



# Definition of Favourable Conservation Status for European Water Vole *Arvicola amphibius*

## Defining Favourable Conservation Status Project

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# Acknowledgements

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This definition substantially draws on an unpublished report prepared for Natural England and completed in 2021 by the authors.

The favourable values were developed utilising species distribution modelling completed for Natural England in 2023 by Dr Frazer Coomber of The Mammal Society.

Members of the GB Water Vole steering group, in particular Mike Dean and Merryl Gelling.

Members of the Natural England Technical Steering Group, in particular Andy Brown, Louise Denning and Dawn Phythian.

The Defining Favourable Conservation Status project team at Natural England.

# Executive summary

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This document sets out Natural England's view on Favourable Conservation Status for Water Vole in England.

Favourable Conservation Status is the minimum threshold at which we can be confident that the species is thriving in England and is expected to continue to thrive sustainably in the future.

This definition has been produced following the Natural England approach to defining Favourable Conservation Status described in the guidance document [Defining Favourable Conservation Status in England](#).

Section 1 of this document describes the species covered by this definition and its ecosystem context.

Section 2 specifies the units used to describe the three Favourable Conservation Status parameters. These are:

- Natural range and distribution (where the species occurs).
- Population (how many there are of the species).
- The extent and quality of habitat supporting the species population.

Section 3 outlines the evidence considered when developing the definition. This definition is based on the best available evidence on the ecology of Water Vole. The evidence covers the current situation, historical changes and possible future changes.

Section 4 sets out the conclusions on the favourable values, that is the value for each of the three parameters when the species has achieved Favourable Conservation Status.

This document does not include any action planning, or describe actions, to achieve or maintain Favourable Conservation Status. These will be presented separately, for example within strategy documents.

## Summary Definition of Favourable Conservation Status

Water Voles are small mammals that typically live along vegetated banks of rivers, streams, ditches, ponds and lakes, and also in terrestrial wetland habitats. They prefer to live alongside relatively deep, slow-flowing water with stable water levels. They excavate extensive burrow systems in the earth banks of these water bodies in which to sleep, nest and evade predators. They feed on grasses, sedges, rushes and other waterside vegetation. Water Voles live in colonies which, in favourable situations, may comprise hundreds of individuals.

Female Water Voles may have up to five litters of six young between April and October. However, average life expectancy is six months to a year, with populations declining by up to 70% over winter. Predation rates are naturally high, even under ideal conditions, with

Water Voles predated by a range of species including various raptors, mustelids, Fox, Grey Heron and large predatory fish.

Water Voles have undergone one of the most severe declines in both numbers and distribution of any wild mammal in Britain during the 20th century due to a combination of habitat loss, degradation and fragmentation and predation by the invasive non-native American Mink *Neogale vison* (formerly known as *Neovison vison*) (hereafter, Mink). Populations declined by 90% between 1995 and 2018, following earlier periods of decline, and distribution has declined by approximately 95% since the beginning of the 20<sup>th</sup> century.

To achieve Favourable Conservation Status populations of Water Voles would have to increase significantly to recover historical losses and occupy their natural range and distribution. Favourable Water Vole populations in England need to consist of viable colonies distributed throughout the natural range. Distribution would require at least 184,000 km of suitable linear riparian habitat in England and sustained presence of populations in terrestrial wetland habitats. The favourable range and distribution is considered to be all hectads (10 km grid squares) in England with suitable habitat for Water Vole, a total of 1,163 hectads. Favourable status would require an expansion of the current range and distribution from 615 hectads.

**Table 1** Confidence levels for the favourable values. © Natural England 2025; This table is published under the [Non-Commercial Government Licence v2.0](#) for public sector information.

<b>Favourable Conservation Status parameter</b>	<b>Favourable value</b>	<b>Confidence in the favourable value</b>
Range and distribution	Populations of Water Vole are present in 1,163 hectads, a near doubling of the current number of occupied hectads (615).	Moderate
Population	<p>A favourable Water Vole population in England consists of viable colonies distributed across 184,000 km of suitable linear riparian habitat in England.</p> <ul style="list-style-type: none"> <li>- A viable Water Vole colony is defined as Water Voles being present at medium or high relative density over a 2km stretch or more (as measured by number of latrines)</li> <li>- Each colony must have functional connectivity to other Water Vole colonies within 2km.</li> </ul> <p>Each wetland area with suitable habitat and more than 1 ha in area should have Water</p>	Low

	Voles present in two consecutive summer seasons and connectivity within 2km to other wetland or linear riparian habitat.	
Supporting habitat	At least 184,000 km of suitable riparian habitat in optimal or good condition to support the favourable population. Habitats need to be well-connected to allow for dispersal and recolonisation.	Low

As of September 2025, based on a comparison of the favourable values with the current values, Water Vole is not in Favourable Conservation Status. Note, this conclusion is based solely on the information within this document and is not on a formal assessment of status based on comprehensive monitoring data.

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# About the Defining Favourable Conservation Status project

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Natural England's Defining Favourable Conservation Status (DFCS) project is defining the minimum threshold at which habitats and species in England can be considered to be thriving. Our Favourable Conservation Status (FCS) definitions are based on ecological evidence and the expertise of specialists.

Through setting our ambition and aspiration for species and habitats, our definitions will inform decision making and actions to achieve and sustain thriving wildlife.

Our Definitions will be embedded into delivery of the UK government's Environmental Improvement Plan, through the Nature Recovery Network, biodiversity net gain and environmental land management schemes.

