



Seasonal movements of the Eurasian otter (*Lutra lutra*) in floodplains of the Gelderse Poort, the Netherlands

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NATIONALE DATABANK

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Abstract

The Eurasian otter (*Lutra lutra*) population in the Netherlands has recently achieved the status of a viable population after its successful re-establishment since the start of the Dutch otter reintroduction program in 2002. Nevertheless, the population remains vulnerable to disturbances, is subject to genetic diversity loss, and disperses limitedly outside of the former release area. To sustain the Dutch otter population, enhanced population connectivity and dispersal is required, for which a better understanding of otter movement patterns and habitat preferences is essential. This study aimed to investigate seasonal migration patterns of Eurasian otters in floodplains of the Gelderse Poort under the influence of fluctuating water levels, water temperatures, and fish stocks. The study analysed dispersal, seasonality, and causality patterns in data collected from 2015 to 2021. Based on analysis of the collected data, the hypothesis of seasonal otter movements in floodplains could not be confirmed, though trends that support the theory were observed. In addition, no causal effects of the studied habitat variables, i.e., water levels, water temperatures, and fish stocks, on otter observations were detected. Possibly, biases in the data and small sample sizes led to nonsignificant results, or other factors, like human disturbance, availability of resources and shelter, and social variables profoundly impact otter movement patterns instead. While there are signs that indicate temporal otter movements between floodplains and inland areas, defining such periodical movements and discovering their underlying incentives remains a challenging task. Complementary research on otter movement patterns could continue to improve conservation efforts that aim to enhance otter dispersal, boost the population's genetic diversity, and protect the viability of this iconic freshwater species in the Netherlands.

Introduction

Up until the 1930s, the Eurasian otter (*Lutra lutra*) was a flourishing semiaquatic freshwater carnivore in the Netherlands, iconic to the Dutch wetlands. However, in the following decades, habitat fragmentation (Kurstjens et al., 2009), severe water pollution (Gutleb & Kranz, 1998; Roos et al., 2001), poaching pressures (Hauer et al., 2002; Kurstjens et al., 2009), intensifying fishing practices with fyke nets (Bekker et al., 2018; Jefferies et al., 1984; Koed & Dieperink, 1999; Madsen, 1991), and increasing numbers of road kills (Hauer et al., 2002; Kruuk & Conroy, 1991; Lammertsma et al., 2008) led to the extinction of the species in 1989. A call from the Dutch public for the return of the otter in the mid-1990s incited efforts for restoring otter habitat, improving water quality, constructing interconnecting corridors, building road underpasses, obliging stop grids on fyke nets, and eventually starting a reintroduction program in 2002 (Koelewijn et al., 2010; Kurstjens et al., 2009).

From June 2002 till November 2008, a total of 31 otters were released in northern Dutch wetlands (Seignobosc et al., 2011). Since the start of the reintroduction program, the otter population has successfully re-established and expanded in the Netherlands and has achieved the status of a viable population that consists of approximately 450 individuals (Kuiters et al., 2020). Nevertheless, given that otter populations have relatively low densities and life expectancies, they remain vulnerable to disturbances and genetic diversity loss (Kuiters et al., 2020; Kurstjens et al., 2009). Genetic variation within the Dutch otter population has declined continuously since the reintroduction in 2002, and new genetic variants, which were added to the population's gene pool via migration and additional reintroductions, have not been able to reach the gene pool's core in Overijssel and Friesland (Kuiters et al., 2019, 2020). Moreover, otter dispersal outside of the former release area is limited (Kuiters et al., 2020; Lammertsma et al., 2008). This restricted dispersal is mainly a result of frequent road kills caused by traffic bottlenecks, which account for 89% of otter mortality in the Netherlands (Kuiters et al., 2020). To sustain the Dutch otter population and maintain its genetic diversity, enhanced population connectivity and dispersal is required. For this reason, a better understanding of otter movement patterns and habitat preferences is essential.

Eurasian otter movements are likely determined by both environmental and social triggers (Carss, 1995), though such movement patterns are relatively undocumented. Otter habitat preferences, on the other hand, have been studied extensively over the past decades (Lanszki & Sallai, 2006; Madsen & Prang, 2001; Ruiz-Olmo et al., 2001, Ruiz-Olmo et al., 2011). In wetlands and floodplains, habitat factors including stream size, water level changes, degree of water pollution and human disturbance, altitude, presence of beaver dams, and availability of shelters, resources, and prey are known to influence otter presence (Kruuk, 2006; Kruuk et al., 1989; Ruiz-Olmo et al., 2002; Ruiz-Olmo & Jiménez, 2008; Yoxon, 2000). These habitat factors may impact otter population dynamics either directly or indirectly through prey density (Martínez-Abraín et al., 2020; Ruiz-Olmo et al., 2011). Otters are typically a food-limited species (Kruuk & Carss, 1996), as prey availability, specifically that of fish, is evidently the most influential criterion for otter presence and reproductive success in suitable habitats (Elmeros & Madsen, 1999; Kruuk, 2006; Martínez-Abraín et al., 2020; Prenda & Granado-Lorencio, 1996; Ruiz-Olmo et al., 2001; Ruiz-Olmo et al., 2001).

Floodplains serve as excellent foraging grounds for Eurasian otters, as floodplains are filled with small, shallow ponds that harbour high densities of slow-swimming fish species and are surrounded by compact vegetation, ideal for catching fish (Carss, 1995; Dorenbosch et al., 2011; Krawczyk et al., 2016; Lanszki & Sallai, 2006). Fish abundances and distributions in floodplains, however, are determined by seasonal patterns and inter-annual fluctuations of, among others, water levels and water temperatures (Dorenbosch et al., 2014; Logez et al., 2016; Thiaw et al., 2017). In Dutch wetlands, water levels rise, and floodplains inundate in winter and spring due to excessive rainfall and incoming melt-water from the Alps. High water levels play an important role in riverine ecosystems by decreasing habitat stability and diluting fish abundance (Ruiz-Olmo et al., 2011). Moreover, at low water temperatures in winter,

fish stocks descend to deeper water columns, which decreases otter hunting success (Logez et al., 2016; Mountain & Murawski, 1992). Therefore, the effects of seasonal water level and water temperature changes on fish stocks suggest incentives for temporal otter movements in and out of floodplain areas (Lanszki & Sallai, 2006; White et al., 2003). Accordingly, temporal otter movements would expectedly shift between floodplains in summer and inland areas in winter.

Studying otter movement patterns, as well as incentives for such movements, enhances a general understanding of otter migration, landscape connectivity, and possible threats from traffic bottlenecks, which contributes to the conservation and restoration of otter populations worldwide. In the Netherlands, an area of particular interest for otter conservation is the Gelderse Poort, a nature reserve situated at the base of the Rhine delta along the German border. The Gelderse Poort has been indicated as critical habitat for otter dispersal from the former release area across the rest of the Netherlands. Also, the Gelderse Poort is an indispensable area for interconnecting the Dutch and German otter populations to facilitate the exchange of genetic material and ultimately counter the threats of continuing genetic diversity loss (Kuiters et al., 2020; Kurstjens et al., 2009). For this reason, this study specifically aims to examine seasonal migration patterns of Eurasian otters in floodplains of the Gelderse Poort under the influence of water levels, water temperatures, and fish stocks.

