixed with urine), which has its own distinctive smell. The components do not differ between sexes (Rosell 1999, Hohwieler et al. 2018), except sometimes an extra sex-specific anal gland secretion on the scent mounds (Schulte 1995). During scent marking in their territory, castoreum is deposited on scent mounds, which can be piles of leaves, aquatic plants, branches, beaver sticks and mud up to 10 centimetres high, or just on the ground (Rosell and Sundsdal 2001). Finding these scented piles is not typical throughout the year, the number of scent marks in proximity of the lodge and at the territorial borders is significantly higher in spring when sub adults disperse (Svendsen 1989, Rosell et al. 1998). Both sexes and all age classes (> 5 months) participate in scent marking (Wilsson 1971) but males scent-mark more frequently than females (Rosell and Thomsen 2006).

2.2.5.3 Sounds

As beavers are crepuscular animals, it is quite difficult to visually confirm the presence of an individual in the dark. Knowing the type of sounds beavers make is crucial. Beavers will be aware of your presence before you are of them because of their excellent hearing and great sense of smell. This will trigger them most of the time to flee or to start to perform territorial protecting behaviour. When a beaver gets startled it will slap its tail against the water, creating a loud splash. If the beaver is really close you could also hear a heavy and loud breathing ("growling") or blowing noise ("hissing"). In the breeding season it is also possible to hear whining noises from the kits in the proximity of the lodge.

2.2.5.4 Beaver droppings

The sighting of beaver faeces on land is quite rare, those that are will generally be found early in the morning at the water's edge. Beaver droppings are predominantly cylindrical with the diameter as an indication of the animal's size. The colour of fresh droppings is dark brown, with lighter-coloured bits of undigested wood, which can be recognized as compressed sawdust. Most of the time they also re-ingest them, this is done to absorb more nutrients out of the food (Müller-Schwarze 2003).

2.2.5.5 Food caches

Beavers, living in cold climates, sometimes create a food stock or also called food caches, which are mainly for the winter months when ice covers the water. They are considered larder-hoarders since usually they store branches in one location (Belova 2012). These are often not seen as they are submerged and shoved in the mud at the bottom of the river/lake or inside the lodge but can occasionally also be seen as piles of wood besides the lodge. The main difference is the species and type of branches, smaller and softer preferred as food source not as building material.

2.3 Timing of fieldwork

Searching for signs of beaver activity in the field is possible throughout the year, although it is important to consider the vegetation height at the moment of field visits. In the report of the RVO the best period starts at the end of the winter and is from March till April (figure 5). Also, according to Dewas, Herr et al. surveys are best carried out during winter, when there is less vegetation. When investigating areas are rich in farmland the report of the RVO also mentions the period of June till October, because the cultivation of crops like maize and sugar beet provide good alternative food sources for beavers. In standard research a location can be confirmed of the presence or absence of beavers by conducting two field visits in one year. The first visit in March – April also called the leafless season and the second in June – October.

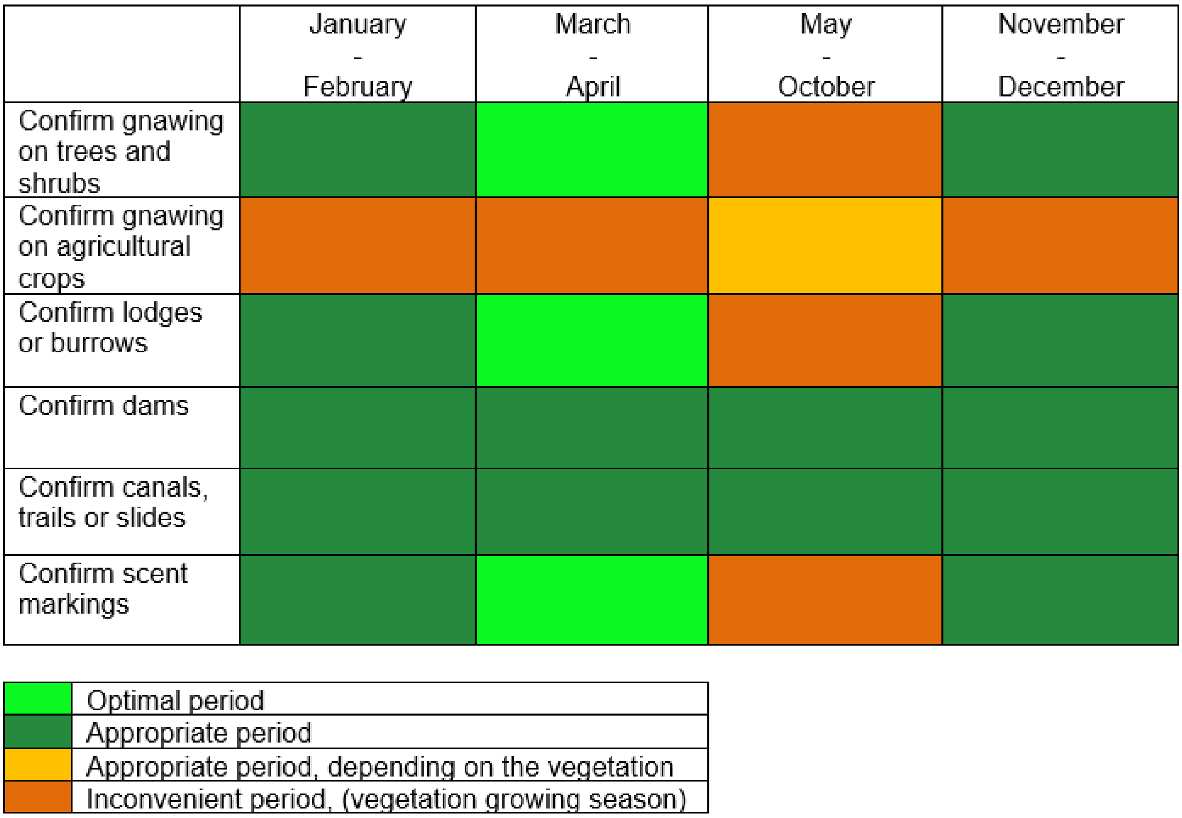


*Figure 5: A visualisation of the recommended field visit periods throughout the year according to the report of the RVO. *These recommendations are based on the ecology of the beaver in the Netherlands and can differ with other countries or regions.**

The period of field observations for this study was timed from August until September and some additional trips in October and November. The choice of this period was because of several rather practical reasons, first that as a student I had no classes during those months and was able to focus entirely on the fieldwork. Second, the period that is advised to go looking for beaver activity was in the middle of the classes in the first year and if the fieldwork was conducted in the second year, it would be too late for processing and writing afterwards. Third and last, all the material and logistics (cars and kayak) where available to use for me at that time, as doctoral researchers and other scientists use less or none of this equipment in that period.

The fieldwork was done when the vegetation was at its highest and densest. This made it more inconvenient to find signs of activity because of less visibility or having inaccessible terrain. Besides having a lush vegetation that hampers the working method, the beavers will also gnaw less on trees and on land vegetation and more on aquatic plants and smaller vegetation on the banks. Except in more urbanised areas with cemented banks where the bank vegetation is less prominent and the beavers gnaw on trees and shrubs throughout the year or when in the proximity of agricultural fields where crops have the preference.

2.4 GIS analysis

The data were processed and analysed with a geographic information system (ArcGIS 10.3.1, Esri, Redlands, California, United States of America, hereafter GIS).

The program was used to combine the two datasets and the HSI model, allowing the production of maps visualising the past and present modelled beaver distribution. Also visualising the present beaver distribution based on the visited locations during the research.

2.4.1 Estimating importance of vegetation type

When combining the data points collected during field visits with the vegetation height map called 'Groenkaart Vlaanderen' (Agentschap voor Natuur en Bos, ANB, 2012), an estimate can be made of the importance of distance to higher vegetation. The classification was based on ortho-photographs dividing the vegetation into three classes; Agricultural land, Low vegetation (< 3 m) and High vegetation (> 3 m) with a resolution if 1 x 1 m.

Beavers require two basic elements in their habitat: fresh water and broadleaved woodland or in general at least woody vegetation. The forage border was set on 100 m, their maximal forage distance from the water and by adding the vegetation heights, it is then possible to determine if there is a significant difference between the vegetation classes.