Conservation bodies will use them to inform their work, including management planning for the land they own. Businesses will have a clear understanding of how their work impacts nature recovery and how they can help contribute to achieving thriving nature.

By considering the evidence for FCS, decisions will be more confident and strategic, with an understanding of their contribution to, or impact on, the national ambition.

# 1. Species definition and ecosystem context

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## 1.1 Species definition

European Water Vole *Arvicola amphibius* (Linnaeus 1758)

Formerly *A. terrestris*.

Water Voles in England and Wales largely derive from an eastern European glacial refugium, genetically distinguishing English and Welsh Water Vole populations from those in Scotland, which are more closely related to Water Voles from western Europe (Piertney and others 2005). However, the ‘Scottish’ haplotype has been identified as far south as the Humber (Brace and others 2016).

## 1.2 Species status

### Red list status

An assessment of the risk of extinction.

**Global:** Least Concern (Batsaikhan and others 2016)

**European:** Least Concern (Temple and Terry 2007)

**GB:** Endangered (Mathews and Harrower 2020)

**England:** Endangered (Mathews and Harrower 2020)

### Conservation status

- UK Biodiversity Action Plan Priority Species 2007.
- Species of Principal Importance under Section 41 of the Natural Environment and Rural Communities (NERC) Act 2006.

## 1.3 Life cycle

In the spring, female Water Voles form a series of contiguous, non-overlapping territories marked by latrines (piles of droppings) and become highly territorial with other females. Males are less territorial, holding territories that are both larger and which overlap with female territories. They will, however, fight with other males over access to females (Strachan and others 2011).

Mating takes place in early spring, with the first young born in March/April, and continues to October where weather conditions are suitable. Female Water Voles may bear up to five litters of, on average, six young. Young leave the nest and disperse at about 22-28 days old when the next litter is born. The average dispersal distance is 2 km. Sexual maturity is typically reached after the first winter but, rarely, early season young may breed in the same autumn (Strachan and others 2011).

Water Voles do not hibernate but become less active over winter and spend a larger proportion of time in nest chambers, often shared with co-nesting females from the same colony. The average life expectancy is six months to a year. Predation rates are naturally high even under ideal conditions, with further losses of up to 70% over winter, particularly affecting dispersing juveniles. Individuals weighing under 170 g are unlikely to survive the winter (Strachan and others 2011).

Water Vole populations vary in size and structure according to habitat. Populations may comprise hundreds of individuals in lowland England, whereas upland populations tend to be smaller and divided into smaller colonies. Where individual colonies in any habitat type are spatially connected, they may form a metapopulation, where loss of one colony will be replaced by dispersing individuals from another, thereby promoting long-term stability.

## 1.4 Supporting habitat

In England, Water Voles are typically associated with wetland ecosystems such as rivers, canals, terrestrial wetland habitats, ponds, lakes and ditches. They show a preference for relatively deep, slow-flowing water with stable water levels and steep (45° or more), uncompacted, earth or silt banks into which burrows are easily dug. Minimal shading by trees or shrubs is important to allow the development of emergent vegetation or reedbeds with at least 60% cover to provide food and cover from predators. Rocky, gravelly and/or spate-prone rivers with sudden and forceful flows are less favoured due to the lack of burrowing opportunities and episodic flooding. Headwaters are known to be used extensively by Water Voles and may comprise a refuge where populations are under threat (Strachan 1997; Strachan and others 2011).

Habitat preferences are influenced by a range of factors including the characteristics of specific habitats, distribution of predators and the proximity of other Water Vole colonies. Water Voles may also be found in less typical locations. In urban areas this may include engineered rivers where sufficient in-channel and emergent vegetation is present. There is some limited evidence to suggest urban areas may also be avoided by Mink, implying urban areas may offer some refuge from predation by this particular species (Brzeziński and others 2012; Brzeziński and others 2018). Increased breeding success of waterfowl in urban areas avoided by mink has also been recorded (Brzezinski and others 2012). However, domestic predators and other factors will have bearing on this potential benefit. Otters may also prey on Water Voles, although likely less effectively than Mink (Dean 2021).

The value of urban areas in supporting Water Vole populations should not be discounted though, particularly in the context of connectivity with and between rural habitats. A study using data in the NBN Atlas records reported presence in 28 out of 64 official cities in the UK, with urban Voles representing 5% of all records (Leivesley and others 2021). Given sufficient vegetation and opportunity to burrow, Water Voles may also survive in relatively polluted water courses (Tansley 2021, pers. comm.). Water Voles are predominantly herbivorous, eating a broad range of riparian vegetation including reeds, grasses, rushes and sedges, often leaving a nibbled “lawn” at the entrance to burrows and berries and other fruits in the autumn. Their winter diet is supplemented with the roots and bark of broadleaved woody species such as willow, and the bulbs, roots and rhizomes of herbaceous species (Strachan and others 2011). Occasionally, invertebrates, small fish, molluscs and crustaceans, depending on availability, season and breeding status, will also be consumed, particularly by pregnant females (Strachan 1997).

Water Voles in England typically inhabit networks of burrows at or above the water’s edge. Above-ground nests of woven vegetation may sometimes be formed in dense tussocks of grasses or sedges, particularly when the habitat is not suitable for burrowing, such as in reedbeds. Burrows and above ground runs in dense vegetation are typically formed within 2-5 metres of the river’s edge; consequently, the extent of riparian habitat from the riverbank is important with regards to both the supply of a diverse food source and the resilience of colonies to predation. Tall, dense marginal herbaceous vegetation provides optimum conditions. Evergreen and woody species provide winter food sources but over-shading by trees, scrub or bramble can create suboptimal conditions by limiting the abundance of both bankside and in-channel vegetation. Tidal rivers, saltmarshes and estuarine habitats may also be utilised, particularly where sufficient reedbed habitat provides stable conditions and food sources, and Water Voles have been recorded on rivers in Essex experiencing 2-3 m or more tidal range (Tansley 2021, pers. comm.).