The present study analyses data collected from January 2015 to March 2021. The incorporated data includes otter observation records collected by ARK Nature, Nationale Databank Flora and Fauna (NDFF), and Netwerk Ecologische Monitoring (NEM) from camera traps and field observations. Complementary data on habitat factors, i.e., water levels, water temperatures, and fish stocks, were obtained from databases of Rijkswaterstaat, Bureau Stroming, Waterschap Rivierenland, Waterschap Rijn & IJssel, and NDFF. Since this study is the first to investigate otter migration patterns over a time period of several years in the Gelderse Poort, this study presents a framework for overcoming the challenges of long-term observational studies that include data collected from multiple parties. To detect otter seasonal movement patterns, this study examines the dispersal, seasonality, and causality (related to habitat factors) of otter observations recorded inland and in floodplains. Finally, the study evaluates which areas are of particular interest for otter conservation efforts and for eliminating traffic bottlenecks in the Gelderse Poort if seasonal migration patterns appear.

Methods

Study Area

The study area is located in the Gelderse Poort (51°52'N, 6°0′E), a nature reserve of about 6000 ha in the eastern Netherlands along the German border. The reserve covers the beginnings of the Rhine delta, where the Rhine splits into the Nederrijn, the Waal, and further into multiple secondary channels. The Gelderse Poort consists of a 20 km long section of the Rhine between Tolkamer and Arnhem and a 12 km section of the Waal between Millingen aan de Rijn and Nijmegen. The reserve contains riverine grasslands, marshlands, clay pits, floodplains, such as the Millingerwaard, and inland subsites, like the Oude Rijnstrangen and Ooijpolder (Natura 2000, 2014). Floodplains are situated between winter and summer dikes, also called primary and secondary flood defences, respectively, and allow episodic flooding when river water levels rise. Water levels on the inland side of winter dikes, on the other hand, are regulated manually by means of pumping stations, weirs, and locks. The Gelderse Poort is subject to several river restoration projects since the establishment of the Kaderrichtlijn Water (KRW) by the European Parliament in 2000. River widening and ecological restoration projects continue to improve the spatial planning and chemical composition of water bodies, as well as the diversity of plant and animal communities of riverine ecosystems in the Gelderse Poort (Rijkswaterstaat, 2018).

A map of the study area, including areas on the floodplain and inland side of winter dikes, was constructed in ArcGIS Pro (Fig. 1). The study area layer was deduced from all otter observations in the Gelderse Poort included in this study, with an added 5 km buffer. Positionings of winter dikes (primary flood defence) and summer dikes (secondary flood defence) were imported into ArcGIS Pro from Nationaal Basisbestand Primaire Waterkeringen from Waterveiligheidportaal. Hereafter, the draw and clip tool were utilised to create separate layers for floodplain and inland areas. These layers were later applied to sort observation data into categories 'Inland' and 'Floodplain' based on their coordinates, as well as to construct a flood map of the Gelderse Poort for the years 2015-2021 ('Databases' in Methods; Fig. 8).

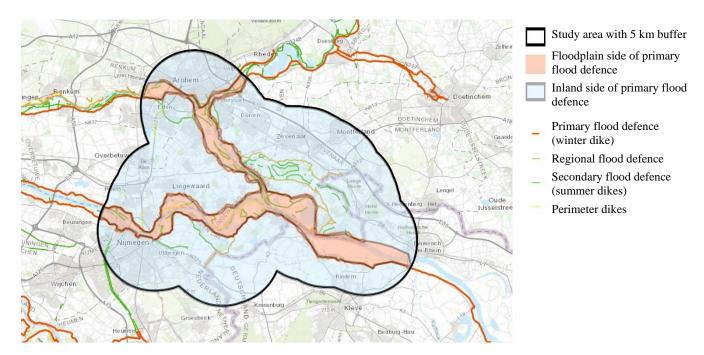


Figure 1: Map of the study area with inland and floodplain areas. The study area of the Gelderse Poort with a 5 km buffer (black outlined area). Floodplain areas outside of primary flood defences (red area) and inland areas of primary flood defence (blue area), based on types of flood defences retrieved from Nationaal Basisbestand Primaire Waterkeringen (see legend).

Data Collection

Camera traps

Camera and field monitoring were executed from January 2021 till March 2021 (supplementary data from previous monitoring were added, see 'Databases'). During the study period, ten camera traps owned by ARK Nature were spread across the Gelderse Poort. Five of these cameras were situated in the Rijnstrangen north of the Nederrijn, whereas the other five were located in the Ooijpolder, Duffelt, and Millingerwaard south of the Waal. Eight of these cameras were placed on the landside of the dikes (land inward from the winter dike), while three cameras were situated in floodplains (between the winter and summer dike). Because of peaking water levels in the Rijn and Waal, four camera traps had to be removed from the Rijnstrangen for a period of four weeks from January 27th to February 28th. The removal or displacement of camera traps due to such water level changes is common, especially in winter. Unfortunately, the removal and replacement of camera traps have not been documented over the past years. Therefore, it is impossible to correct for recording time biases.

Each Bushnell camera trap had a 32GB SD memory card and eight rechargeable AA batteries, which were replaced at least once every two weeks. The camera traps were attached to trees at about 0.5 metres

above ground level and were angled downward at about 20 degrees. The cameras responded to changes in temperature and movement and were set to record 30-second videos at intervals of one second once a temperature or movement trigger initiated the filming. Temperature and movement sensitivity settings differed per camera, depending on the site, e.g., sensitivity was lowered at very windy sites with moving vegetation to avoid false video recordings. Following the collection of the memory cards, each otter video fragment recorded by the camera traps was counted (n_{obs}) and registered at Waarneming.nl (exact observation coordinates were blurred at Waarneming.nl to prevent theft of camera traps).

Field observations

Along with camera trap monitoring, field patrols were carried out at least once every two weeks to check the area for otter signs, mainly footprints, tracks, and spraints. Spraints are otter droppings used for species communication that are usually 2 – 7cm long, dark green to black-grey, smell strongly of fish, and contain fish bones and scales. Fresh spraints were collected to subtract DNA-containing material used for genetic monitoring. This study, however, does not wield genetic data, so spraint collection methods are not discussed here. Occasionally, feeding signs, paths and slides, dens, and castlings (raised areas created by otters, usually by scraping together grass, mud, sand or gravel, for spraint deposition) were also recorded as observations. In the study area, otter signs were searched for under and near bridges, on banksides, on boulders or rocks near rivers and streams, on old tree stumps or logs, on gravel banks or sandy and muddy areas, around ponds and lakes, in marshes or reed beds, at river junctions or intersections, and at either end of otter paths (Dijkstra et al., 2012). All otter signs were photographed and registered at Waarneming.nl, where corresponding information on the date and location of the observation was documented as well. Recorded otter observations, concerning mainly footprints, tracks, and spraints, were counted (nobs) and included in the data analysis. Again, the amount of time spent on field patrols has not been documented over the past years. Therefore, it is impossible to correct for field patrol monitoring biases.

