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ORIGINAL PAPER

Reconstruction of Eurasian beaver (*castor fiber*) recolonization in moor habitats using digital orthophotos

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Abstract

Moors remaining in western European landscapes are habitats of high nature conservation value. Moors are abundant in the alpine foothills of southern Germany. However, most of the moor habitats have been degraded through drainage in the course of former peat exploitation and human land use activities. Since moor restoration programs have been proven to be expensive and complex, conservationists have considerable expectations regarding the potential rewetting effects of beavers on these habitats. Supported by conservation legislation and reintroductions, the formerly eradicated species has since returned to many waterways in Germany. This provides the opportunity to explore the potential of this so-called 'eco-engineer' in relation to moor restoration. However, data on the recolonization process – which are necessary in order to analyze the impact exerted by the species on moor habitats – are very limited. We investigated whether the colonization of a peatland by beavers can be sufficiently reconstructed through analyses of digital orthographical aerial photographs (DOPs). We found that beaver canals, on the basis of their characteristic shape, are reliably identifiable on aerial photographs. Therefore, the canals are characteristic indicators of actual beaver presence. Further, our results suggest that the development of beaver populations in moor habitats can be tracked closely by assessing the abundance of beaver canals identified on DOP time series.

Keywords Beaver · Population development · Remote sensing · Moor

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Introduction

Beavers are renowned for their potential to modify water systems and riparian habitats. Prior to being virtually eradicated across Europe in the latter half of the nineteenth century, the Eurasian beaver influenced the development of waters and riparian zones in many parts of Eurasia. Since the middle of the twentieth century, reintroductions and improved conservation legislation have led to the restoration of the species (Halley et al. 2012, 2020). In the meantime, the beaver has successfully recolonized large parts of its former range (Nolet and Rosell 1998; Pillai and Heptinstall 2013; Swinnen et al. 2017). In this process, the species has resettled into heavily degraded water systems within landscapes that are under intensive anthropogenic land use. Particularly in areas intensively used by humans, the return of the beaver is accompanied by human-wildlife conflicts (Nolet and Rosell 1998). Yet, conservationists hold great expectations about the restoration effects of the species on degraded riparian habitats. In fact, in addition to the impacts on plants, invertebrates, and vertebrates on population and community, the beaver can affect hydrological processes and support carbon storage (Rosell et al. 2005; Wohl 2013; Johnston 2014; Nummi et al. 2018). Overall, the recovery of the so-called 'eco-engineer' species is linked to a range of restoration effects and ecosystem services (Jones et al. 1994, 1997; Anderson et al. 2014; Hood and Larson 2015; Karran et al. 2018; Smith et al. 2020; Larsen et al. 2021; Thompson et al. 2021). While these effects have been well documented for many riparian habitats, information about the potential influence of beavers particularly on moor habitats is less comprehensive. The role of the beaver for peatland formation after the last glaciation and thus for enhancing carbon storage is demonstrated (Gorham et al. 2007) as well as various research show the potential of the beaver to support paludification under certain environmental conditions (Johnston 2001; Charman 2002). Moors are essential for providing habitat for many highly specialized organisms, and they have a key function in global carbon storage. However, a huge number of moors have been degraded by drainage to allow for peat exploitation, agricultural land use and forestry. This is also the case for many moors in the Alpine foothills at the northern side of the European Alps. In recognition of the outstanding ecological importance of the moors, considerable restoration efforts have been conducted since the mid-1980s with rewetting as the central measure. These measures can be extremely expensive and complex. Against this background, it is increasingly discussed to what extent the eco-engineering potential of the beaver can support or even substitute technically based moor restoration. However, to substantiate the potential benefits of the beaver for moor restoration, it is necessary to conduct detailed research in areas where the activities and effects of beavers can be compared with technical measures. Such a rare opportunity is provided in the moor reserve of the Wurzacher Ried in the very south of Germany, where we started our research in 2010. As it is the case for almost all moors in Germany and even western Europe, reliable information about the timing of initial beaver colonization was not available for our study area. However, information about the duration of beaver presence is a prerequisite for reliable estimation of the impacts and effects of the species on a habitat over time. Beaver-induced disturbances can show changing dynamics in the short term that result into a habitat mosaic with intrinsic spatiotemporal heterogeneity on landscape level (Kivinen et al. 2020). Thus, there is a need for analytical procedures that allow for distinguishing the effects of rather immediate habitat-beaver interactions from indicators which reflect the population dynamics of the species. In this paper, we describe our experiences and results in reconstructing beaver colonization of a moor habitat through an interpretation of aerial images. The aim of the study is to analyse if certain habitat features visible on digital orthographical aerial photographs (DOP) can be used as indicators for beaver presence, distribution, and population development and therefore to trace former colonisation processes of moor areas where no beaver data is available.