Reedbeds, away from main channels, are regarded as good refuges from Mink (Carter and Bright 2003) due to the difficulty for Mink to hunt non-linear populations to extinction. Large reedbeds form a useful part of a resilient landscape for Water Voles, particularly in a well-connected wetland habitat. Water Vole populations in such habitats may serve as a source for metapopulations in the wider landscape where these are spatially connected to the wetland habitat (Macpherson and Bright 2010, 2011). However, there is uncertainty over how useful this habitat is over winter when reeds have died back.

Island refuges of dense scrub or bramble thickets above the flood line in floodplains have been found to be important during major flooding events, where Water Voles would otherwise drown if their fur became waterlogged (Roberts 2021, pers. comm.).

Across continental Europe fossorial populations of Water Voles (that is, living underground and away from riparian habitat), are more common than their riparian counterparts, but there are confirmed and substantial fossorial populations on the mainland and some islands of Scotland. Fossorial populations are likely to have once been widespread in England as fossil evidence from the Mesolithic suggests Water Voles in Britain were originally associated with terrestrial rather than aquatic habitats (Yalden 2006). It is

thought that persecution in the 18<sup>th</sup> and 19<sup>th</sup> centuries (they can be significant crop pests), combined with changes in land use type and intensity may have largely cleared fossorial Water Voles from England (Cooper 2021).

Anecdotal evidence from the Wildlife Trusts and others suggests that within the last 30 years there have been fossorial populations, or Voles exhibiting fossorial behaviours, in Yorkshire, the Peak District, Newcastle upon Tyne, Brownsea Island and Cambridgeshire (Cooper 2021). More recently, a small group of juveniles were found in Kent in 2016 on grassland some distance from any waterbody, of an age that suggests they could have been born there (Cooper 2021).

It is unclear whether fossorial behaviour is generally precluded by land use and habitat availability in England, whether riparian habitats are preferentially selected due to abundance, or whether some other factor(s) determines fossorial behaviour. As no dedicated fossorial surveys are known to have been carried out, it is also possible that such behaviour simply has not been recorded or has been overlooked, due to confusion with the similar behaviours of Rats and Moles in these habitats. Given the lack of evidence and understanding of fossorial Water Vole populations in England, this definition focusses on Water Voles inhabiting terrestrial riparian and wetland ecosystems. This will be updated should new evidence come to light.

## 1.5 Ecosystem context

Globally, the range of Water Voles is thought to extend over much of Europe and Russia, from France and Great Britain in the west, to the Lena Basin and Lake Baikal in Siberia (Russia), and from north of the Arctic Circle to Iran and the Middle East in the south (Batsaikhan and others 2016). They occupy a broad range of habitats at elevations between sea level and 3,210 m above sea level, including wetland habitats, pasture, boreal and temperate forests, semi-deserts, irrigated land, and mountain forests, grasslands and steppes, and are important grazers and prey species in these areas (Batsaikhan and others 2016). Populations appear to be less dense in aquatic habitats than terrestrial habitats in these areas (Stewart and others 2018).

Water Voles are present across England, Wales and Scotland, including the Isle of Wight and Anglesey, but absent from Ireland, the Isle of Man and some Scottish islands.

Water Voles are ecosystem engineers and a keystone species, influencing the riparian landscape in Britain, the spatial dynamics of plant communities and the composition of ecological communities.

Through grazing, the deposition of nitrogen-rich faeces and burrowing activity Water Voles play a key part in plant community structure and composition/diversity, and thus the diversity and complexity of higher trophic levels. Grazing activity reduces competition between plant species and so increases the diversity of wetland plant communities, and burrowing activity throughout a territory supports the cycle of nitrogen back to the soil, supporting vigorous plant growth (Bryce and others 2013). The burrow systems of Water

Voles increase soil aeration and microbial activity in the vicinity of the burrow which, in combination with natural management of bankside vegetation and distribution of seed and root material by Water Voles, results in greater habitat heterogeneity (Bryce and others 2013). In areas where Water Vole populations are thriving, this effect may be realised at the landscape scale due to the natural extinction-colonisation dynamics of Water Vole metapopulation structure, whereby the movements of colonies create a patchwork of habitats in different successional stages (Bryce and others 2013). The decline of Water Voles in Great Britain may have reduced habitat heterogeneity and created greater abundance of dominant grass species, resulting in lower community diversity than comparable sites occupied by Water Voles (Bryce 2006).

Disused burrow systems offer refugia for several other species including other small mammals, reptiles, amphibians and insects. The eventual erosion and collapse of extensive burrow systems alters river dynamics by creating scalloped edges that serve as new habitat for additional species such as bank-nesting birds and burrowing insects, as well as diversifying river flow patterns (Gow 2018). Their effects have been likened to those of Beavers in influencing the habitats of floodplains, though on a smaller scale.

Water Voles are a known prey component for a range of species including various raptors, mustelids such as Stoat *Mustela erminea* and Weasel *Mustela nivalis*, Fox *Vulpes vulpes*, Grey Heron *Ardea cinerea* and large predatory fish such as Pike *Esox lucius*. Crucially, a more recent and now key predator of Water Voles is the introduced Mink which has contributed to the catastrophic decline of Water Vole in the latter part of the 20<sup>th</sup> century (Jefferies and others 1989).