Databases

Otter monitoring in the Gelderse Poort has been executed by ARK Nature interns and volunteers since 2014, following the same monitoring protocol as stated above. To investigate seasonal migratory patterns over the course of several years, available observation data collected by ARK Nature dating from September 2017 to March 2021 were included in the analysis. Additionally, observation datasets from the Nationale Databank Flora and Fauna (NDFF) and Netwerk Ecologische Monitoring (NEM) from 2015 to 2020 were incorporated in the analysis. Data collected by NDFF involved validated observation records from several databases, as well as individual observations reported at Telmee, Waarneming.nl, and Invoerportaal NDFF. The NEM dataset contained natural data from Rijkswaterstaat, the Ministry of Agriculture, Nature and Food Quality, the Ministry of Infrastructure and Water Management, and Statistics Netherlands.

Recorded observations could only be included in the analysis if the data included both the date and coordinates of the observation. Additionally, observation records obtained from Waarneming.nl and Observation.org could only be included in the analysis if validated. The combination of the three datasets led to a total of 2008 validated observations ($n_{obs} = 2008$). Since the NDFF dataset also included observations from NEM and ARK Nature registered at Waarneming.nl, the complete dataset was checked for double observations. Observations with identical observation type (camera trap/spraint/tracks/etc.), date (and time if available), and coordinates were removed from the dataset. Finally, this resulted in a total of 1483 unique observations ($n_{obs} = 1483$).

For statistical analysis, the observations ($n_{obs} = 1483$) were categorised into 'Binnendijks', i.e., inland observations (IL), or 'Buitendijks', i.e., floodplain observations (FP), based on the observation coordinates. Inland and floodplain coordinates were determined by means of clipping the data in ArcGIS Pro for the inland and floodplain regions in the study area (Fig. 1). Data sorting resulted in 1345 inland

observations (n_{IL} = 1345) and 137 floodplain observations (n_{FP} = 137). Hereafter, the observations were categorised per season, according to the recorded observation date, i.e., winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, November). December observations were included with the winter of the following year, e.g., observations from December 2017 were scored as winter 2018, along with observations from January 2018 and February 2018.

Finally, data on habitat variables, i.e., water levels, temperatures, and fish stocks, were collected from databases of Rijkswaterstaat, Bureau Stroming, Waterschap Rivierenland, Waterschap Rijn & IJssel, and NDFF. Data on water levels, water temperatures, and surface water oxygen concentrations at Lobith, the monitoring station closest to the Gelderse Poort near Millingen aan de Rijn, were retrieved from Rijkswaterstaat for the years 2015 till 2021. Conversion tables for water levels in secondary channels were provided by Bureau Stroming. Data on inland water levels, which are regulated manually, were retrieved from Waterschap Rivierenland and Waterschap Rijn & IJssel. Data on water levels (maximum water level in m per season) were applied to construct a flood map of the Gelderse Poort in ArcGIS Pro (refer to www.doc.arcgis.com/use-flood-impact-analysis for specific method). Finally, data on fish stocks in kg/ha over the years 2015 till 2021 were collected from Waterschap Rivierenland and Waterschap Rijn & IJssel. Additional data on freshwater fish observations in the Gelderse Poort from 2015 to 2021 were retrieved from NDFF.

Data Analysis

Detection and treatment of outliers

As outliers in data can drastically bias the fit of estimates and affect the accuracy of statistical analysis, especially in regression models, all the datasets were checked and treated for outliers (Altman & Krzywinski, 2016). The multivariate model approach was applied to detect outliers in the data, where Cook's distance D_i for each observation i measured the change in \hat{Y} (fitted Y) for all observations with and without the presence of observation i. The Cook's distance displays how much observation i impacts the fitted values. Plotting the Cook's distance for each dataset showed that row 13 in the dataset for the inland otter observations per season conflicts with the other observations in the dataset (Fig. 2). An outlier test (R studio, 'outlier' package) confirmed that row 13 of column 'Inland' in the otter observation dataset was a strong outlier.

Cook's distance otter data before imputation

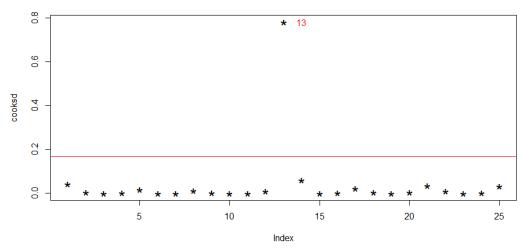


Figure 2: Influential otter observation data by Cook's distance before imputation. Cook's distance of row values for dataset 'Inland otter observations per season'. Cook's distance for row 13 is about four times higher than the mean Cook's distance for the dataset (red line). Therefore, the value of row 13 is influential and is treated accordingly.

To treat the detected outlier, the imputation method was applied. Since mean imputation (replacement of the outlier with the mean of all column values), median imputation (replacement of the outlier with the median of all column values), and k-Nearest Neighbours imputation (replacement of the outlier with the mean value of k neighbouring rows) would result in values that represented estimates of all seasons combined, these methods would be inappropriate to estimate the true value of the outlier, which was observed in winter. Therefore, the outlier was manually imputed with the value of the second-highest number of observations in winter, i.e., the outlier of 618 observations in winter 2018 was substituted by the second-highest value of 99 observations in winter 2017.

After the imputation, plotting Cook's distance for the altered dataset showed that the value of row 14, column 'Inland', conflicted with the other observations in the dataset (Fig. 3a). An outlier test (R studio, 'outlier' package) confirmed that row 14 of column 'Inland' in the otter observation dataset was an outlier in the adjusted dataset. The same imputation method, as stated above, was applied to substitute the outlier value, which was observed in spring, with the second-highest number of observations in spring. Therefore, the outlier of 174 observations in spring 2018 was substituted by 50 observations in winter 2016. After this imputation, the data did not contain any more outliers and was ready for analysis (Fig. 3b).

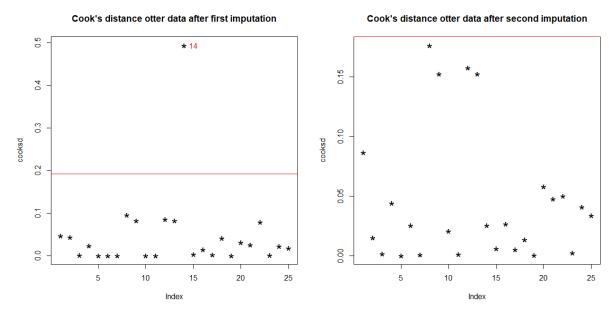


Figure 3a-b: Influential otter observation data by Cook's distance after first (a) and second (b) imputation. (a) Cook's distance of row values for dataset 'Inland otter observations per season' after manual imputation of row 13. Cook's distance for row 14 is about 2.5 times higher than the mean Cook's distance for the dataset (red line). Therefore, the value of row 14 is influential and is treated accordingly. (b) Cook's distance of row values for dataset 'Inland otter observations per season' after manual imputation of row 13 and 14. None of the Cook's distances for row values is higher than the mean Cook's distance for the dataset (red line).

Wilcoxon signed-rank test for dispersal

First, otter dispersal across inland areas and floodplains over seasons was examined. The null hypotheses (H_0) for each season state that the number of observations is equal between inland and floodplain areas. In other words: the difference between the number of inland and floodplain observations is equal to zero for each season. As the data of inland and floodplain observations are interdependent, i.e., the samples are assumably taken from the same population of otters, a dependent t-test was applied. Assumptions of normality and equal variance of the observation data were tested with Shapiro-Wilk tests and Levene's tests, respectively (R Studio, 'car' package). Since the data were not normally distributed, a nonparametric Wilcoxon signed-rank test compared the number of inland and floodplain observations per season from 2015-2021 (R Studio, 'car' package). All plots were constructed in Python 3.9.