Methods and material

Study area

The study was conducted in the moor and wetland reserve "Wurzacher Ried" located in the Alpine foothills within the federal state of Baden-Württemberg, southern Germany (Figs. 1 and 2). The reserve has an area of 20 km^2 with a corresponding drainage catchment extending over about 60 km^2. Mean altitude is 650 m a.s.l., mean temperature is 7 °C, and annual precipitation is 1100 mm. The peatland evolved in a glacial basin eroded in the 'Würm' ice age (~20.000 years ago). The evolution of the moor began with a silting lake enclosed by moraines. Today, about one third of the area consists of raised bog, which is surrounded by fens. Whereas about one third of the area is still intact moor habitat, many parts of the moors and fens are affected by former drainage, peat mining, agricultural land use, and forestry. Peat exploitation started in 1730 and was intensified around 1880 for industrial peat extraction. Drainage ditches were built until the beginning of the 1960s. During the 1960s, exploitation was reduced, with peat extracted for medical purposes only. Peat exploitation ceased completely in the Wurzacher Ried in 1995.

Today, the area is protected by various legal categories, e.g. Natura 2000 and RAMSAR convention. Certified by the European Council (European Diploma for Protected Areas) since 1999, the Wurzacher Ried is a focus of nature conservation politics and

Fig. 1 The location of the study area in Europe (smaller graphic) and the location of the study area (hatched red) in the German Alpine foothills (enlarged)

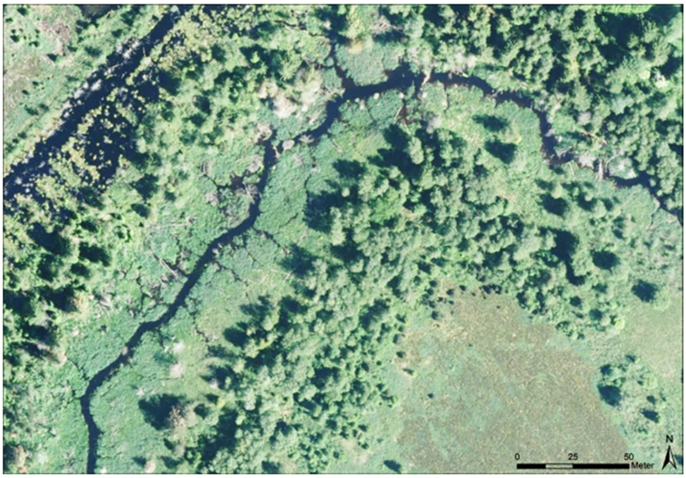

Fig. 2 Beaver canals visible on DOP. Beaver canals branching off from a creek (centre). Upper left corner: section of a drainage ditch showing characteristic linear geometry

administration. The prominent conservation status of the area provides the opportunity to explore long-lasting effects of the returning beaver on degraded moor habitats situated within an intensively used cultural landscape.

The water system of the study area includes natural creeks as well as manmade ditches and comprises a total length of about 90 km. Three small third-order rivers make up about one quarter of the total length of the water system. The remainder of the waterways in the reserve are a wider network of ditches originating from past drainage activities. Mean flow velocity is 0.1 m/s within the small rivers and 0.03 m/s in ditches. All three small natural rivers obtain their water supply from aquifers in the moraine sediment, with their headwaters located immediately within the study area. Accordingly, water levels of the rivers are seasonally and annually stable.