## 2. Units

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### 2.1 Natural range and distribution

Hectad (10 km square).

This unit has been used since 2009 in the National Water Vole Database and Mapping Project, consistent with original UK BAP target metrics, and will allow comparative analysis with an extensive, annually updated, national dataset.

### 2.2 Population

Relative density estimates of populations per kilometre for linear habitats. Many studies do not record population numbers but are based on relative density estimates.

Relative population size is indicated by the number of latrines found during a survey (Table 2). Although it is not possible to make robust estimates of absolute numbers of animals from latrine counts, they do provide relative indices of activity (Dean and others 2016).

**Table 2.** Guide to relative population density taken from the number of latrines present at different times of the survey season (taken from Dean and others 2016). This table is published under the [Deed - Attribution-NonCommercial 4.0 International - Creative Commons](#).

	Approximate number of latrines per 100 m of Bankside habitat	
Relative population density	First half of survey season (mid April to end of June)	Second half of survey season (July to September)
High	10 or more	20 or more
Medium	3-9	6-19
Low	≤ 2 (or none, but with other confirmatory field signs)	≤ 5 (or none, but with other confirmatory field signs)

## 2.3 Habitat for the species

Kilometre

Many Water Vole habitats in England are linear and the ranges of Water Voles within these are also generally linear. As such, territories may be measured in terms of length in many instances. On large rivers, this may require measurement along both banks as separate colonies may exist on each bank (Harris and others 1995).

### 3. Evidence

All blocks of evidence are assigned one of three confidence levels (High, Moderate, Low), based on the quality of the evidence, its applicability and the level of agreement.

The matrix in Figure 1 is used to assess the confidence level assigned to blocks of evidence. White = High confidence; Light blue = Moderate confidence and Dark blue = Low confidence.

Limited evidence Strong agreement	Medium evidence Strong agreement	Robust evidence Strong agreement
Limited evidence Medium agreement	Medium evidence Medium agreement	Robust evidence Medium agreement
Limited evidence Weak agreement	Medium evidence Weak agreement	Robust evidence Weak agreement

**Figure 1** Matrix used to assign confidence to blocks of evidence © Mastrandrea and others 2010.

Quality of evidence is defined as follows:

- Robust evidence is that which has been reported in peer-reviewed literature, or other reputable literature, from well-designed experiments, surveys or inventories that shows signs of being applicable generally.
- Medium evidence is that reported from well-designed experiments, surveys or inventories but from only one or a small number of sites, with uncertainty over its more general applicability, or is correlational or circumstantial evidence.
- Limited evidence includes ‘expert opinion’, based on knowledge of ecological factors that plausibly suggest an effect, but there is no circumstantial or direct evidence available.

Agreement is defined as follows:

- Strong agreement is consensus across the literature and amongst those with expertise on the habitat or species.
- Medium agreement is common consensus across the literature and amongst experts but there are some differing papers or reports and/or some differences of opinion.

- Weak agreement is little consensus across the literature and amongst experts and, possibly, many different findings and/or opinions.

### 3.1 Current situation

Since 2008, the National Water Vole Database and Mapping Project (NWVDMP), led by The Wildlife Trusts and delivered by Hampshire and Isle of Wight Wildlife Trust, has collated records of Water Voles and Mink, as well as records of Water Vole reintroduction projects, and is the best available national dataset for these species. The dataset comprises verified records with a minimum accuracy of 100 m, from Local Environmental Records Centres, Wildlife Trusts, People's Trust for Endangered Species and other organisations, and is used to map and understand the changing distribution of Water Voles over time and to assess progress against the original UK Biodiversity Action Plan targets for distribution of Water Voles.