Second, seasonal patterns of otter observations, both inland and in floodplains, were inspected. The null hypothesis (H₀) states that the number of observations on the landside and floodplain side of the dike is equal over seasons. Assumptions of normality and equal variance of the observation data were tested with Shapiro-Wilk tests and Levene's tests, respectively (R Studio, 'car' package). Since the data were not normally distributed, a nonparametric Kruskal-Wallis rank-sum test was applied to compare the mean number of observations per season over the years 2015-2021 for both inland and floodplain observations (R Studio, 'dplyr' package). All plots were constructed in Python 3.9.

General instrumental variables regression model for causality

Finally, the relationship between water level X_{WL} (mean water level per month), water temperature X_{WT} (mean water temperature per month), fish stocks X_{FS} (mean number of fish records per month), and otter observations Y (mean number of otter observations per month) over the years 2015-2021 was investigated by means of a general instrumental variables regression model. The null hypothesis (H_0) states that the number of otter observations per month is unrelated to water level, and/or water temperature, and/or fish stocks per month. A standard linear regression model would study the effects of X on Y (Fig. 4a). However, the covariance between X and Y is affected by several unknown/unobserved variables in the model that influence both variable X and Y, represented as error term u. In other words: the variables X and Y share a common confounder u. This 'confounder bias' creates the illusion that X has a causal effect on Y, which is not necessarily correct. This type of causality inference is extremely common in studies of complex systems and dynamics, like ecosystem and population dynamics studies in ecology (Creel & Creel, 2009; Kendall, 2015; Larsen et al., 2019; Loney & Nagelkerke, 2014).

The correct way to adjust for such a confounder bias is by controlling for error term u (Steiner et al., 2017). A method for controlling for error term u is the use of an instrumental variable, represented here as variable Z (Fig. 4b). The instrumental variables method allows computing unbiased relationships between endogenous variables X and response variables Y through instrumental variables Z if an unknown confounding variable u is suspected (Didelez et al., 2010). To estimate the effect of endogenous variables X on response variables Y, the model must adhere to the assumptions that instrumental variables Z are directly related to variables Z, are unrelated to variables Z, and are independent of the unobserved variable Z (Fig. 4b; 'Assumptions'). Also, the number of instrumental variables Z in this model (Z_{WL} , Z_{WT} , Z_{FS}) the model requires at least one instrumental variable for each endogenous variable so that the number of instrumental variables Z in this model (Z_{WL} , Z_{WT} , Z_{TS}) the model requires at least one instrumental variable for each endogenous variable so that the number of instrumental variables Z in the strict assumptions and abstract nature of the instrumental variables method, selecting appropriate instrumental variables for a general instrumental variables regression model is one of the method's main challenges (Windmeijer et al., 2015).

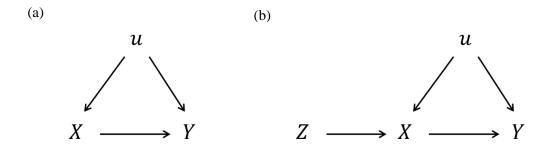


Figure 4a-b: Causal diagrams without (a) and with (b) instrumental variable, based on the causal graphs of Steiner et al. (2017). (a) Causal diagram without instrumental variable. Regressor X and response variable Y are both influenced by unknown/unobserved variables represented as error term u. Thus, the covariance between X and Y is biased by the error term u. (b) Causal diagram with instrumental variable Z. Regressor X and response variable Y are both affected by error term u, while instrumental variable Z is independent of error term u. *Instrumental variable Z is directly related to X and is only related to Y through X.*

Assumptions of the generalised instrumental variables regression model:

(i)
$$Cov(Z_i \rightarrow X_i) \neq 0$$

(ii) $Cov(Z_i \rightarrow u_i) = 0$
(iii) $m \geq k$

(ii)
$$Cov(Z_i \rightarrow u_i) = 0$$

(iii)
$$m > k$$

For the endogenous variable X_{WL} (mean water level), the model requires an instrumental variable that impacts water levels of the Rhine in the Gelderse Poort but is unrelated to error u and the number of otter observations Y. Factors that impact water level are local precipitation and evaporation (Coops & Hosper, 2002). However, these variables might directly influence the number of otter observations Y, as rainfall and evaporation may lead to the flushing away or accelerated degradation of otter traces like spraints and tracks, which impacts the number of recorded observations (Dijkstra et al., 2012; Jansman et al., 2001). Therefore, these factors were rejected as instrumental variables. Instead, precipitation along the Rhine outside of the Netherlands or snow-melt in the Alps near the origin of the Rhine would serve as excellent instrumental variables, as they determine water levels of the Rhine but do not affect otter traces in the Gelderse Poort. The city of Basel, Switzerland, is situated directly along the Rhine so that precipitation in Basel reflects fluctuating water levels of the Rhine. Data on precipitation at Basel (rainfall and snowfall) were retrieved from World Weather Data online (Basel Monthly Climate Averages, n.d.). Spearman correlation tests in R studio confirmed that assumptions for instrumental variables were met for both total precipitation and snowfall in Basel, but total precipitation showed a stronger correlation to the water level in the Gelderse Poort. Therefore, total precipitation in Basel was selected as the instrumental variable Z_P for the endogenous variable X_{WL} .

Similarly to the variable X_{WL} , for the endogenous variable X_{WT} (water temperature) the model requires an instrumental variable that impacts water temperatures of the Rhine in the Gelderse Poort but is unrelated to error u and the number of otter observations Y. Though local air temperatures or solar radiation are factors that impact water temperature, these factors could again affect the degradation of otter spraints and other traces, which influences the number of otter observations and makes these factors unsuitable as instrumental variables (Dijkstra et al., 2012; Jansman et al., 2001). Snowfall in Basel, along the Rhine in Switzerland, was selected as the instrumental variable for water temperatures in the Gelderse Poort. Spearman correlation tests in R studio confirmed that snowfall was indeed strongly correlated with water temperatures X_{WT} and was unrelated to the number of otter observations Y. Therefore, snowfall in Basel was selected as the instrumental variable Z_S for the endogenous variable

Finally, the endogenous variable X_{FS} (fish stocks) calls for an instrumental variable that influences fish numbers but has no effect on the number of otter observations Y and is independent of error u. Factors such as stream size, vegetation in the water column, and fishery activity, which affect fish stocks but may also impact otter population sizes, were rejected as instrumental variables (Madsen & Prang, 2001; Radinger & Wolter, 2014; Welcomme & Hagborg, 1977). Alternatively, the oxygen concentration of surface water at measuring station Lobith was selected as the instrumental variable for fish stocks, as oxygen concentrations limit fish population sizes and, therefore, impact the number of recorded fish observations (Maes et al., 2007). Otters, on the other hand, do not depend directly on oxygen levels in water for their survival so that the number of otter observations is not directly affected by oxygen concentrations in the water. Spearman correlation tests in R studio confirmed that oxygen concentration was strongly correlated with the number of observed fish X_{FS} and was unrelated to the number of otter observations Y. Accordingly, oxygen concentration of surface water at measuring station Lobith was selected as the instrumental variable Z_0 for the endogenous variable X_{FS} .