2.5 Statistical analysis

Statistical analysis has been conducted with the statistical program R (The R Foundation for Statistical Computing, Vienna, Austria) and RStudio (Foundation for Open Access Statistics (FOAs), Boston, United States of America).

Throughout the study, a significance level of 0.05 was used. If results were significant, three different p-values can be assigned; <0.05, <0.01 and <0.001 to demonstrate larger significant differences. When data were not normally distributed, non-parametric tests were used.

HSI model validation tests

Size adjustments to the Habitat Suitability Index (HSI) model have been made to make statistical analysis more plausible for the current spread of the beaver, only including the 5 x 5 km Universal Transverse Mercator (UTM) squares that have observational data of our own fieldwork or in combination with the presence only datasets.

The McNemar's Chi-squared test was performed on the 2 x 2 matrix, showing predicted and observed absence and presence, for symmetry of rows and columns. One drawback to this test is that it may fail if there are 0’s in certain locations in the matrix, therefore lumping the classes might be needed to acquire results.

For restricted area 1 (Flanders without the province of West-Flanders), restricted area 1 with no border squares covering more than 50% of neighbouring countries or Wallonia (Flanders without the province of West-Flanders with no borders) and restricted area 2 (the observation only area including only the UTM squares visited for this study) a Chi-squared test and a Wilcoxon Signed-Rank test were performed.

The Wilcoxon Signed-Rank test was also conducted on the table, with the model differentiated into the individual classes, to decide whether the corresponding data from the predictions and the observations are identical without assuming them to follow the normal distribution.

On site preferences

With the use of the vegetation height/type map called ‘Groenkaart Vlaanderen’ (Agentschap voor Natuur en Bos, ANB, 2012). An accurate determination of importance of vegetation type in the UTM squares could be calculated using a Chi-squared test.

3 Results

An overview of all available data, combining the HSI model and both the presence only datasets, on beaver locations and spread (figure 6) was used to determine the areas that should be visited.

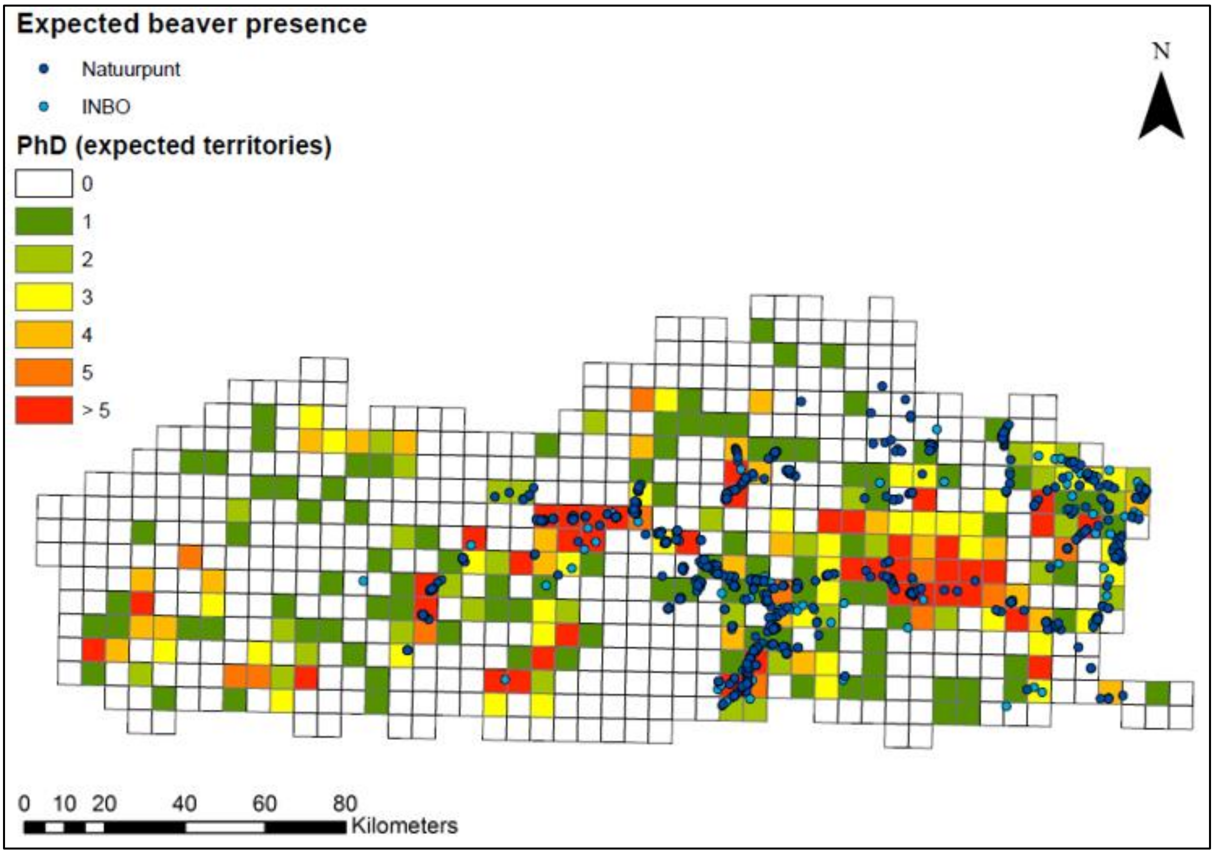


Figure 6: A map visualising the combination of the HSI model and the two presence only datasets, used to determine observation sites, all overlapping on the map of Flanders. Each UTM square is given a colour for the number of expected beaver territories to be present. Furthermore, the presence only datasets are shown, in dark blue the data points from Natuurpunt and in light blue the data points from INBO.

A more detailed visualisation of the colonisation progress during the last 8 years is visualised in figures 7 A & B. The collection of data, including both the presence only datasets from Natuurpunt and INBO, give an estimate of the spread starting from 2010 until 2017 (figure 7 A). After conducting all the field visits a new estimate of the spread could be made with the colonised area observed in this study, so representing the spread from 2017 until 2018 (figure 7 B). Both maps give a view on the restricted colonisation in a certain time period. Some areas for 2018 do not overlap or go beyond the area for 2017, this is due to a lack of observational data within this area (most Northern part of the polygon) and no sightings of beaver signs confirmed by other sources.