The water system of the study area and the corresponding drainage basin discharge into the 'Wurzacher Ach' river. Emerging at the very south bounds of the moor, the Wurzacher Ach is interconnected with the greater Danube water system and is assumed to have provided the immigration route for the beavers that founded the population currently existing in the study area. Exterminated all over southern Germany in the middle of the nineteenth century, beavers have been reintroduced into the Danube in the nearby federal state of Bavaria since the 1960s (Weinzierl 1973, 2003). Originating from these releases, beavers subsequently dispersed over the Alpine foothill region of southern Germany and adjacent Austria (Kasperczyk 1987, German Federal Agency for Nature Conservation 2008).

Monitoring of dams and lodges

From 2010 until 2015, we studied the impact of the returning beaver on the moor habitat in the study area. During this period, the population development of the beaver was monitored. Beaver dams and lodges were field surveyed in 2010, 2011, 2012, 2013, 2015, and additionally in 2019. A further assessment exclusively of beaver lodges was carried out in 2014. Beyond the field trials, we attempted to estimate the number of lodges present in the area before the beginning of our field studies. This estimate was based on knowledge of how beaver lodges emerge. During our studies, we observed the emergence of beaver lodges from the outset and were able to explore how these processes were visibly expressed on digital orthographical aerial photographs. Based on the positions of lodges detected during the first field trial in 2010, we explored older DOPs in search of signs of evolving lodges. Signs characteristic of emerging lodges were detectable on images from 2006. We did not find any indicators for beaver lodges in older DOPs.

As mentioned above, dams and lodges were assessed directly in the field starting in 2010. In each trial, fieldwork was carried out from December until February of the following year. This involved kayaking and wading to search through the complete network of streams and ditches in the study area. Positions of dams and lodges were GPS located. Dams were measured and assessed according to their functionality. The dimensions of lodges were also measured. Building conditions of the lodges as well as tracks and signs of beavers were used to estimate if the lodges were inhabited. This approach to estimation proved reliable on the basis of previous tests where we observed beaver lodges with photo traps.

Calculation of the retention area of beaver dams

Calculations of the areas that are hydrologically affected by the beaver dams were carried out based on a digital elevation model (DEM) with a 1×1 m resolution. The DEM was derived from airborne LIDAR data. In a first step, the DEM was used to topographically identify the waterways and to evaluate already available digital layers of the drainage network. In combination with information gained from fieldwork, we were then able to produce a differentiated digital layer of the actual waters in the study area.

An intersection of the digital layer of waterways and the DEM allowed for exploration of the rewetting effects of the beaver dams. Therefore, each dam position was defined as a catchment outlet. Based on this, we calculated the respective catchment area for the dams. Within these areas, the rewetted zones were then calculated in relation to dam height and groundwater distance equal to zero. We used QGIS (QGIS Development Team 2020) and the hydrological software tool WASIM-ETH (Schulla and Jasper 1998; Schulla 2019) for this procedure. The analyses resulted in a spatially explicit depiction of the zones affected by the dams and allowed for tracing the retention effects developing throughout the study period.

Assessments of beaver canals

Verification of canal structures in the field showed that beaver-dug canals can be reliably distinguished on DOPs and thus might serve as an indicator of beaver presence. Aerial photogrammetric surveys of the study region have been carried out on behalf of the federal administration since the 1980s. DOP series with 0.1 m and 0.2 m ground resolution, respectively, are available in three- to five-year cycles. To reduce the time gaps between these standardly conducted overflights, we initiated additional photogrammetric aerial surveys in 2012 and 2015. Beaver canals were identified on the DOPs through a systematic visual census of the watercourses on a computer screen. Canals were digitally located in a GIS. Verification in the field showed that precise identification of canals on the DOPs was feasible throughout the study area.