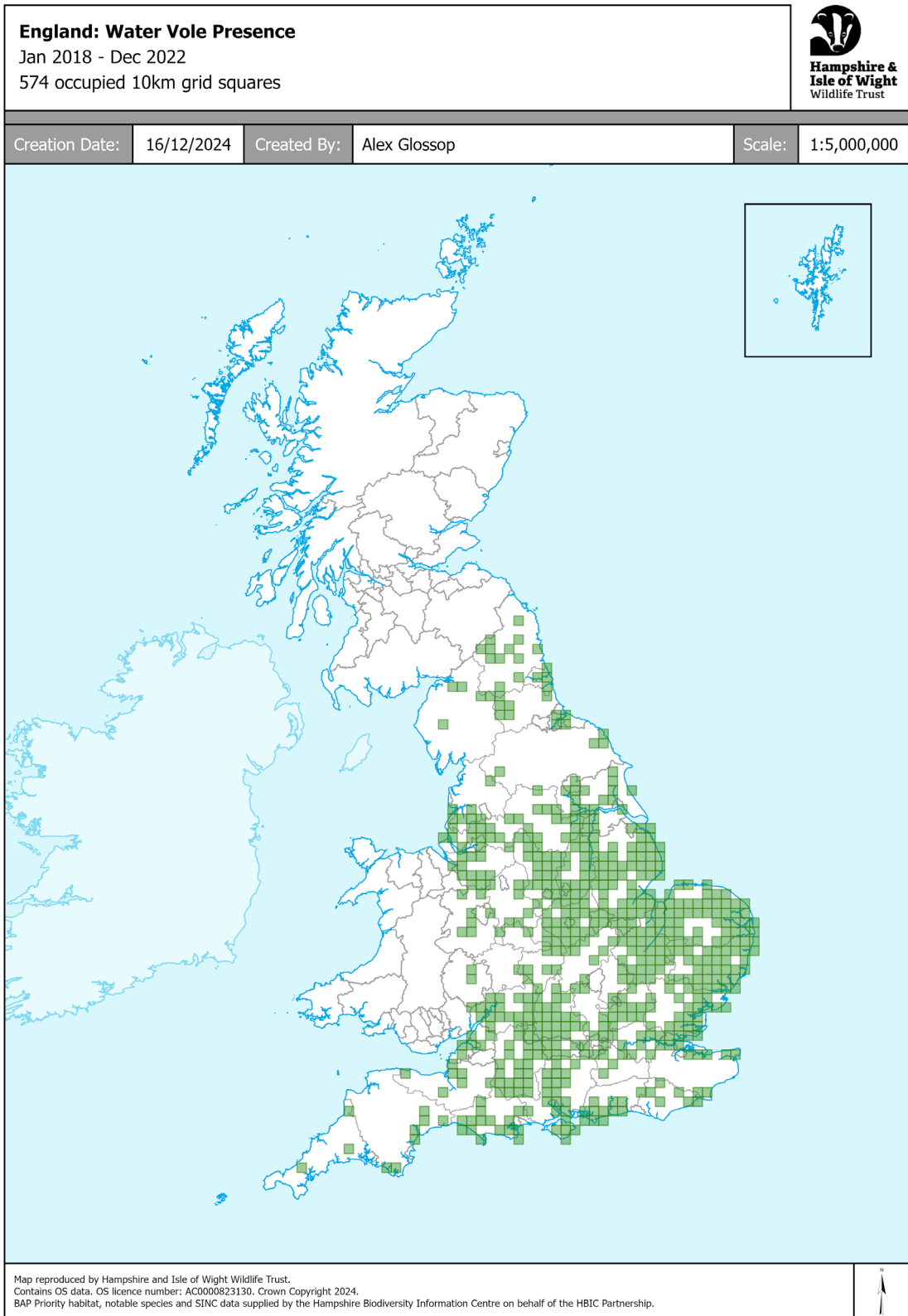
The results of the NWVDMP can be expressed as a suite of maps: distribution maps at hectad scale, and three tiers of alert mapping – Alert Areas, Local Key Areas and Regional Key Areas. Alert Areas are 2 km buffers of water courses/bodies where Water Voles have been recorded as present within the last 10 years. Local Key Areas are Alert Areas 6 km<sup>2</sup> or greater in area and are likely to be important for maintaining the sustainability of local Water Vole populations. Regional Key Areas are Alert Areas 35 km<sup>2</sup> or greater in area and are likely to play a strategic role in the recovery of the species; populations here are more likely to survive the impacts of stochastic events and to persist for more than 40 years.

#### Natural range and distribution

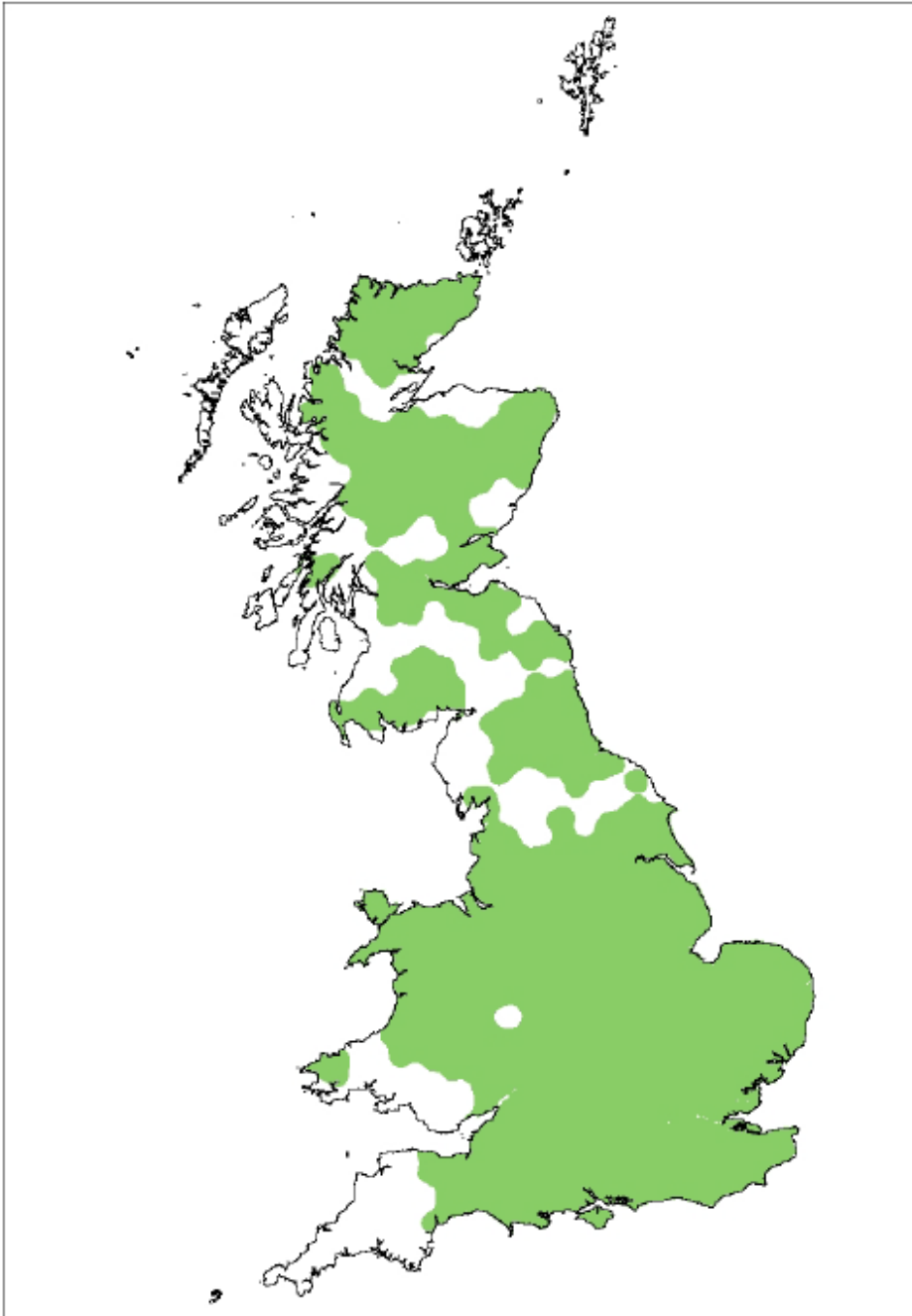
Water Voles have been recorded in 574 hectads in England in the 5-year period between 2018 and 2022 (Figure 2).