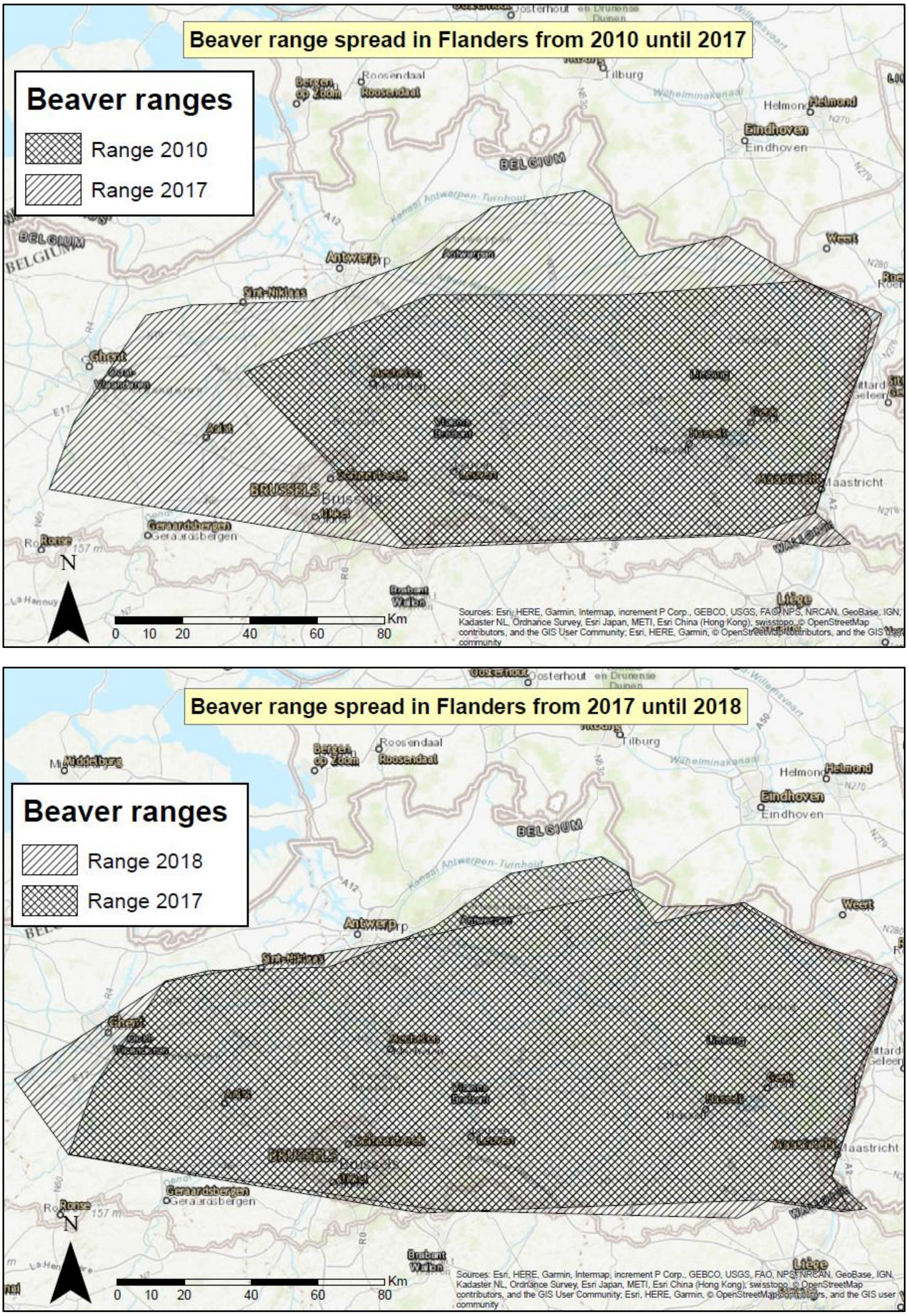


Figure 7: A. The expansion of the area colonised by beavers starting from 2010 till 2017. B. The expansion of the area colonised by beavers starting from 2017 until 2018. These polygons are made based on observed beaver sign data points, thereby the edges give a maximal estimation of the spread. Within the polygon it is important to notice that the area is not entirely colonised or inhabited.

3.1 HSI model for Flanders without the province of West-Flanders

When using a smaller version of the original HSI model of Flanders, restricted area 1, without the province of West-Flanders, including the observations of this study (figure 8), the matrices presented in tables 1 and 2 were drawn up, holding a total of 500, 5 x 5 UTM squares. This reduction takes into account the fact that area and colonisation spread by beavers has had a restriction in time.

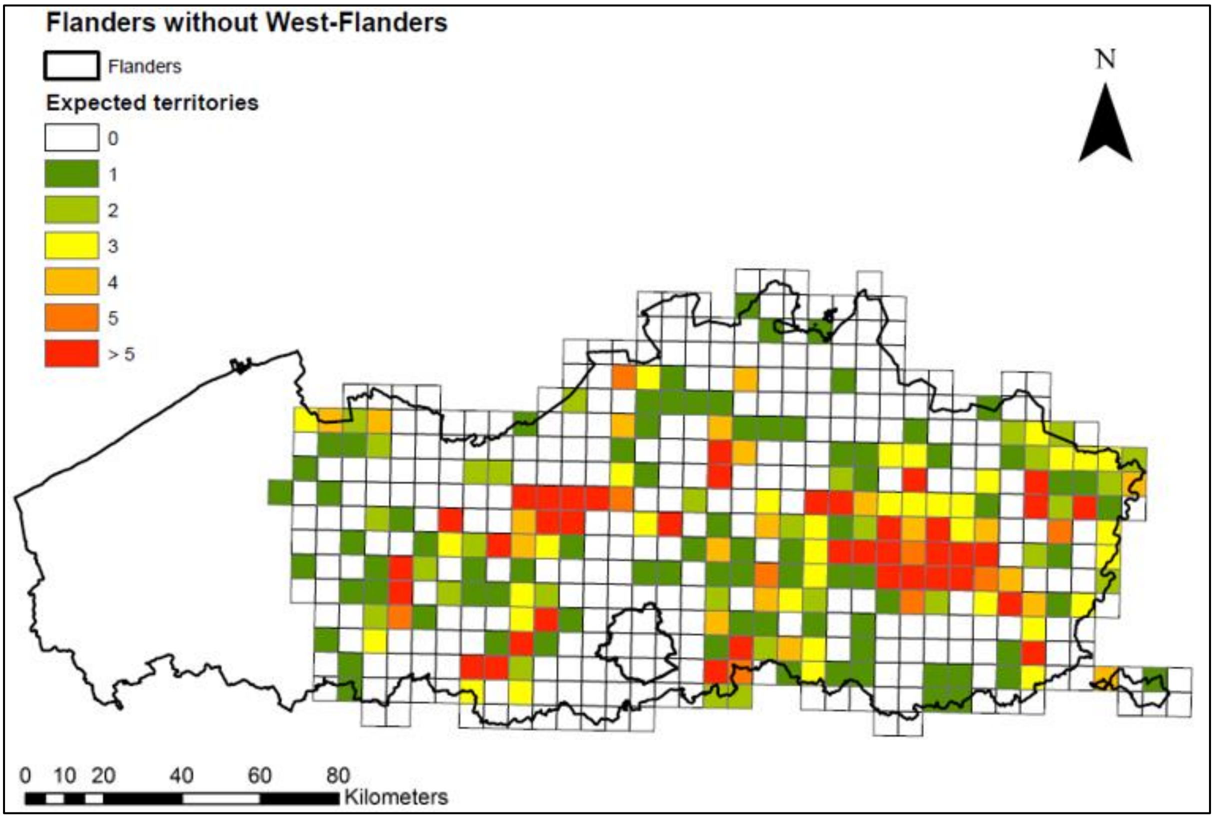


Figure 8: A visualisation of the first reduced version of the original HSI model of Flanders, excluding the province of West-Flanders, with a total of 500, resolution is 5 x 5 km, UTM squares. Each UTM square is given a colour for the number of expected beaver territories to be present.

The HSI model that covered the whole of Flanders also includes border areas, which overlap with neighbouring countries (Germany and the Netherlands) and Wallonia could give a possible bias. Therefore, the restricted area 1 was tested for both with and without border squares. Restricted area 1 without border squares, excluded UTM squares with less than 50% of their surface located in Flanders, lowering their number of 500 to 440 squares compared in table 3.

Table 1: Presence/absence matrix showing the predicted number of territories in the UTM squares (present or absent) versus the observed number of territories (yes or no) for Flanders excluding the province of West Flanders. Tested with the McNemar's Chi-squared test for accuracy, p-value, sensitivity, specificity, positive- and negative prediction value.

		Predicted	
		Present	Absent
Observed	Yes	88	23
	No	130	259

The McNemar's Chi-squared test, that was performed on the 2 x 2 matrix, reveals different point of views on the matrix. Accuracy shows how much of the diagonal were correctly predicted, with a high value of 69 % (347 out of 500 squares). The Mcnemar's Test P-Value is <2e-16, which means there is a significant difference (p-value < 0.05) and that the model made no good predictions. Sensitivity stands for the probability that the positive observation (yes) was the same as the positive prediction (present) and had a high value of 79 % (88 out of 111 squares). Specificity stands for the probability that the negative observation (no) was the same as the negative prediction (absent) and had also a high value of 67 % (259 out of 389 squares). The positive prediction value, 40 % (88 out of 218 squares), shows a lower success of predicting the presence of a beaver, whereas the negative prediction value, 92 % (259 out of 282 squares), shows a high success predicting the absence of a beaver.

Table 2: Presence/absence matrix, with different classes, of the predicted versus the observed number of beaver territories for Flanders without the province of West Flanders divided in UTM squares, tested with a Chi-squared test.

		Predicted						
		0	1	2	3	4	5	>5
Observed	0	259	59	18	24	8	5	18
	1	17	12	5	6	5	2	10
	2	5	5	6	3	3	2	6
	3	1	4	2	3	1	0	3
	4	0	2	0	0	1	1	1
	5	0	0	0	0	0	1	2
	> 5	0	0	0	0	0	0	0

Conducting a Chi-squared test on table 2 shows no results, only when lumping it down to 3 categories (0, 1 and > 1) with a p-value < 0.001 which reveals that the predictions are not following the observations in the field.