'Pearson's product-moment' was used to explore correlation between the development of the numbers of lodges, dams, and beaver-built canals, and the area affected by beaver dams as calculated for the different years (Freedman et al. 2007). Tests for normal distribution were carried out according to Shapiro–Wilk (Shapiro and Wilk 1965). To describe the changes in numbers of lodges and beaver canals, respectively, over time, the time series were fitted to a Weibull growth function (Yang et al. 1978). The model fit was estimated by applying the Akaike information criterion with correction for small sample size (Burnham and Anderson 2002). Statistical analysis was performed using R (R Core Team 2020).

Results

Initial occurrence and colonization process

By digging canals, beavers connect potentially suitable forage habitat to waters. In our study area, the average length of beaver canals was about 14 m. However, beaver canals connected woods and shrub areas with the river network over distances of up to nearly 100 m (min.: 0.9 m; max.: 94.9 m; mean: 14.1 m; SD 14.9 m). Our analyses of DOPs showed that beaver canals are reliably distinguishable from other water-bearing structures like drainage ditches and streamlets on the digital images. Thus, systematic assessment of the drainage network on DOP sets from different years provided the opportunity to reconstruct and explore beavers' colonization of the study area. No beaver canals or hints of beaver presence were detectable on DOPs acquired in the 1990s. Canal structures characteristic of beaver presence appeared for the first time on images dating from 2001 (Fig. 3). There, a few canals indicated initial beaver activities in the south-western and north-eastern ranges of the area. Over the years, the abundance of canals increased throughout the water system of the area. Tracing of individual canals according to their visibility on the aerial photographs across different years revealed that they became revegetated and were covered again at most two years after they had been abandoned by beavers. Thus, detecting beaver canals on DOPs provides reliable proof of beaver presence, and the assemblage of canals visible on a respective DOP can consistently represent the actual beaver distribution at a certain time.

Indicators of population development

To estimate the development of the beaver population in the study area, we assessed different variables potentially reflecting the dynamics of the beaver population. Starting with low numbers in 2001 ($n = 19$), the rate of beaver canals increased during the following years with a peak in 2015 ($n = 1469$; Fig. 4). In addition to canal numbers obtained from DOP analyses, we explored the number of lodges and dams. Moreover, we assessed the area rewetted by the beavers' damming activities. These data were derived from field trials conducted between 2010 and 2019. Additionally, the presence of beaver lodges in 2006 was reconstructed by remote sensing (see methods). Concerning beaver lodges, we differentiated between the total number of lodges and the number of lodges inhabited by the animals at the time of the survey in winter. Two lodges estimated for 2006 and four inhabited lodges out of a total of five lodges revealed by our first field survey in 2010 suggest a slowly increasing population during the first decade of beaver presence in the study area. After 2010, the number of beaver lodges increased more rapidly, whilst from 2014 to 2019, the growth rate in the number of lodges inhabited by beavers slowed down again considerably (Fig. 4).