It should be noted that likely absence of Water Voles is less frequently recorded and so whilst Glossop (2024) (Figure 2) represents the most comprehensive dataset at present, derived from the NWVDMP dataset of 1042 hectads across Great Britain, 'white' squares cannot confirm absence of Water Vole in that location. However, by grouping records by 5-year period, the impacts of recorder effort are minimised as much as is possible for this type of dataset.

Distribution mapped in this way differs from that published in Mathews and others (2018) (Figure 3), which shows presence across much of England, and absence from areas such as Cornwall and Devon using data from a far longer period and more records. In addition, it used a smoothing methodology, which will assume presence in some squares where there is no underlying data. Together these factors account for the differences between the two maps.



**Figure 2** Glossop, A. (2024) Water Vole distribution in England by hectad 2018-2022. Hampshire and Isle of Wight Wildlife Trust. © Hampshire and Isle of Wight Wildlife Trust 2025. © Crown Copyright and database rights 2025. Ordnance Survey AC0000823130; AC0000851168. © Natural England 2025; Published under the Open Government Licence.  
<https://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/>



**Figure 3** Smoothed British distribution using alternative methodology and dataset, 2005-2016. Data from the National Water Vole Database and Mapping Project, © Fiona Mathews 2025. This map is published under the [Open Government Licence v3.0](https://www.nationalarchives.gov.uk/doc/open-government-licence/version/3) for public sector information.

**Confidence:** Moderate

## Population

Definitive population data for Water Voles is minimal as routine surveys attempt to detect the presence of Water Voles and rarely include counts of individuals. There is no definitive current population estimate for England. Better understood is distribution, but this again is limited by lack of up-to-date, systematic survey at the national level. In addition, as roughly 70% of Water Voles die off over winter, over the course of a year the national population will fluctuate substantially.

Various population estimates have been derived from distribution data. Caution is needed in applying these figures as they rely on modelling of density estimates rather than physical counts, but they represent the best available estimates and use consistent methodologies to enable comparisons to be made over time. Modelling linear populations using the length of suitable habitat within the species range, multiplied by a population density estimate of 4 individuals per kilometre (the median density estimates from published literature) and adjusted for known occupancy rates, produces a figure of 77,200 individuals in England (57,900 -95% CI to 193,000 +95% CI) (Mathews and others 2018), based on data held in the NBN Atlas. Using peak density estimates ranging from 2.4 per 100 m to 14.0 per 100 m (Strachan and others 2011), produces substantially higher estimates of 463,200-2,702,000 individuals (based on Mathews and others estimate of 19,300 km of suitable linear riparian habitat with known occupancy in England). These figures do not account for populations in area-based (that is, non-linear) habitats such as reedbeds, where the population density may be between 25 and 50 individuals per hectare (Strachan and others 2011).

**Confidence:** Low

## Habitat for the species

Modelling completed for Natural England by the Mammal Society in 2022 (see Appendix 1) concluded that there are 184,224 km of riparian habitat with climate, hydrology and terrain suitable for Water Vole in England, significantly more than the 115,000km estimate of Mathews and others (2018). Given that the more recent modelling (Appendix 1) used more recent and robust habitat data layers than Mathews and others (2018) this is taken to be more accurate and is the figure that will be used in the definition.

An equivalent figure is not currently available for non-linear wetland habitats that are suitable for Water Vole. This is due to the variation within the habitats encompassed by the term 'wetlands' and the dynamic and transitional nature of such habitats.

**Confidence:** Low

## 3.2 Historical variation in the above parameters

### Drivers of change

Water Voles have undergone one of the most severe declines in both numbers and distribution of any wild mammal in Britain during the 20th century (PTES 2021). The causes of this decline are considered to be agricultural intensification, afforestation, the naturalisation and spread of non-native Mink, and an increasing human population (Harris and others 1995; Mathews and others 2018). These factors cause decline both as individual drivers and cumulatively (Harris and others 1995).

Following the Second World War, agriculture and silviculture intensified significantly. Widespread tree planting in the north and west of England and the resultant acidification of waterways is thought to have contributed to early declines in Water Vole numbers (Harris and others 1995). Intensification of agriculture resulted in significant loss, degradation, and fragmentation of suitable habitat through wetland drainage, overgrazing, encroachment of cultivated land into riparian habitat, and the degradation of structural and vegetative suitability of banks for burrowing due to poaching by farmed animals (Mathews and others 2018).