Furthermore, a Wilcoxon Signed-Rank test was done on the different classes, the following p-values were calculated and are shown in table 3.

Table 3: Validation of the HSI model by a Wilcoxon Signed-Rank test showing the calculated p-values of predicted-observed for the entire model and for each of the different classes' individual, this for the area of Flanders without the province of West Flanders (With border). This was also tested for the area of Flanders without the province of West Flanders and excluding any UTM square covering less than 50% of Flemish territory (No border).

	With border		No border	
Classes	**N predicted**	**p-value**	**N predicted**	**p-value**
All classes	500	< 0.001	440	< 0.001
0	282	< 0.001	229	< 0.001
1	82	< 0.001	79	< 0.001
2	31	< 0.001	27	< 0.001
3	37	< 0.001	36	< 0.001
4	18	< 0.001	18	< 0.001
5	11	< 0.01	11	< 0.01
>5	40	< 0.001	40	< 0.001

The Wilcoxon Signed-Rank test shows that the complete model is equally bad as each class individually in predicting the number of beaver territories for a certain UTM square. Not including the border squares is only lowering the number of squares in the lower classes, but showing no significant effect compared to when the border squares were included.

3.2 HSI model for the visited UTM squares

When another, even smaller, version of the original HSI model for Flanders was used, restricted area 2, including only those UTM squares with observational data points gathered during this study (figure 9). The matrices presented in tables 4 and 5 were drawn up, with a total of 129, 5 x 5 UTM squares. Combining the accurate data points from this study and takes into account the fact that area and colonisation spread by beavers has had a restriction in time and excludes possible presence only observer mistakes from obtained datasets.

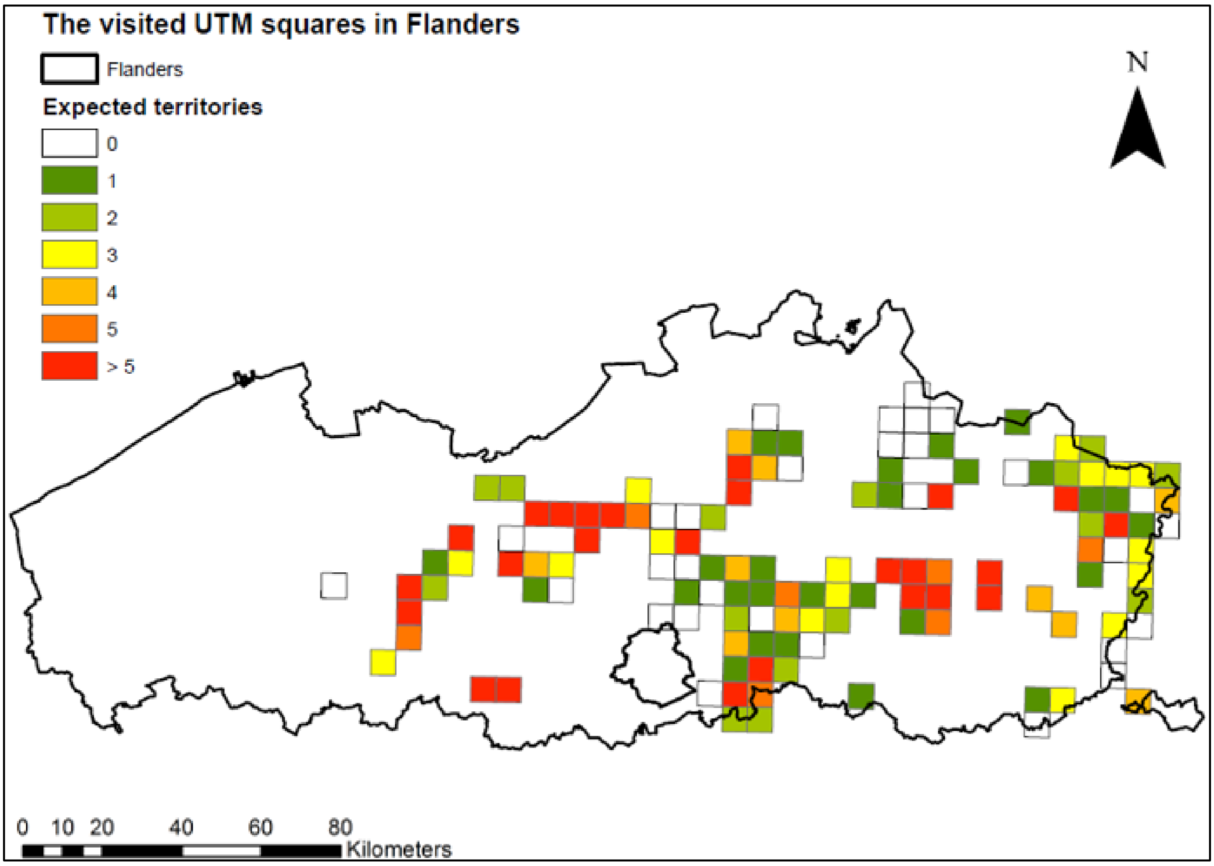


Figure 9: A visualisation of the second reduced version of the original HSI model of Flanders, including only the visited UTM squares, with a total of 129, resolution is 5 x 5 km, UTM squares. Each UTM square is given a colour for the number of expected beaver territories to be present.

The HSI model that covered the whole of Flanders also includes border areas, which overlap with neighbouring countries (Germany and the Netherlands) and Wallonia could give a possible bias. Therefore, the same procedure as in restricted area 1 was followed, namely testing for both with and without border squares. Restricted area 2 without border squares, excluded UTM squares with less than 50% of their surface located in Flanders, lowering their number of 129 to 121 squares compared in table 6.

Table 4: Presence/absence matrix showing the predicted versus the observed number of territories in the UTM squares (present or absent) and observed number of territories (yes or no) for Flanders including only the observed squares. Tested with the McNemar's Chi-squared test for accuracy, p-value, sensitivity, specificity, positive- and negative prediction value.

		Predicted	
		Present	Absent
Observed	Yes	88	23
	No	12	6

The McNemar's Chi-squared test that was performed reveals different point of views on the matrix. Accuracy shows how much of the diagonal were correctly predicted, with a high value of 73 % (94 out of 129 squares). The Mcnemar's Test P-Value is 0.09097, which means there is no significant difference (p-value > 0.05) and that the model made a good prediction. Sensitivity stands for the probability that the positive observation (yes) was the same as the positive prediction (present) and had a high value of 79 % (88 out of 111 squares). Specificity stands for the probability that the negative observation (no) was the same as the negative prediction (absent) and had a low value of 33 % (6 out of 18 squares). The positive prediction value, 88 % (88 out of 100 squares), shows a high success of predicting the presence of a beaver, whereas the negative prediction value, 21 % (6 out of 29), shows a low success predicting the absence of a beaver.

Table 5: Presence/absence matrix, with different classes, of the predicted versus the observed number of beaver territories for Flanders including only the visited UTM squares, tested with a Chi-squared test.

		Predicted						
		0	1	2	3	4	5	>5
Observed	0	6	4	2	3	1	1	3
	1	17	12	5	6	5	2	10
	2	5	5	6	3	3	2	6
	3	1	4	2	3	1	0	3
	4	0	2	0	0	1	1	1
	5	0	0	0	0	0	1	2
	> 5	0	0	0	0	0	0	0

Conducting a Chi-squared test on table 5 shows no results, only when lumping it down to 4 categories (0, 1, 2 and > 3) with a significant p-value of 0.46. Meaning that the model is in line with the observations for the lower classes but not for the higher classes.

Furthermore, a Wilcoxon Signed-Rank test was done on the different classes, the following p-values were calculated and are shown in table 6.