With the selection of the instrumental variables, the biased multiple regression model (Equation 1) was replaced by the unbiased generalised instrumental variables regression model (Equation 2), as stated below.

where,

- Y_i is the response variable otter observations
- $X_i^{(k)}$ is the endogenous regressor correlated with u_i
- $\beta_{X^{(k)} \to Y}$ is the regression coefficient of $X_i^{(k)}$ affected by u_i
- u_i is the unknown error term

Unbiased instrumental variables model:
$$Y_i = \beta_{Z^{(P)} \to Y} X_i^{(WL)} + \beta_{Z^{(S)} \to Y} X_i^{(WT)} + \beta_{Z^{(O)} \to Y} X_i^{(FS)} + u_i$$
 (2)

where,

- Y_i is the response variable otter observations
- $X_i^{(k)}$ is the endogenous regressor correlated with u_i $\beta_{Z^{(k)} \to Y}$ is the regression coefficient of the instrumental variable
- u_i is the residual error term

The model of equations for each of the three endogenous regressors could be solved, so that the desired regression coefficients $\beta_1 = Cov(X_i, Y_i)$ were estimated as stated below (Fig. 5).

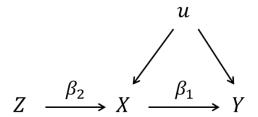


Figure 5: Causal diagram for instrumental variables with regression coefficients β_1 and β_2 . The covariance β_1 between regressor X and response variable Y is influenced by error term u, while the covariance β_2 between instrumental variable Z and regressor X are independent of u.

$$\beta_1 = Cov(X_i, Y_i) \tag{3}$$

$$\beta_2 = Cov(Z_i, X_i) \tag{4}$$

$$\beta_1 \cdot \beta_2 = Cov(Z_i, Y_i) \tag{5}$$

$$\beta_1 \cdot Cov(Z_i, X_i) = Cov(Z_i, Y_i) \tag{6}$$

$$\beta_1 = \frac{Cov(Z_i, Y_i)}{Cov(Z_i, X_i)} \tag{7}$$

Solving the model (R studio, 'ivpack' package) provided the estimates for regression coefficients β_1 , standard errors, and p-values. All plots were constructed in Python 3.9.

Results

Dispersal

To examine otter dispersal across inland and floodplain areas over seasons, the average number of inland and floodplain observations was compared (Fig. 6). In winter, the average number of inland otter observations was about 12 times higher than the average number of otter observations in floodplains (Wilcoxon signed-rank test, V = 27, P = 0.031). For the other seasons, i.e., spring, summer, and autumn, the average number of observations between inland and floodplain areas did not differ significantly (Wilcoxon signed-rank test, P > 0.05 for all conditions). The null hypothesis for equal otter dispersal between inland areas and floodplains could, therefore, only be rejected for winter observations.

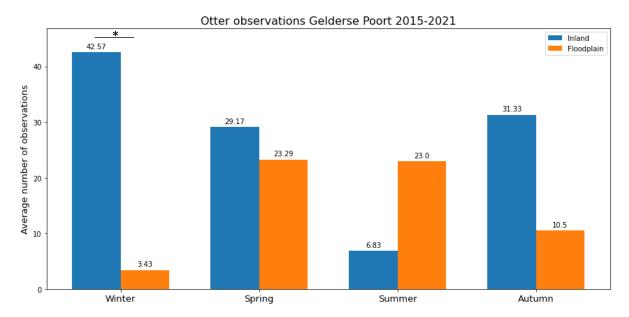


Figure 6: Inland versus floodplain otter observations Gelderse Poort 2015-2021. The average number of otter observations recorded inland (blue bars) and in floodplain areas (orange bars) per season from 2015 to 2021. The average number of observations is indicated above bars. According to Wilcoxon signed-rank tests, the data showed a difference between the number of inland and floodplain observations in winter * (V = 27, P = 0.031) but showed no difference between the number of inland and floodplain observations in spring (V = 20, P = 0.063), summer (V = 11, P = 0.418), and autumn (V = 14, P = 0.563).

Seasonality

To detect recurrent seasonal patterns of otter observations, both inland and in floodplains, the occurrence of otter observations over seasons was investigated (Fig. 7). Inland otter observation numbers appeared to peak in winter periods and drop in summer periods. Patterns in floodplain observation numbers were difficult to detect due to a lack of data. Still, a slight oscillating pattern can be observed from summer 2018 to summer 2020. However, otter observation data did not correspond significantly to seasons, both for inland observations (Kruskal-Wallis rank-sum test, $\chi^2(3) = 4.14$, P = 0.246) and floodplain observations (Kruskal-Wallis rank-sum test, $\chi^2(3) = 1.65$, P = 0.647). Therefore, the null hypothesis for the absence of seasonality could not be rejected.

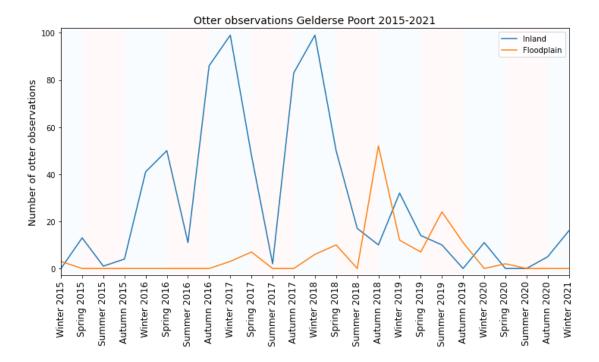


Figure 7: Seasonal otter observations Gelderse Poort 2015-2021. The number of otter observations recorded per season from January 2015 to February 2021. Inland otter observations are plotted in blue, floodplain observations are plotted in orange. Coloured bars in the background represent 'winter' periods (blue), i.e., the period between autumn and spring, and 'summer' periods (orange), i.e., the period between spring and autumn. According to Kruskal-Wallis rank-sum tests, the number of otter observations, both inland ($\chi^2(3) = 4.14$, P = 0.246) and in floodplains ($\chi^2(3) = 1.65$, P = 0.647), did not correspond to seasons.

Causality

First of all, to illustrate seasonal river flow in the Gelderse Poort and visualise how seasonal changes in water levels may affect otter habitat, a flood map was constructed in ArcGIS Pro (Fig. 8). Since inland water levels are, for the most part, manually regulated, the flood map only depicts floodplain areas, in which water levels are directly dependent on river flow of the Rhine. At maximal water levels, measured between 2015 and 2021 at measuring station Lobith, the area flooded almost completely in winter. In spring and summer, the number of flooded areas at maximal water levels was considerably less than in winter, though the number of flooded areas was clearly lowest in autumn.