Compounding this, the escape and deliberate release of Mink from fur farms since at least the late 1920s led to a rapid increase in the numbers and range of this invasive, non-native species which became well-established along rivers by the 1950s (Dunstone 1993). Mink are a key predator of Water Voles (Carter and Bright 2003) and numerous studies have found their decline to be strongly and negatively correlated with the presence of Mink (for example, Barreto and others 1998a, 1998b; Strachan and others 1998; Woodroffe and others 1998). As well as direct predation it is thought the presence of Mink induces avoidance behaviour in Water Voles due to the perception of predation risk, affecting movement and distribution and precluding recolonisation of areas with Mink presence (Brzeziński and others 2019).

The human population of England and Wales increased by nearly 50% between 1921 and 2021 (ONS 2022), and with this, the demand for additional housing, places of work and places for recreation increased. Water abstraction and pollution have also risen, putting further pressure on already fragile and fragmented habitats. In England, 86% of rivers are still failing to meet 'good ecological status' (GES) (Defra 2020a). Whilst it is unclear how GES, or specific elements of it, may impact habitat suitability for Water Voles, it is pertinent as a broad measure of the decline in the state of England's water environment. There is currently no mechanism for assessing the in-combination effects of multiple planning developments on Water Vole habitats or populations.

Widespread in-combination effects are likely to have reduced the robustness of populations, making them more susceptible to the impacts of disease and stochastic events.

## Natural range and distribution

At the start of the 20<sup>th</sup> century, Water Voles were considered widespread and abundant, being found in suitable aquatic habitat throughout England (Harris and others 1995).

Between 1989 and 1998 The Vincent Wildlife Trust carried out two national Water Vole surveys of 2,970 sites, including 1,926 baseline sites and 1,044 sites with historic records of Water Vole presence. The baseline sites were selected by creating a grid pattern of 18 10km squares within each 100km square across Great Britain. Within each of the selected 10km squares, five sites were chosen using the Ordnance Survey map to ensure a representative sample of the waterways available would be covered. The surveys found a significant decline in distribution of 94% since 1900 (Strachan and others 2000). The NWVDMP has subsequently estimated a further 39% decline in distribution between 2006 and 2022 for Great Britain and 31% for England alone (Glossop and Morse 2024a). Although there was an apparent small increase in distribution since 2013 (McGuire and Morse 2020), the most recent analysis indicates a subsequent recommencement of decline with 652 10km grid squares recorded as occupied between 2018 and 2022, the lowest number since the calculation of the baseline in 2006 (Glossop and Morse 2024a).

Figure 4 shows the cumulative distribution of Water Voles since the late nineteenth century (though the great majority of records are from the mid-1990s onwards): a combined distribution of 1,689 hectads across Great Britain. Clearly, suitable habitat was once widely distributed. This map is useful to illustrate the widespread distribution of potentially suitable habitats and the potential for Water Vole distribution but should not be taken to imply actual distribution at a specific point in time.

Mapping of distribution relies on available data and there are distinct areas of data paucity, notably for Devon, Cumbria and Yorkshire/Lancashire. Data pre-2006 for Devon are absent from the dataset as the species became extinct in this county in the early 2000s due to predation by Mink and loss of suitable habitat (Natural Devon 2014). Similarly, data are absent for Cumbria, though it is known Water Voles were once common throughout the area but have suffered significant declines due to habitat degradation, fragmentation and loss, and predation by Mink (Cumbria Biological Data Network 2010). It is thought that the potential for Water Voles throughout Cumbria does exist, but widespread Mink presence precludes natural recolonisation (Cumbria Biological Data Network 2010). Efforts are underway to source historical and current data to identify past and existing use of suitable habitats in all three areas.