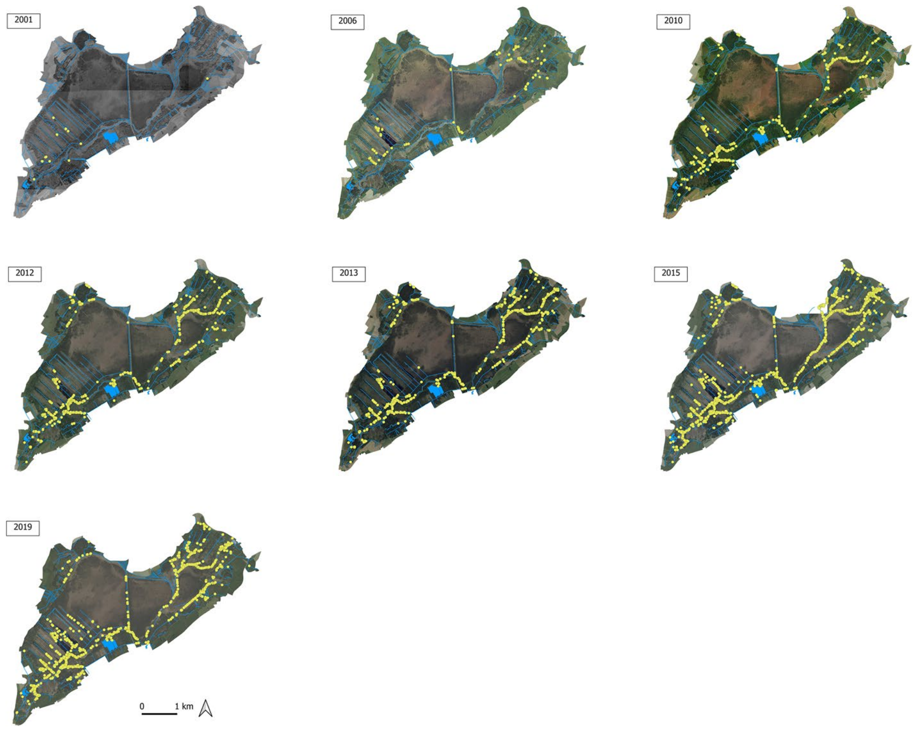

Fig. 3 Occurrence of beaver canals identified on DOPs from different years between 2001 and 2019. Dots (yellow) indicate the location of the canals branching off from creeks and ditches in the study area

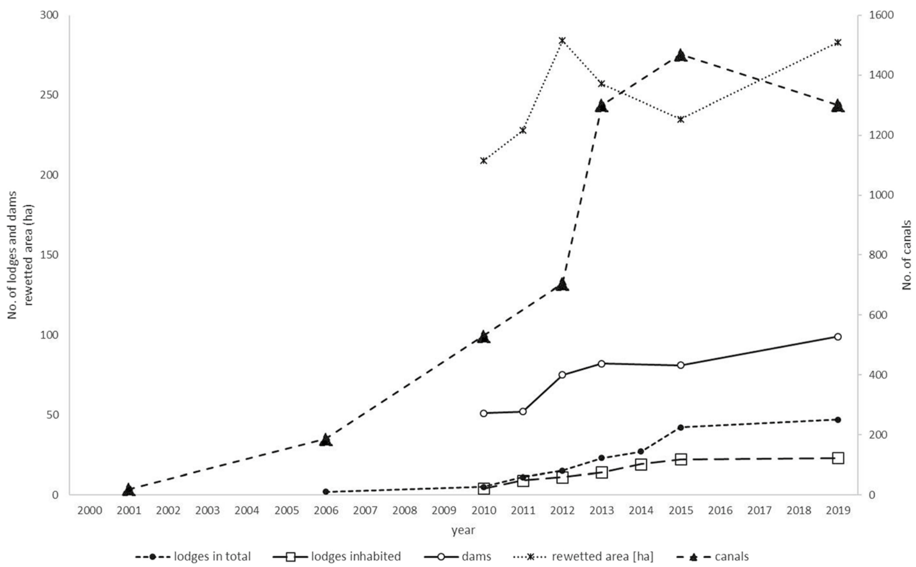

Fig. 4 Different indicators of beaver presence 2001–2019

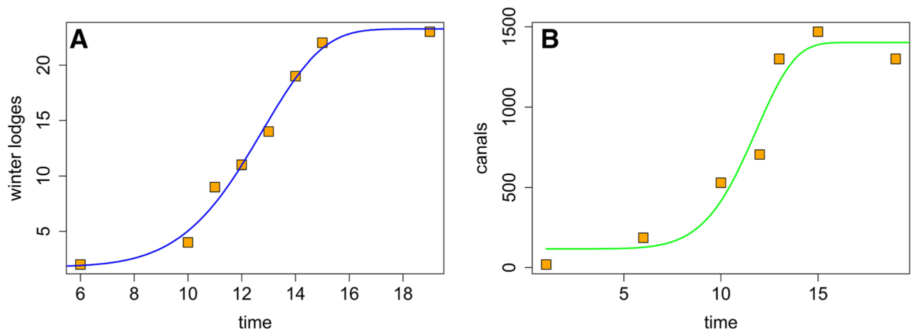

Fig. 5 Development of the number of beaver winter lodges (**A**) and of beaver built canals (**B**) over time. Time steps correspond to years