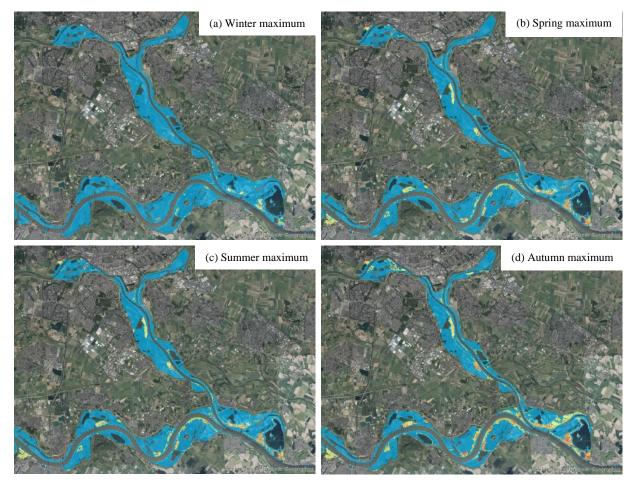


Figure 8a-d: Seasonal flood maps of floodplains in the Gelderse Poort at maximal water levels between 2015 and 2021. Flood maps illustrate floodplains in the Gelderse Poort at maximal water levels in m per season. Coloured planes represent flooded areas (blue), areas 0-2 m above water level (yellow), areas 2-4 m above water level (orange), and areas 4-6 m above water level (red). Maximum water levels for each season were measured between 2015 and 2021 at Lobith and were set at 15.15 m in winter (a), 13.34 m in spring (b), 13.61 m in summer (c), and 12.25 m in autumn (d).

To inspect causal relationships between the number of inland and floodplain otter observations and water levels, water temperatures, and fish stocks, the variability of these habitat factors over time was explored (Fig. 9). Generally, water levels peaked at the end of winter and beginning of spring, while water temperatures were lowest during the same period. Spearman correlations showed that seasonal patterns in water levels and temperatures ($\rho = -0.444$, P = 0.0001), water levels and fish stocks ($\rho = -0.350$, P = 0.002), and water temperatures and fish stocks ($\rho = 0.607$, $P = 1.26 \cdot 10^{-8}$) were related.

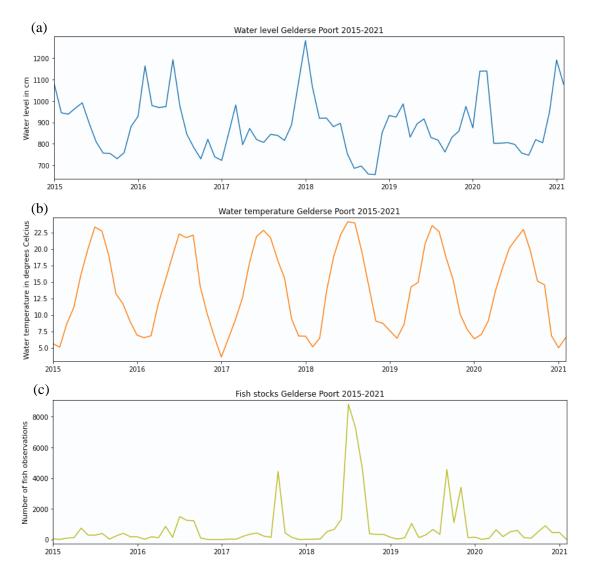


Figure 9a-c: Water level, water temperature, and fish stocks Gelderse Poort 2015-2021. (a) Mean water level per month in cm of the Rhine at measuring station Lobith in the Gelderse Poort from January 2015 to February 2021. (b) Mean water temperature per month in degrees Celsius of surface water of the Rhine at measuring station Lobith in the Gelderse Poort from January 2015 to February 2021. (c) Number of recorded fish observations per month in the Gelderse Poort from January 2015 to February 2021.

The relationship between the number of otter observations and habitat variables water level, water temperature, and fish stocks was investigated by means of a generalised instrumental variables regression model (Fig. 10). The instrumental variables regression model showed that there was no significant effect of water level on inland otter observations, estimated by instrumental variables regression coefficient β_1 with standard error 0.286 ± 0.193 (t-test of coefficients, t = 1.48, P = 0.143), as well as of water level on floodplain otter observations $9.938 \cdot 10^{-5} \pm 1.785 \cdot 10^{-2}$ (t-test of coefficients, t = 0.006, P = 0.996). Similarly, the model indicated that there was no effect of water temperature on inland otter observations -0.502 ± 0.725 (t-test of coefficients, t = -0.69, P = 0.491) or on floodplain otter observations 0.131 ± 0.069 (t-test of coefficients, t = 1.905, t = 0.061). Finally, fish stocks appear to have no effect on inland otter observations -0.040 ± 0.023 (t-test of coefficients, t = -1.789, t = 0.078) or floodplain otter observations -0.001 ± 0.010 (t-test of coefficients, t = 0.099, t = 0.922). Therefore, the null hypothesis for the absence of causality could not be rejected.

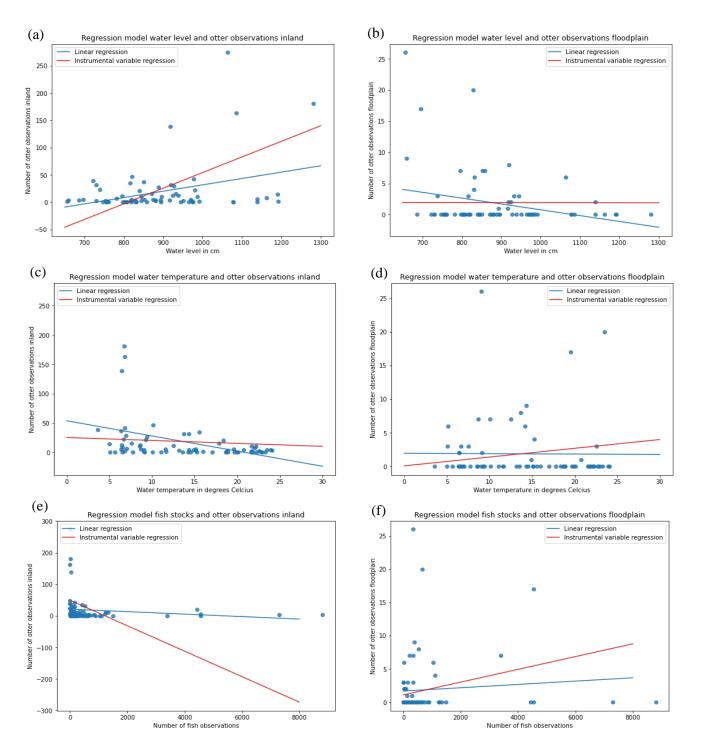


Figure 10a-f: Regression models of habitat variables and otter observations. Subplots present otter observation data, either inland (left column) or in floodplains (right column), against water level in cm (a-b), water temperature in degrees Celsius (c-d), or number of fish observations (e-f). Each frame contains plots of the standard regression model (blue), with biased regression coefficient β_1 , and the generalised instrumental variables regression model (red), with unbiased regression coefficient β_1' . None of the unbiased regression models showed significant causal effects of habitat variables on otter observations (t-test of coefficients, P > 0.05 for all conditions). (a-b) With increasing water levels, an increase in inland otter observations ($\beta_1 = 0.136 \pm 0.039$; $\beta_1' = 0.286 \pm 0.193$) and increase in floodplain otter observations ($\beta_1 = -0.010 \pm 0.004$; $\beta_1' = 9.938 \cdot 10^{-5} \pm 1.785 \cdot 10^{-2}$) is observed. (c-d) With increasing water temperature, a decrease in inland otter observations ($\beta_1 = -2.678 \pm 0.780$; $\beta_1' = -0.502 \pm 0.725$) and increase in floodplain otter observations ($\beta_1 = -0.010 \pm 0.087$; $\beta_1' = 0.131 \pm 0.069$) is observed. (e-f) With increasing numbers of fish observations, a decrease in inland otter observations ($\beta_1 = -0.003 \pm 0.0004$; $\beta_1' = -0.001 \pm 0.010$) is observed.