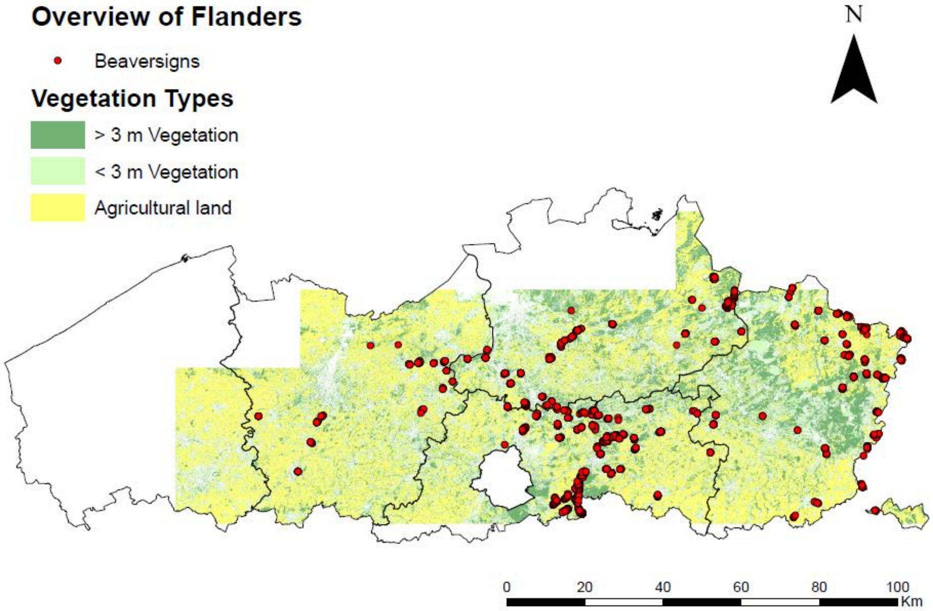
Table 6: Validation of the HSI model by a Wilcoxon Signed-Rank test showing the calculated p-values of predicted-observed for the entire model and for each of the different classes' individual, this for the area of Flanders including only the visited UTM squares (with border). This was also tested for the same area excluding any UTM square covering less than 50% of Flemish territory (No border).

	With border		No border	
Classes	**N predicted**	**p-value**	**N predicted**	**p-value**
All classes	129	< 0.001	121	< 0.001
0	29	< 0.001	26	< 0.001
1	27	0.05	27	0.05
2	15	0.49	12	0.484
3	16	< 0.05	16	< 0.05
4	11	< 0.05	9	< 0.05
5	7	< 0.05	7	< 0.05
>5	24	< 0.001	24	< 0.001

The Wilcoxon Signed-Rank test shows that the complete model and most of the classes individually are equally bad in predicting the number of beaver territories for a certain UTM square, except for the classes 1 and 2. Where one shows a significance of 0.05 and two an even larger significance of 0.49 in estimating the right number of territories. Not including the border squares just leaves out 8 squares and shows no significant effect compared to when the border squares were included.

3.3 Linking presence with vegetation types

To see if there is a certain importance of vegetation type in the territory of a beaver, the vegetation map of Flanders (Groenkaart van Vlaanderen) was used (Agentschap voor Natuur en Bos, ANB, 2012). This map divides the vegetation in three types; Agricultural land, Low vegetation (< 3 m) and High vegetation (> 3 m) with a resolution of 1 x 1 m (figures 10 A&B). By combining only the gnawing activity data points and the vegetation map, an accurate estimate can be made on what type of vegetation is most seen in areas occupied by beavers.



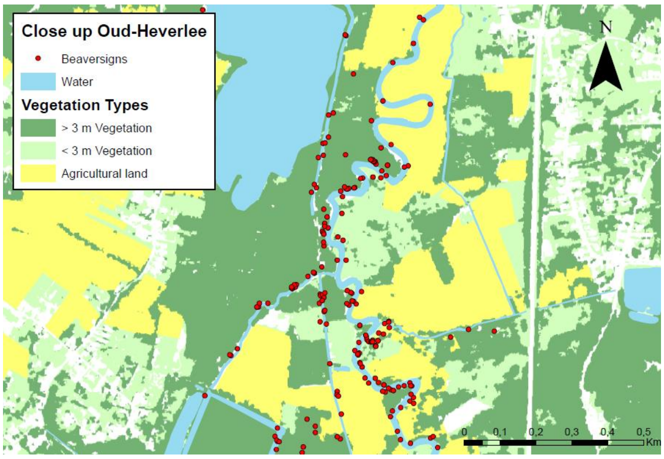


Figure 10: A. An overview of the vegetation map of Flanders (Groenkaart van Vlaanderen), that divides vegetation in three types; Agricultural land (yellow), Low vegetation (< 3 m) (light green) and High vegetation (> 3 m) (dark green) with a resolution of 1 x 1 m (Agentschap voor Natuur en Bos, ANB, 2012). With the red dots showing observed beaver signs throughout the landscape. B. A close up of the vegetation in Oud-Heverlee (Groenkaart van Vlaanderen), which is a more densely colonised area in Flanders. With the red dots showing observed beaver signs throughout the landscape.

The gnawing activity points are clearly not distributed evenly over all vegetation types (Chi-square test, p-value <0.001). They are clearly concentrated in the High vegetation type (Fig 10 B).

4 Discussion

4.1 Model validation

HSI models are frequently used and have been developed throughout North America to map suitable beaver habitat characteristics. These models predict current suitable beaver habitat but are less suited for predicting where beavers could be if they modify the landscape, or where appropriate restoration actions or land-use management actions were taken (Dittbrenner et al. 2018). The use of this HSI model in Flanders aimed to predict where and how many beavers could inhabit the area. After four years the main expected difference was that of a population growth combined with a larger spread of beavers throughout Flanders. As predicted beavers have been found at many new locations, where they were absent at the time of the study by Swinnen (2015). The focus in this study was the validation of the HSI model's predictive power, which is normally used to determine habitat suitability, in relation to the further colonisation of Flanders. Starting with an estimation of the current spread based on the HSI model for Flanders and adjusting the assumptions of the HSI model based on the additional presence only datasets obtained from Natuurpunt and INBO, a list was made with areas for validation of presence or absence of beavers. Here the public presence only datasets demonstrated their additional value in the selection of areas, because Flanders is such a densely populated area with a lot of urbanisation and few places where nobody lives. For this reason and because beavers leave distinctive structures and signs in their environment, the presence of beavers is hard to miss. In a recent study by Rutten et al. the wildlife observation chance was linked to the importance of the search effort from wildlife observations. The analysis of observers' characteristics based on their past observational records has been found useful to correct for population trends (Rutten Submitted). The reasoning behind this is that an active observer, someone who often reports wildlife observations, would report sightings of beavers if they would be present in the area. This means that if there are observations of other mammals reported by active observers for a certain area, but no beaver observations, it is quite safe to say that these effectively are areas where there are no beavers present at that time.

The HSI model output shows that the colonisation is still far from its maximum capacity as many suitable habitats are not yet occupied and population densities are in general still reasonably low. For this reason, it is important to separate some of the components and inspect them separately. The complete area of Flanders was reduced to two restricted areas: one where the province of West-Flanders was excluded out of the model and an even smaller one that only included the visited UTM squares. Both reduced areas were determined based on the amount of time needed for the colonisation of such a large area and the growth in density at a colonised site.

The model's predictions for the area of Flanders without the province of West-Flanders show a lot of incorrect estimations. Splitting up the model in its two components of presence or absence and the number of territories reveals two parts of the model's predictions. On the one hand, the predictions for a beaver to be present or not and on the other hand, the number of territories or the density in that UTM square. The presence or absence of beavers is well predicted in the model for the area of Flanders without the province of West-Flanders, except for the fact that there are lots of empty squares that have never been visited by beavers. This indicates that the number of absences is not solely due to the selectivity of the beaver, but also other factors like earlier mentioned such as time needed and distance to cover. Therefore, the results showing that the chance of a good prediction for the absence of a beaver is more likely to be correct than incorrect, should be interpreted with certain caution. In contrary the chance of a good prediction for the presence of a beaver is more likely to be incorrect than correct. This can be due to the large area that remains in the model but will mostly also be because of the lack of time for a complete colonisation of the area. Regarding the number of territories predicted in the UTM squares, the entire model performed equally well as for the separated classes. Once more the large area that remains in the model is something to take into account, but for the number of territories the local density is the most important factor and this also takes time to grow. Compared to the full model with 645 UTM squares only 500 squares with a resolution of 5 x 5 km remained. However, the UTM squares at the edge of the map sometimes included area of neighbouring countries (Germany and the Netherlands) or, parts of Wallonia. When calculating the expected number of territories for a certain UTM square only data from the part in Flanders was used. The neighbouring UTM parts outside Flanders also formed part of the model but lacked map data and did thus not contribute to the HSI model output. This resulted in inaccurate estimations because of possible suitable habitat in the UTM square that is not used for the estimation.