During the field trials, the beaver dams were assessed throughout all the natural creeks and drainage ditches in the study area. The mean frequency of dams in the area was 0.9 dams per km of waterway. The density of dams was higher in the natural creeks than in the ditches in all years ([dams/km] in creeks, min.: 1.2; mean: 1.5; max.: 1.7; SD: 0.2 vs. [dams/km] in ditches, min.: 0.4; mean: 0.6; max.: 1.0; SD: 0.2). Based on the dam data, we calculated the size of the rewetted area resulting from the beavers' damming activities. As described above, the number of lodges was still low in 2010. Against this background, the 51 dams already counted at this time seemed like a considerably high number, making up nearly 50% of the maximum number of dams, which was recorded later in 2019 ($n=99$). The area rewetted by beaver dams in 2010 (209 ha) accounted for 74% of the maximum extension of the rewetted area, which was recorded in 2012 (284 ha) and 2019 (283 ha), respectively (Fig. 4). This means that the size of the rewetted area had already peaked in 2012, and the increasing dam numbers and dam abundance that we recorded later in 2019 did not result in a further increase in the rewetted area compared to 2012 (Fig. 4).

We used the number of lodges, particularly numbers of inhabited winter lodges, as an indicator of beaver population density. We found that the time series of winter lodges is significantly correlated with numbers of beaver-built canals (Pearson's product-moment correlation, $t=3.5097$, $df=3$, $p=0.03921$, $r=0.897$) and with the number of dams (Pearson's product-moment correlation, $t=3.7803$, $df=4$, p-value$=0.01943$, $r=0.884$). In contrast, the size of the area rewetted by beaver dams and the numbers of inhabited lodges do not appear to be correlated (Pearson's product-moment correlation, $t=1.2182$, $df=4$, p-value$=0.2901$, $r=0.520$).

The development over time in the numbers of inhabited lodges can be very well described using a growth function (Fig. 5; Table 1). The model suggests that the population density is near carrying capacity. The model also fits well to the canal data. However, it cannot accommodate a drop in y values once the asymptote has been reached (Fig. 5; Table 1).

Table 1 Parameters of non-linear models describing the development of the numbers of winter lodges and the numbers of beaver built canals over time

Parameter	Estimate	SE	t-value	Pr(>|t|)	Conv. tol	AICc
Model: nls_winterlodges						
Asym	23.250	1.017	22.856	0.0000217		
Drop	21.449	1.561	13.739	0.000163		
nlog	−17.310	2.655	−6.519	0.0029		
pwx	6.731	1.037	6.493	0.0029		
					0.0000028	58.29852
Model: nls_canals						
Asym	1401.867	144.195	9.722	0.00231		
Drop	1284.939	204.826	6.273	0.00818		
nlog	−17.424	9.035	−1.928	0.14939		
pwx	6.990	3.634	1.923	0.15014		
					0.0000097	157.0705

Asym Horizontal asymptote, *Drop* Difference between the asymptote and the intercept (of y at x = 0), *nlog* Natural log. of the rate constant, *pwx* The power to which x is raised, *conv. tol* Achieved convergence of tolerance, *AICc* Akaike information criterion with correction for small sample sizes

Discussion

To estimate the effects that a returning beaver population will exert on degraded moor habitats over time requires detailed information about the dynamics and the development of the population of the rodent species. However, at the starting point of our studies in 2010, such information was not available. Even the point at which the beavers first arrived in the reserve was unknown.