Discussion

The present study investigated seasonal migration patterns of Eurasian otters in floodplains of the Gelderse Poort under the influence of water levels, water temperatures, and fish stocks. To detect temporal movements of the otter population in the Gelderse Poort, the dispersal, seasonality, and causality (related to habitat factors) of inland and floodplain otter observations were examined. The otter population, which was assumably food-limited (Kruuk & Carss, 1996), was expected to migrate between floodplains in summer and inland areas in winter due to periodical changes in water levels and water temperatures that affect fish stocks. During winter, when water levels are high, and water temperatures and fish abundances are low, otter observations were predicted to shift from floodplains to inland areas, while the opposite pattern was expected in summer periods.

Firstly, the observation data did not display any differences in otter dispersal between inland and floodplain areas in spring, summer, and autumn but did show such a difference in winter (Fig. 6). The higher number of inland observations in winter supports the hypothesis of temporal migration to inland areas. However, observation data of the other seasons do not confirm the migration hypothesis. Though the number of observations in summer was higher in floodplains than inland, which is in line with the hypothesis, this difference proved nonsignificant. Similarly, otter observations, both inland and in floodplains, appeared unrelated to seasons (Fig. 7). While the pattern of inland and floodplain observations seems to oscillate over seasons, the hypothesis of seasonality for otter movements remains unconfirmed. These results could possibly be explained by several biases in the data. For instance, the relatively high number of observations in winter may be a result of extended field patrols by CaLutra volunteers, who are mainly active during winter. Also, as otters search for territory and mates during winter periods (October to March), marking prominent structures in their habitat with spraints, otter activity is generally higher in winter periods, leading to detectability biases (Kuiters et al., 2019). These type of observation biases may lead to invalid results and could conceal evidence of seasonal otter movements.

Other biases that may have impacted the outcomes of statistical tests result from monitoring defects. For instance, recording times of camera traps and the amount of time spent on field patrols were undocumented so that a correction for monitoring time was impossible. Of course, since the datasets of NDFF and NEM included observations from field patrols executed by volunteers and random observations registered at portals like Waarneming.nl, one cannot expect such monitoring documentations. Still, since there is no way to know how much time was spent on monitoring during each season, it is impossible draw solid conclusions based on this data. Additionally, camera traps were not spread evenly over inland and floodplain areas and field patrols probably took place more inland, as floodplains flood completely at high water levels and inland areas are generally more easily accessible. As a result, the observation records were obviously skewed toward inland observations, as $n_{\rm IL} = 1345$ and $n_{\rm FP} = 137$. Furthermore, the sample size of the otter population in the Gelderse Poort, which is currently estimated at about 5 individuals, is probably too small to detect any significant differences in otter observations between inland and floodplain areas or between seasons (Kurstjens et al., 2009; van der Spek, 2017). Complementary research in areas with larger otter populations, like Friesland and Overijssel, could lead to more valid results and may display seasonal migration patterns more clearly.

Secondly, the generalised instrumental variables regression model generated no evidence of causality for the effects of water levels, water temperatures, and fish stocks on otter observations. Though coherent seasonal patterns of water levels, water temperatures, and fish stocks occurred (Fig. 8; Fig. 9), these factors did not significantly affect otter movements in and out of floodplains (Fig. 10). Nevertheless, trends that support the hypothesis of temporal otter migration in floodplains were observed. On the one hand, for higher water levels, lower temperatures, and lower numbers of fish, the number of inland otter observations increased. On the other hand, the number of floodplain observations increased at higher water temperatures and with higher numbers of fish. For all of these variables, the unbiased instrumental variables regression coefficients β'_1 revealed stronger effects of the habitat

variable on otter observations than was indicated by the biased standard regression coefficients β_1 . The only result that was not in line with the expected movement patterns was the effect of water level on floodplain otter observations, as the instrumental variables model indicated that otter observations in floodplains increased slightly at higher water levels. This unexpected result is possibly caused by the limited number of floodplain observations ($n_{FP} = 137$).

The lack of evidence for causal effects of water levels, water temperatures, and fish stocks on otter observations may be the result of inconsistencies and biases in the datasets, but it may also point toward other explanations for possible otter migration. For instance, the amount and intensity of human disturbance may be of greater influence on otter movements than fish densities (Prenda & Granado-Lorencio, 1996). Furthermore, as water levels do not only affect the density of prey but also impact the availability of other resources and shelters, it is possible that the availability of resources and shelter influence temporal otter movements more than fish densities do (Kruuk, 2006; Kruuk et al., 1989; Ruiz-Olmo et al., 2002; Ruiz-Olmo et al., 2011). For further research it could thus be valuable to construct flood maps of the area in more detail, i.e., also for inland areas and from recorded water levels at multiple measuring points, and to study the habitat suitability of non-flooded patches. Another alternative explanation for seasonal otter movements could be the social interaction between individuals of otter populations. Migratory behaviours that are led by social components, such as breeding, rearing pups, expanding territory, and intraspecific competition behaviours, may have more significant effects on seasonal movement patterns than environmental factors (Garshelis & Garshelis, 1984; Sjoasen, 1997). Seasonal movements may also differ between male and female otters (Kuiters et al., 2019; Sjoasen, 1997). Thus, charting the sex of individual otters in the study area by means of DNA sequencing may help to understand observed movement patterns. Further research on social variables as incentives for otter movements may contribute to a better understanding of otter seasonal migration patterns.

Although this study cannot confirm seasonal migration between inland areas and floodplains of the Gelderse Poort, movements in and out of floodplains due to fluctuating water levels are still suspected. With this assumption in mind, some specific areas in the Gelderse Poort become of particular interest for otter conservation efforts and tackling traffic bottlenecks. First of all, as otters appear to move between inland areas and floodplains, otters need to cross the winter dikes that separate these areas. Especially around December and June, when these movements likely occur, precautions around winter dikes to prevent otter road kills could be valuable. Though it is impossible to place fauna passages through winter dikes, considering their flood protecting function, other methods to reduce road-kill mortality, such as speed-limiting measures and mowing grass at roadsides, could contribute to protecting otters that cross winter dikes periodically (Kuiters & Lammertsma, 2014; Niewold & Beekers, 2011). Secondly, as otters likely move to inland areas during winter, thus entering areas with increased human activity, efforts to reduce the impact of human disturbances on otters in these areas could be favourable. Examples of reducing human impact are implementing speed-limiting measures, confining accessibility of certain areas, restricting fishing practices, and setting rules for keeping dogs on a leash during specific time periods, in this case, during winter (Clavero et al., 2010; Kurstjens et al., 2009). Complementary research on inland otter dispersal could contribute to defining which inland areas are of particular importance for otter populations during winter and where such precautious measures would be beneficial.