When the area of Flanders without the province of West-Flanders is narrowed down to only the UTM squares visited during this study, then the predictions are slightly better. Looking at the two parts of the model's predictions for this even smaller area, there are some contesting findings compared to the area of Flanders without the province of West-Flanders. Here the presence or absence of beavers is well predicted in the model for the only visited UTM squares, where every square that was visited could also have been visited by beavers. In this case the results show that the chance of a good prediction for the presence of a beaver are more likely to be correct than incorrect, contesting the predictions for absence in the model for the area of Flanders without the province of West-Flanders. Also visible in the results for this smaller area is that the squares where absence was predicted, more presence than absence was observed. This indicates that the areas where the colonisation process is active, beavers might tend to be picking suboptimal habitat and are less selective. Important to keep in mind, the only visited UTM squares count just 129 squares compared to 500 squares in the area of Flanders without the province of West-Flanders. The predictions made for the number of territories in the model covering only the UTM squares that were visited, have a noticeable difference between the complete model and its different classes. The complete model is still not able to make the correct predictions for only the visited area. When dividing the predictions for each number of expected territories in the UTM squares, a trend of correct predictions was found. The predictions were good for one territory and even better for squares where two territories were expected. These results are plausible, considering the time needed for colonisation of such a large area and if a distant UTM square is reached one or two can settle reasonably quick. At the moment, the prediction of more than two territories in the same UTM square have a low chance of being correctly estimated. Nonetheless, beavers are present in areas where they were expected, but population density gradually increases over time. This all could imply that the prediction for most of the UTM squares is correct, but just require more time.

In addition to the underestimation in predicted occupied territories, the model potentially also overestimates unoccupied territories. This refers to territories where the predicted absence of beavers is contested by an observed presence. These presences could reveal certain flaws in the HSI prediction model, either by necessary parameters not incorporated in the model or by non-predictive parameters that were used. For the area of Flanders, a set of eight habitat and land-use variables was selected based on general ecological knowledge about beaver habitat requirements (Swinnen 2015). Including three forested habitat types [Willow (*Salix sp*.), Poplar (*Populus sp*.), other deciduous forest]; one shrub-like category: [mainly Hawthorn (*Crataegus sp*.) and Common broom (*Cytisus scoparius*)], two non-woody vegetation types [grassland and wetland vegetation (mainly *Phragmites australis* and *Filipendula ulmaria*)] and semi-natural environments (parks, cemeteries, …). Finally, distance from the nearest water was included as an eighth variable. Agricultural crops were not considered since they are frequently rotated over the years (Swinnen 2015). Vegetation often does not meet criteria that a traditional HSI model would identify as suitable, many potentially suitable areas are often not considered for restoration planning or relocation actions. Additionally, and perhaps more importantly, in most regions, vegetation data is not mapped on a sufficient spatial resolution to allow for landscape-scale HSI models to be applied over larger spatial extents (Dittbrenner et al. 2018). The study of Swinnen (2015) had the availability of detailed, fine-scale area-wide vegetation and land-use maps, which allowed them to assess beaver habitat selection in more detail and to formulate detailed predictions of areas at risk of colonization by re-introduced beavers. Environmental predictors were prepared at a cell size of 10m (a smaller resolution was not realistic given the spatial accuracy of the BVM land-use database) (Swinnen 2015). Flanders, as a relatively small area, has now even more detailed data, 1 x 1 m resolution, called the 'Biologische Waarderingskaart' (BWK), which is based on the vegetation, land use, … and the 'Groenkaart Vlaanderen' dividing the vegetation according to its height (Agentschap voor Natuur en Bos, 2012). Potentially contributing to better estimates based on these more accurate data. Still the variables which are used in previous HSI models are often good predictors of current or historical beaver presence. However, they fail to identify areas that may become suitable if transformed by beavers into high quality habitat. Demonstrated by vacant areas meeting minimal habitat requirements that experience a very gradual expansion as beavers transform each site's morphology and vegetation composition. Thereby areas denoted as unsuitable surrounding currently occupied sites have the potential to become suitable in the future. HSI models are therefore less useful in areas reaching carrying capacity or areas altered by anthropogenic impacts (Dittbrenner et al. 2018).

A possible logic reason for these false absences or false presences might be explained by an edge effect of the UTM squares. All UTM squares are adjacent to each other and can sometimes share the same territory of a certain beaver or a family home range living on the edge of two UTM squares. For example, one UTM square predicted to have zero territories was neighbouring a UTM square predicted having one, but on-site visits revealed that both UTM squares show beaver activity. Therefore, data analysis will assign both UTM squares with having one territory present, when in fact there is just one that overlaps both UTM squares. As previously mentioned, beavers can occupy foraging ranges from 500 m going up to 12 km (bank length) and on average territories are 3 km in length. When considering that a UTM square is just 5 x 5 km, this can cause for some bias in both the analysis as in the model. Which can lead to a misinterpretation of the data and can help to explain a possible overestimation of the presences in UTM squares where absence was expected and also the number of territories present.

Intrinsic potential models could provide an alternative to HSI models (which generally use both intrinsic and extrinsic predictors) by using geomorphic variables that are less prone to change through time (Dittbrenner et al. 2018). Beaver Intrinsic Potential (BIP) models identify sites where the hydro-geomorphic, or underlying intrinsic physical conditions, are suitable for beavers. Making it able to identify sites as suitable or unsuitable based on the potential situation of the inspected area and not only on the present situation. This in contrast with the HSI model that only considers the actual situation. BIP models will additionally mark sites as suitable when habitat restoration, management changes, or beaver modifications could allow the beaver to thrive in those locations. Intrinsic potential models have been previously used to inform fish habitat restoration work, and some have proposed using intrinsic potential for non-fish species, including the beaver (Benda et al. 2007). BIP models may be more appropriate than HSI models for predicting where beavers are likely to occur within a watershed given the ability of beavers, being ecosystem engineers, to modify variable habitat characteristics such as vegetation density and type. Intrinsic variables appropriate for use in BIP models are those that cannot be readily altered by beaver colonization. These include site features such as regional climate, precipitation regime, stream gradient, stream width, and valley width. In the study of Dittbrenner (2018) they developed and applied a BIP model that can predict where high quality beaver habitat currently exists and where colonization will occur as population levels increase or if management changes are made (e.g., expansion of a riparian buffer or greater implementation of non-lethal beaver management options). This approach offers a straightforward method for developing accurate estimates of potential beaver habitat using readily available data. The accuracy of this model makes it particularly useful for identifying sites that are suitable for beaver relocation and beaver-assisted restoration (Volk et al. 2014). The effects of beaver colonization (e.g., dam building, pond formation, and subsequent aggradation of stream channels) have the potential to increase the suitability of surrounding habitat. The use of BIP models has the advantage over traditional HSI models for detecting potential habitat, regardless of the current vegetative cover or land use and without extensive field surveys or complex modelling (Dittbrenner et al. 2018).

It is most likely that the further development of models for the prediction of beaver populations will have to take into account many variables that contribute to the change in the beaver’s regulating factors. Including for example geomorphologic characteristics of the terrain, recovery rate of feed resources and the extent and rate of development of beaver settlements.

4.2 Spatial distribution and population size

During the initial phases of recolonization, beaver populations are relatively sparse and optimal habitats are the first ones to be selected. As population density gradually increases, preferred habitats are occupied, forcing beavers to occupy less-attractive territories (Zwolicki et al. 2019). A broad range colonisation was seen in a study in the Czech Republic, where beavers appeared to be following a dispersal pattern in which distant sites were often colonized before sites closer to the introduction site (John et al. 2010). A same trend was seen in the Netherlands, as a sequential release of beavers into a previously unoccupied area, showed that they successively settled in good habitat, before inhabiting poor habitat. In a final stage, so called floaters were observed, the term used to describe a beaver that doesn't settle in a strict territory and roams in between different occupied territories, ready to adopt one when it comes available (Nolet and Rosell 1994). This being consistent with the idea of a preference for more qualitative habitat further away over nearby sites with suboptimal habitat characteristics. Hartman documented in 1994 how the increasing number of occupied areas developed during the colonisation by beavers of the Swedish province of Värmland; he reported a gradual increase during the first decades, speeding up after about 30 years and then approaching its maximum. We investigated the potential growth rate of the beaver population in different ways.