Our first attempts to clarify when beaver occurrence in the study area had first begun were aimed at tracing the age of beaver lodges using dendrochronological approaches. These trials were unsuccessful based on the fact that sample trees felled in the study area did not show any characteristic growth-ring patterns within their life span. Thus, comparisons of growth-ring patterns of sample trees and limb material extracted from the beaver lodges did not make it possible to determine when the lodges had originated. However, the uniform growth-ring patterns of the sample trees indicate stable environmental conditions and water supply prevailing even at the outer edges of the study area.

The analyses of DOP series from different years provides a basis on which to estimate retrospectively that the beaver arrived in the study area around 2000 or 2001. As we learned later, this estimate is consistent with anecdotal reports from these years. For example, we received information about gnaw marks detected in the western part of the moor reserve and, for the first time, a beaver dam was reported from the eastern part of the study area (Weisser pers.). In addition to identifying the time of initial occurrence, analyzing DOP time series provided information to reconstruct the beavers' colonization process across the moor. To explore beaver presence, aerial surveys and remote sensing techniques had already been applied in previous research. Fuller (1953) reports on aerial survey experiments carried out in the late 1940s in the Mackenzie District, Northwest Territories, and describes trials to refine these approaches. The basic method underlying the surveys was to directly spot beaver signs such as lodges, dams, and feed beds from an aeroplane. The aerial surveys were aimed at assessments of current population trends, where the proportion of lakes with signs of beavers (i.e. those occupied by beavers) was used as an indicator. However, as a starting point, we needed to retrospectively reconstruct the beavers' colonization of the study area. Thus, we were dependent on data that could allow for the identification and chronological allocation of beaver signs from years or decades ago. In this situation, the availability of regularly generated DOP series potentially provides the information needed. Arial images have frequently been used to identify beaver occurrence and for population census (Dickinson 1971; Kirby 1976; Broschart et al. 1989). Particularly beaver-induced impoundments, e.g. ponds as well as food caches, have been identified on aerial images and used to conduct censuses of beaver populations over large areas in North America and Russia (Rebertus 1986; Broschart et al. 1989; Johnston and Naiman 1990a, 1990b). The occurrence of impoundments depends partially on topography, and the location of beavers' work sites is determined by the distribution of suitable vegetation e.g. softwood. Nevertheless, such signs can reasonably be used as indicators of beaver distribution and abundance at a large spatial scale. Our study area extends over just 20 km^2, and today most of the wetlands and moors in human-dominated landscapes of Western Europe are even smaller. Therefore, indicators that occur more frequently in the landscape and provide higher spatial resolution are required. Particularly in bog areas and peatlands, canals dug by beavers are abundant (e.g. Zavyalov 2011b). Beavers create canals to achieve safe access to e.g. feeding places that are located at greater distances from waterways (Anderson et al. 2015; Hood and Larson 2015). Such canals are visible on aerial photographs (e.g. Rebertus 1986). The canals made by the beavers have a characteristic shape, which makes it easy to distinguish them from other habitat features visible on the DOPs. By tracing the fate of individual canals on DOP series, we found that canals are covered by vegetation after two years at most after being abandoned by the beaver. Thus, unlike beaver ponds that potentially remain for longer periods in the landscape (Johnston and Naiman 1990b), the canals visible on the DOPs represent the current distribution of the species within the area of concern. The capability to reflect the distribution at a given time is relevant because the frequency of standardised aerial surveys will not necessarily reveal short-term dynamics of beaver-induced disturbances (Kivinen et al. 2020). We therefore judge beaver canals identified on DOPs to be reliable indicators for reconstructing the initial occurrence and subsequent distribution of the beaver in moors and comparable habitats. This is important because information about beaver occurrence in peatlands of Western Europe is very limited. Human access to bogs can be difficult per se and is further restricted by law since many moor habitats are protected areas in EU countries.