In conclusion, there are signs that indicate temporal otter movements between floodplains and inland areas, but defining such periodical movements and discovering their underlying incentives remains a challenging task. This study presents a framework for future research on otter migration patterns and provides insights on overcoming the challenges of long-term observational studies, especially for handling inconsistent data and unobserved biases. Complementary future research on otter movement patterns could continue to improve the efficiency of conservation efforts for enhancing otter dispersal and boosting the population's genetic diversity. While there is a long way to go to secure the long-term viability and stability of the Dutch otter population, conservation initiatives remain inexhaustibly committed to protecting this iconic freshwater species, so that the Eurasian otter will hopefully continue to flourish and roam the Dutch wetlands once again.

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Appendices

Appendix I: otter observation data per season

Season_Year S		illiana Otter Observations	Floodplain Otter Observations	Absolute difference
Winter 2015 V	Winter	0	3	3
Spring 2015 S	Spring	13	0	6
Summer 2015 S	Summer	1	0	1
Autumn 2015 A	Autumn	4	0	4
Winter 2016 V	Winter	41	0	41
Spring 2016 S	Spring	50	0	50
Summer 2016 S	Summer	11	0	11
Autumn 2016 A	Autumn	86	0	86
Winter 2017 V	Winter	99	3	96
Spring 2017 S	Spring	48	7	44
Summer 2017 S	Summer	2	0	2
Autumn 2017 A	Autumn	83	0	83
Winter 2018 V	Winter	618	6	612
Spring 2018 S	Spring	174	10	164
Summer 2018 S	Summer	17	0	17
Autumn 2018 A	Autumn	10	52	42
Winter 2019 V	Winter	32	12	20
Spring 2019 S	Spring	14	7	7
Summer 2019 S	Summer	10	24	14
Autumn 2019 A	Autumn	0	11	11
Winter 2020 V	Winter	11	0	11
Spring 2020 S	Spring	0	2	2
Summer 2020 S	Summer	0	0	0
Autumn 2020 A	Autumn	5	0	5
Winter 2021 V	Winter	16	0	16

Appendix II: variables data per month

Month_Year	Snowfall (mm)	Painfall (mm)	Total precipitation (mm)	Average water level (cm)	Average Water Temperature (oC)	Average O2 concentration (mg/L)
January 2015	3110W14II (11111)	46.74		1077.24	5.63	
February 2015	24			944.28	5.09	
March 2015	0	26.00	26.00	937.81	8.62	13.15
April 2015	0			965.41	11.09	
May 2015	0			991.02	16.01	
June 2015	0			894.95 808.91	19.92 23.29	
July 2015 August 2015	0			756.64	23.29	
September 2015	0			754.83	18.90	
October 2015	0			730.54	13.17	
November 2015	15	32.38	47.38	758.49	11.65	11.50
December 2015	18	13.71	31.71	880.32	9.03	11.80
January 2016	33			927.89	6.91	
February 2016	15			1162.81	6.52	
March 2016	8			977.77	6.81 11.55	
April 2016 May 2016	0			969.12 973.07	15.11	
June 2016	0			1191.88	18.74	
July 2016	0			975.59	22.26	
August 2016	0	19.90	19.90	843.75	21.69	9.00
September 2016	0	16.70	16.70	781.97	22.08	8.61
October 2016	0			729.66	14.29	
November 2016	1			820.73	10.10	
December 2016	1			738.78	6.68 3.59	
January 2017 February 2017	69 4			722.75 850.26	6.37	
March 2017	0			980.79	9.23	
April 2017	0			795.95	12.52	
May 2017	0	54.10	54.10	871.38	17.83	10.01
June 2017	0	77.06	77.06	819.24	21.86	9.09
July 2017	0	48.62	48.62	806.46	22.81	
August 2017	0			843.75	21.69	
September 2017	0			839.05	18.35	
October 2017 November 2017	22			815.73 887.57	15.53 9.38	
December 2017	27			1084.97	6.77	
January 2018	1			1280.60	6.74	
February 2018	35	25.14	60.14	1064.24	5.12	14.00
March 2018	30	28.06	58.06	918.52	6.45	12.40
April 2018	0			919.99	13.71	
May 2018	0			879.83	18.87	
June 2018	0			895.58 754.03	22.18 24.10	
July 2018 August 2018	0			685.62	23.93	
September 2018	0			696.41	19.56	
October 2018	0			658.92	14.29	
November 2018	20	9.20	29.20	656.12	9.03	8.51
December 2018	0			852.86	8.69	
January 2019	113			931.56	7.56	
March 2019	43			924.43 986.02	6.43	
April 2019	3			831.29	8.52 14.21	
May 2019	C			892.93	14.21	
June 2019	C			915.89	20.75	
July 2019	C	148.20	148.20	829.26	23.52	9.32
August 2019	C			817.02	22.59	9.03
September 2019	C			761.74	18.65	
October 2019	C			830.25	15.26	
November 2019 December 2019	42			859.00 973.76	10.06	
January 2020	43			874.27	7.76 6.34	
February 2020	42			1138.33	7.00	
March 2020	30			1139.01	9.09	
April 2020	C			802.25	13.56	
May 2020	C	121.30	121.30	802.85	17.03	
June 2020	C			805.54	20.13	
July 2020	C			796.94	21.58	
August 2020	C			756.82	22.94	
September 2020	0			746.69	19.65	
October 2020 November 2020	0			819.31 804.67	15.11	
December 2020	249			950.50	14.53 6.79	
January 2021	673			1190.21	4.99	
February 2021	159			1077.51	6.51	

Month Year	Otter Observations Inland (nr)	Otter Observations Floodplain (nr)	Fish Observations (na)
Month_Year January 2015	Otter Observations inland (III)		
February 2015	0		50
March 2015	12		_
April 2015	0	0	
May 2015	1	0	738
June 2015	0	0	283
July 2015	0		
August 2015	1		550
September 2015	0		
October 2015	3		233
November 2015 December 2015	4		101
January 2016	29		115
February 2016	8		27.5
March 2016	42	0	
April 2016	5	0	119
May 2016	3	_	999
June 2016	1		2
July 2016	0		1133
August 2016	10 7		
September 2016 October 2016	32		1251
November 2016	47		
December 2016	23		
January 2017	39	0	
February 2017	37	0	26
March 2017	22	0	15
April 2017	11		
May 2017	15		545
June 2017	0		72.1
July 2017	0		
August 2017 September 2017	21		111
October 2017	35		
November 2017	27		123
December 2017	163	0	
January 2018	181	0	12
February 2018	274		17
March 2018	139		
April 2018	32		323
May 2018 June 2018	3 10		
July 2018	3		1552
August 2018	4		0010
September 2018	5	17	
October 2018	4	9	374
November 2018	1	26	339
December 2018	5		
January 2019	15		113
February 2019	12 10		
March 2019 April 2019	0		113
May 2019	4		1045
June 2019	4	. 1	
July 2019	4	20	
August 2019	2	3	
September 2019	0		T330
October 2019	0		1105
November 2019	0		3333
December 2019 January 2020	5		124
February 2020	6		147
March 2020	0		0
April 2020	0		/0
May 2020	0	0	
June 2020	0		302
July 2020	0		332
August 2020	0		111
September 2020	0		
October 2020 November 2020	0		510
December 2020	2		093
January 2021	14		440
February 2021	0		
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