- Survey data from Flanders

With the available data on the number of territories over the past years in Flanders an estimation could be made of the growth rate (R) (table 7), calculated by dividing the number of territories of the current year with the number of territories of the previous year. The growth rate seems to be fairly high but stable over the past years, suggesting that the population is not yet nearing the carrying capacity.

Table 7: The estimated number of colonies during the past five years with the growth rate (R) for that year. Data was obtained from Swinnen (2015) and given to us by the Agency for Nature and Forest (ANB).

Year	Estimated number of colonies	Reference	Calculated R
2014	71	Swinnen (2015)	1.13
2015	80	Swinnen (2015)	1.20
2016	96	ANB estimate	1.35
2017	130	ANB estimate	1.15
2018	150	ANB estimate	1.25
2019	187	ANB estimate	

- Demographic model

Solid demographic data for *Castor fiber* are not easily available. However, McTaggart & Nelson (2003), published survival and reproductive rates for a population of *Castor canadensis* in Illinois. We used the data from his study to parameterise a population growth matrix, using 15 age classes of one year. There is a considerable variation in survival rates over different age classes. The studied population was near carrying capacity and commercial beaver hunting was happening. The calculated growth rate from the matrix is R=1.07 (table 8).

Table 8: Population growth matrix based on demographic data for *Castor canadensis* (McTaggart & Nelson 2003). The top row of the matrix (green) represents average production of young by each age class, the values below the diagonal (blue) represent survival of an age class to the next year, the diagonal cell at the bottom (orange) represents survival for animals in age class 15 or older.

0	0,11	0,9	1,62	1,62	1,62	1,62	1,62	1,62	1,62	1,62	1,62	1,62	1,62	1,62
0,43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0,6	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0,66	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0,75	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0,88	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0,76	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0,82	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0,8	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0,75	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0,67	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0,5	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0,5	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0,5	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0,5	0,01

To what extent the data from McTaggart & Nelson (2003) can be informative for our study remains of course a question. The data originate from North American beavers and it has been reported before that they have on average a somewhat larger litter size than *Castor fiber* (Rosell and Parker 1995, Pollock et al. 2003). Moreover, demographic values can differ between populations, for example beavers living in a more urbanised area versus those in a more natural environment. Moreover, as mentioned before, growth rates decrease as populations reach the carrying capacity.

- Future development

When projecting the growth of the beaver population in Flanders, logistic growth is expected. We used both values above, i.e. the rather high R = 1.20, assumed to be representative of the rapid increase phase of the population, and the lower R = 1.07, when the growth is levelling off towards carrying capacity. Swinnen (2015) predicted that there was suitable habitat available in Flanders for 924 territories. Starting from the current (2019) estimated number of beaver territories in Flanders, and with a growth rate of R=1.20, all territories will be occupied in less than 9 years (187*(1.2)^9 = 965). Using the more conservative growth rate of 1.07 it would take around 24 years (187*(1.07)^24 = 948) to reach this maximum occupancy.

Counting back in time from 71 territories in Flanders in 2014, with a fixed growth rate of 1.20, it can be calculated that there would have been 9 or 10 territories in 2003 ($71/(1.2)^{11} = 9.6$). In reality, 41 beavers were re-introduced in 2003 but under the assumption that not all released individuals managed to settle and an average number of 4 individuals per territory (Zahner 2005), this calculated number of starting territories seems realistic. The risk of under crowding effects, also referred to as Allee effects, has sometimes been mentioned in connection with introductions and has been suggested as the reason why many re-introduction attempts have failed (Hartman 1995). High dispersal rates from the reintroduction site were considered to be a major cause behind the problems with reintroducing beavers but this problem did not occur in the case of the population in Flanders.

The different scenarios regarding the period of colonisation until reaching carrying capacity reveal a similar trend as in the study of Hartman (1994), with a population that is still increasing and plenty of vacant habitat still available. However, depending on the phase of colonisation we are currently expected to be in, this maximum number of territories predicted by the model of Swinnen (2015) could be reached within 9 or 24 years. Important to keep in mind, the HSI model was based on the environmental parameters of territories that were inhabited by beavers during the study of Swinnen (2015). Two caveats are justified here. On the one hand, ongoing urbanisation in Flanders (at rates of 6.4 to 7.33 hectares a day, Pisman 2018, Statistiekvlaanderen 2019), suitable beaver habitat may have disappeared since Swinnen (2015) made his predictions. On the other hand, beavers may also start settling in less optimal sites that were still unoccupied when Swinnen (2015) collected his data, and that therefore have been classified as unsuitable.

The current status of the beaver in the rivers of Flanders can be compared to the results of a study by Dewas in 2012 in France. There the number of beavers varied depending on the river system. Four different types of population were identified: (i) saturated, with all available habitat, from optimal to marginal, occupied; (ii) optimal, with the populations expanding and colonizing new habitats; (iii) unstable, with expansion very slow and/or available habitats fragmented; and (iv) precarious, with populations declining and previously occupied habitat becoming vacant. The same overall trends are generally observed for beavers in neighbouring countries (Dewas et al. 2012). Beavers have never been completely extinct in France unlike in Belgium and already started recolonising France in the beginning of the 20th century much earlier than the 21st century as is the case for Flanders. This may explain why in Flanders categories (ii) and (iii) are more dominant.

According to the predictions of the HSI model, Flanders has a high level of suboptimal habitat for beavers that are now still empty but which, with the expected strong population growth, will probably become inhabited in the near future. This being in line with the colonisation progress, the other catagories (i) and (iv) require some more time to emerge. Representing areas where suboptimal sites incapable of permanently sustaining beaver occupation are depleted of their food resources. Because of that, beaver numbers can decrease and more or less stabilize at lower levels (Halley and Rosell 2002). This pattern suggests that territorial behavior can limit beaver density, something that is also mentioned in other studies, where changes in population density are reported to affect social structure (increase in the mortality of juveniles, changes in family composition and inter-family relations) (Belova 2012). Besides population growth and rate of expansion also these intraspecefic interactions are important to consider when estimating the colonisation.

4.3 Importance of higher vegetation

Flanders contains a vast network of waterways providing lots of suitable beaver habitat. Only the fact that Flanders is one of the most densely inhabited regions with quite a lot of urbanized area which diminishes the total semi-natural area. All this makes the complex waterway network of Flanders less attractive than expected. Colony density on a large scale is often influenced by habitat quality, newly established populations and harvesting in populations (Wilsson 1971). However, when looking at a smaller scale, the local density of a beaver population is influenced largely by habitat quality. Even though, beavers being able to alter many habitat factors, which may affect habitat suitability (Jones et al. 1994), still need some parameters which are crucial for first settlement. One crucial factor of a suitable beaver habitat is the vegetation, impacting family home ranges. This implies that an extensive amount of preferred plant growth on riverbanks is needed to maintain a beaver population (Fustec et al. 2003). Habitat selection is the result of the preference for particular food sources, which for beavers, comprises of deciduous woody plants, and in European riparian habitats, this is mostly represented by willow-scrub communities (Zwolicki et al. 2019). In the present study a classification of the vegetation was used that separated the following classes; agricultural land, low vegetation and high vegetation. The results show that there is one type of vegetation, high vegetation, that has a significant preference to beavers in comparison to both other types.

Considering the way of collecting data in the field and the analysis of the data points, there could be some incorrect assigned data points. This because gnawing activity on aquatic or herbaceous vegetation compared to the characteristic notches and cuttings in woody vegetation are more difficult to spot and can be missed when collecting data in the field. Having in mind a possible bias in the data points, the results still show a significant difference with the higher vegetation clearly having the most gnawing activity. This indicates that higher vegetation and presumably woody vegetation is of major importance for habitat preference in beavers. Since the high vegetation type contains mostly woody vegetation, it is a food source that is available throughout the year, whereas the low vegetation type or agricultural land offer more seasonal availability. The availability of woody plants is therefore one of the most important factors in determining beaver range and distribution (Wilsson 1971, Rosell and Parker 1995).