A huge amount of moor habitat throughout Western Europe has been depleted by former drainage and anthropogenic land use. Restoration e.g. of moors is difficult and expensive. Increasingly recolonizing its historic range in the now human-dominated landscapes (Swinnen et al. 2017), the beaver is assumed to provide considerable support for the rehabilitation of wetland habitats (Willby et al. 2018; Nummi and Holopainen 2020; Smith et al. 2020). However, effectively involving the returning beaver as a driver of moor restoration schemes will require more detailed information about the effects of beaver populations on moor and bog habitats (Lang and Wieder 1984; Rebertus 1986; Zavyalov 2011a). As is the case for many moors in Western Europe, habitat alterations in our study area have either been well documented over previous decades by diverse research or can be reconstructed (Gremer 1991; Kohler et al. 1992; Böcker et al. 1994; Schwineköper 1997; Schall 1998). In contrast, complementary information about the development of beaver populations in moor habitats is mostly absent. Thus, it is of specific interest if the beaver canals, which can be retrospectively identified on DOP series, can also serve as indicators of population trends.

Since the beginning of our field research in the study area in 2010, we regularly monitored beaver dams and lodges. Active winter lodges are supposed to be a robust indicator of the number of family groups (Brommer et al. 2017). Comparing the data over time, we found a significant correlation between inhabited winter lodges and numbers of beaver canals as well as between winter lodges and dam numbers. In contrast, the size of the rewetted area for all dams in total that we calculated for each of the different study years does not closely correspond with the dam numbers. However, the sizes of the rewetted areas differ between the various dams, depending on the topographic circumstances prevailing at the respective dam site. Thus, decay or emergence of only a few dams can considerably impact the total size of the rewetted area.

With the initial occurrence of beavers having been dated to around 2000 or 2001, the fact that only five beaver lodges were found during our first field survey in 2010 suggests that growth of the beaver population between 2000 and 2010 was rather slow. After 2010, the number of active winter lodges and, correspondingly, the number of dams and canals grew more rapidly, peaking around 2013 for dams and 2015 for winter lodges and canals. Another four years later, the numbers of dams, lodges, and canals remained at high levels. The somewhat earlier peak in dam numbers can be explained by the finding that upon initially arriving in the study area the beavers first extended their activities over the available habitat and then increased their population density during subsequent years. Such time-delayed population congestion subsequent to area-wide colonization has also been found in previous research (Zavyalov 2011b).

Documenting the development of the beaver population in the Wurzacher Ried for 20 years since the initial occurrence of the species in the area, our data suggest an approximation of the population density to the carrying capacity. However, a more definitive interpretation of beaver population dynamics in the study area will require more data. Notwithstanding, the temporal dynamics of the beaver population that we have identified in our study area corresponds with the findings of previous research documenting that colonization maxima in newly established beaver populations were reached after 13 to about 20 years (Busher 1987; Busher and Dzięciolowski 1999; Starikov and Anchugov 2009; Korablev et al. 2011; Zavyalov 2011b), between 25 and 29 years (Novakowski 1965; Broschart et al. 1989; Johnston and Naiman 1990b; Busher and Dzięciolowski 1999; Hartman 2003; Zavyalov 2011a), and after about 40 years, respectively (Hartman 1994).

We conducted for the first time, to our knowledge, a systematic approach to explore the potential of beaver canals as an indicator for beaver population dynamics. According to our results, we believe that beaver-built canals identified on DOP series can be used to trace back the distribution and development of beaver populations in moor habitats. Thus, these remote sensing data can contribute to a better understanding of the impact and the restoration effects that the returning beaver potentially exerts on moor habitats in western European landscapes. Such an understanding can facilitate an efficient involvement of the beaver into restoration planning and improve the conservation of moors in western Europe.

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Author contributions TK: study design and conception, data collection, data analyses, writing the paper. VE: data collection, data analyses, writing the paper. YC: study design, data collection, data analyses. UK: data analyses.

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Data availability All relevant data result from the manuscript.

Code availability Not applicable.

Declarations

Conflict of interest There are no conflicts of interest or competing interests related to the submitted manuscript.

Ethical approval Not applicable.

Consent to participate All listed authors agree to participate the publication process.

Consent for publication All listed authors agree to the publication of the submitted manuscript.

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