With increasing foraging resources, territory size may decrease, because an animal is expected to defend the smallest area that can provide sufficient resources for maximization of reproduction. Although benefits from foraging resources increase with territory size, costs, such as patrolling effort and border conflicts, increase as well, reducing the net benefit of increased territory size (Brown 1964). Perhaps, given the possible underestimation of the population size, carrying capacity in Flanders has not been reached yet. There is still ample possibility to roam freely and find vacant territories, so larger territories may still be economically defendable because competition is low. Depending on the degree of colonisation or population size, in a certain area, this can affect the preference in type of food source.

In an earlier study Campbell et al. (2005) it was shown that larger beaver territories were proportionately richer in terms of food abundance and had been colonized for a longer period than smaller ones. This can be explained by settlement patterns: since beavers appear to select the best available site, beavers introduced early occupied territories which offered food in greater abundance and which were bigger in size than those occupied by beavers that were introduced later or arrive later during colonisation (Pulliam and Danielson 1991, Campbell et al. 2005). Considering the same hypothesis, but applied to this study, with an area at the start of the colonisation and at its present situation. Less dense colonised areas would show larger territories, where the chance of depleting food sources is lower. When population growth stimulates colonisation and density increases, colonised areas would show smaller territories, where the chance of depleting the food source is higher. The occupation of large territories reduces the rate of foraging resource depletion, and hence elongates the time until a new territory must be found. As a result, costs of increased predation risks and intraspecific competition which may arise while searching for a new territory, are reduced (Stamps and Tollestrup 1984, Campbell et al. 2005). Sometimes the species can play a role in the depletion, feeding on willow species provides potential to re-sprout when beavers cut them, and therefore, depletion of their foraging resources is slowed down (Fustec et al. 2001). These results and findings combined indicate that sufficient amounts of higher vegetation type do not only play a role in the early stages of colonisation but also determines the timeframe a territory can be used over the longer term.

5 Conclusion

The starting point of whether an HSI model is appropriate to estimate the colonisation of an area is not confirmed, nor disproved. Most of the predictions made by the HSI model did not correspond to the observed values in the field. Nevertheless, results are promising for the future use of the HSI model, as the areas with low predicted number of beaver territories are approximately in line with the observations. The HSI model output shows that the colonisation is still far from its maximum capacity as many suitable habitats are not yet occupied and population densities are in general still reasonably low. These findings can be assigned to two important factors in the progress of colonisation; time and area. The recent re-introduction of the beaver and slow growth rate at the start of colonisation, indicate that beavers did not have enough time to cover large distances and reproduce at the same time. For these reasons more time is needed to properly validate if the current HSI model is correct.

Furthermore, the model shows an overestimation in areas that were predicted to be unsuitable for supporting beaver territories. As contesting presences of beavers were found in multiple areas where the absence was expected by the model. These unexpected presences could reveal certain flaws in the predictions by the model, identifying factors that are missing or that are not necessary for determining if an area is suitable habitat for beavers. Taking into account that beavers may also have start settling in less optimal sites that were still unoccupied when Swinnen (2015) collected his data and therefore have been classified as unsuitable. Maybe even that beavers show new ecological features in more urbanised areas, which we were unaware of. Still vegetation, and more specific higher vegetation, has proven it is an important parameter in where beavers will settle. Beaver Intrinsic Potential (BIP) models could possibly offer a solution for the flaws found in the HSI model. BIP models offer additional assessment factors, identifying sites based on the potential situation of the inspected area and not only on the present situation. Therefore, BIP models will also mark a site as suitable when habitat restorations or modifications by man or beaver could allow the beaver to thrive here.

More accurate data is needed to fully understand and follow up on the colonisation of the beaver through Flanders. A possible example of a similar approach was developed in 1989, when the French government’s National Agency of Hunting and Wildlife started a large-scale beaver monitoring programme. This included systematic surveys of beaver distribution and expansion in which all water courses belonging to river systems potentially occupied by beavers were inspected each year (Dewas et al. 2012).

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The reason I have chosen this subject is out of a combination of various interests in different study fields; the behavioural aspect, the conservation/restoration aspect and of course the environmental impact which is my main master. As everything is divided in different classes and disciplines in the theory, a thesis can show you that in practice it can all fall together and become a mix of everything. This became clear to me because I worked with different organisations along the way. For this cooperation I thank Natuurpunt and INBO.

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8 Appendix

8.1 Present/Absent location table

Table 9: The 131 in total different locations visited during the fieldtrips with confirmation of presence or absence of beavers. With a confirmed total of 103 presences and 28 absences of the visited locations.

	Location	Present	Absent
1	Arendonk		X
2	As		X
3	Baasrode	X	
4	Babbelaar		X
5	Balen		X
6	Bazel	X	
7	Bel	X	
8	Bilzen	X	
9	Blaasveld	X	
10	Boeretang		X
11	Bokrijk	X	
12	Bonheiden	X	
13	Boom	X	
14	Boortmeerbeek	X	
15	Bornem	X	
16	Brasel	X	
17	Bree	X	
18	Broechem	X	
19	Dessel	X	
20	Destelbergen		X
21	Diest	X	
22	Dilsen-Stokkem	X	
23	Donk		X
24	Duffel	X	
25	Dunberg	X	
26	Eizer	X	
27	Eksaarde		X
28	Emblem	X	
29	Gavere	X	
30	Geel		X
31	Geetsbets	X	
32	Gelrode	X	
33	Gijzegem		X
34	Grammene	X	

35	Grobbendonk		X
36	Grote Heide	X	
37	Hamme	X	
38	Heikant	X	
39	Herk De Stad		X
40	Herstappe	X	
41	Heusden		X
42	Hever	X	
43	Hodonk	X	
44	Hofstade	X	
45	Holsbeek	X	
46	Hombeek	X	
47	Houwaart	X	
48	Idegem		X
49	Kampenhout	X	
50	Kanne	X	
51	Kerkhoven	X	
52	Kinrooi	X	
53	Klein Willebroek	X	
54	Kleine-Brogel	X	
55	Korbeel-Lo	X	
56	Kortrijk-Dutsel	X	
57	Krijkelberg	X	
58	Kruibeke	X	
59	Kruishoeve	X	
60	Lammersberg		X
61	Langdorp	X	
62	Lauw	X	
63	Lebbeke		X
64	Leuven	X	
65	Lier	X	
66	Linkhout	X	
67	Lokeren	X	
68	Lovenjoel	X	
69	Lozen	X	

70	Lummen		X
71	Mal	X	
72	Mechelen	X	
73	Meerhout		X
74	Meldert	X	
75	Melle		X
76	Melsen	X	
77	Mespelare	X	
78	Moelingen	X	
79	Moerzeke	X	
80	Mol	X	
81	Molen	X	
82	Molenbeersel	X	
83	Muizen	X	
84	Munsterbilzen	X	
85	Neerhoven	X	
86	Neeroeteren	X	
87	Niel	X	
88	Oelegem		X
89	Oksdonk	X	
90	Olmen	X	
91	Opglabbeek	X	
92	Opoeteren	X	
93	Oppitter	X	
94	Oudenaarde	X	
95	Overijse	X	
96	Peltheide	X	
97	Postel	X	
98	Pulderbos		X
99	Putkapel	X	
100	Puyenbroeck	X	

101	Reppel	X	
102	Rotem	X	
103	Rumst	X	
104	Schilde		X
105	Sint-Joris-Weert	X	
106	Sint-Joris-Winge	X	
107	Sint-Huibrechts-Lille	X	
108	Sint-Pieters-Rode	X	
109	Terlo		X
110	Tielt-Winge	X	
111	Tienen	X	
112	Tongeren	X	
113	Tremelo	X	
114	Veldhoven	X	
115	Veltem-Beisem		X
116	Viersel	X	
117	Vlasselaar	X	
118	Vogelhoek		X
119	Vorselaar	X	
120	Waasmunster	X	
121	Webbekom	X	
122	Werchter	X	
123	Wespelaar	X	
124	Willebroek	X	
125	Winkelomheide		X
126	Wintam	X	
127	Zaffelare	X	
128	Zandhoven		X
129	Zevergem	X	
130	Zingem	X	
131	Zoersel		X