**Great Britain: Water Vole Presence**

Jan 1861 - Dec 2022

1,689 occupied 10km grid squares

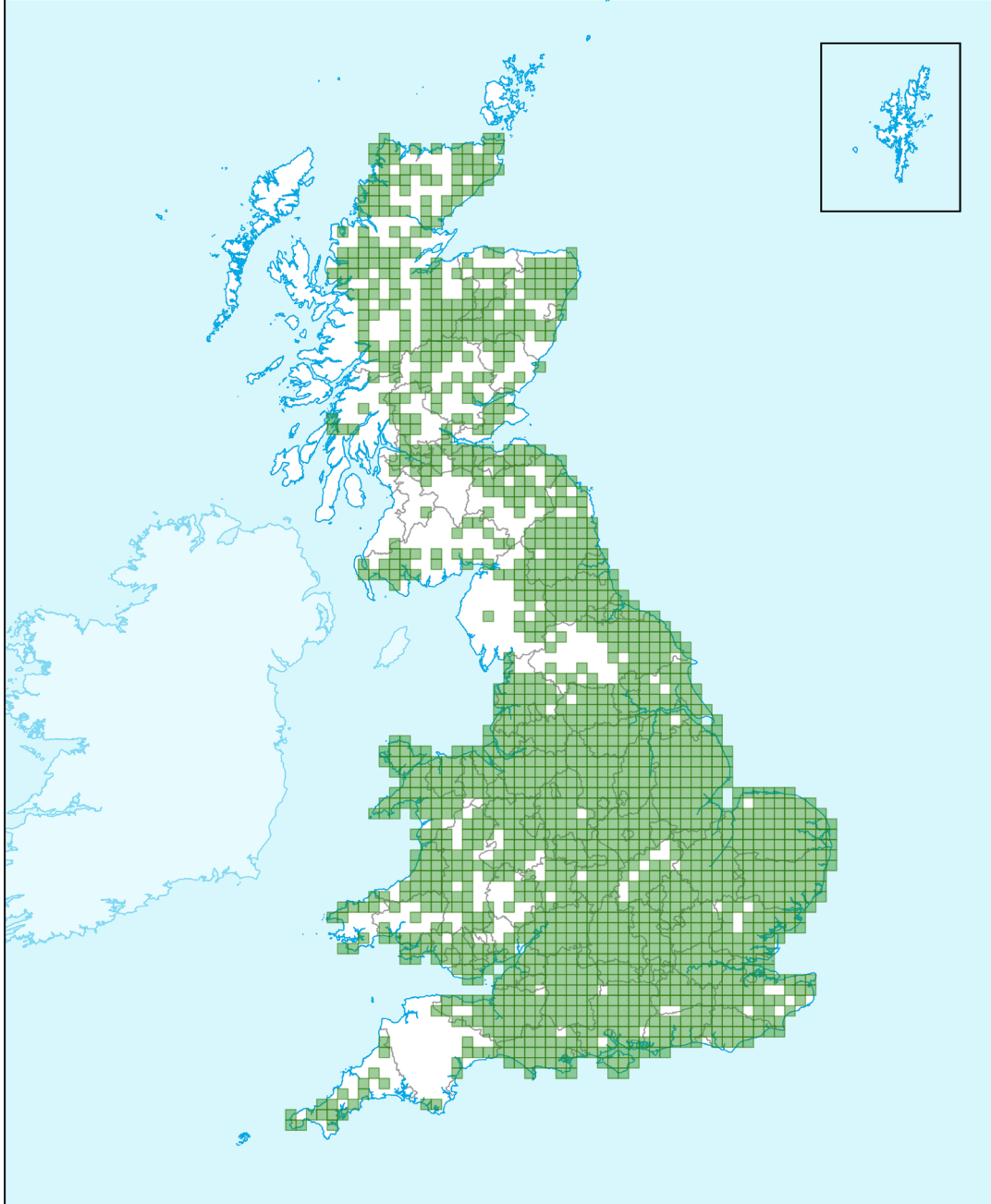


**Hampshire &  
Isle of Wight**  
Wildlife Trust

Creation Date: 18/03/2024

Created By: Alex Glossop

Scale: 1:5,000,000



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BAP Priority habitat, notable species and SINC data supplied by the Hampshire Biodiversity Information Centre on behalf of the HBIC Partnership.



**Figure 4** Cumulative historical Water Vole distribution in England by hectad 1861-2022. From Glossop and Morse (2024b). © Hampshire and Isle of Wight Wildlife Trust 2025. © Crown Copyright and database rights 2025. Ordnance Survey AC0000823130; AC0000851168. This map was produced under [Deed - Attribution-NonCommercial 4.0 International - Creative Commons](#).

**Confidence:** Moderate

## Population

The 1989/90 national survey of Water Voles found there had been a steady decline in Water Voles over the 20<sup>th</sup> century, with periods of accelerated loss in the 1940s and 1980s (Strachan and Jeffries 1993). The 1995 review of British mammals estimated the Water Vole population in Britain to be 1,169,000 of which 752,000 were estimated to be present in England (Harris and others 1995). Subsequent analysis by Strachan and others (2000), using comparable methodology, estimated the population of Water Voles across the whole of the Britain had declined by 78% between 1989-1990 and 1996-1998. The current population estimate of 77,200 by Mathews and others (2018), again using a comparable methodology to Harris and others (1995), suggests a further 50% decline in Britain for the period 1998-2016. Overall, the decline in England is estimated at 90% between 1989 and 2018. As this estimate is based on loss of range rather than the more sensitive and direct loss of numbers, the true scale of loss is likely to be larger still and taking the estimates for the decline in distribution prior to 1989 and the decline in population since that year suggests an overall decline in population of over 99%.

**Confidence:** Low

## Habitat for the species

The extent of riparian habitat varies little over time, but quality and suitability are widely known to have declined considerably through fragmentation, degradation, draining of wetland areas and increasing establishment of invasive non-native species. Consequently, past occupancy can be attributed to having more suitable habitat previously. However, there is no information available on the historical extent of habitat suitable for Water Vole.

**Confidence:** Low

## 3.3 The future for the species and its conservation

### Pressures and threats

Whilst substantial efforts have been made to halt and reverse past damage to Water Vole habitat and control Mink populations, many of the pressures and threats that caused the decline of Water Voles in England remain a significant problem today.

Mink predation is the overriding factor likely to lead to continued decline and localised extinction of populations with knock-on impacts of avoidance behaviours, for example, reduced foraging time leading to increased winter mortality.

Intensive agriculture and forestry, together with further population expansion, development the continued decline of our water treatment infrastructure and the mis-management of sewage, are likely to lead to the continued decline in availability and connectivity of suitable habitat. The continued spread of invasive non-native species, for example Japanese knotweed, Himalayan balsam, also has the potential to contribute to a reduction in suitable habitat.

Many English habitats are highly fragmented with semi-natural land cover in England comprising mostly small and fragmented patches (Natural England 2015). Whilst watercourses remain largely intact in themselves, the quality of riparian and adjacent habitats is highly variable. Habitat fragmentation may be one of the most critical overarching threats to Water Voles as populations are less able to cope with other threats if unable to expand, move away or recolonise adjacent habitats. Small, isolated populations are at greatest risk of extinction due to their greater vulnerability to fluctuations in breeding or predation rates, or environmental events such as flooding or drought. Water Vole colonies occupying small water bodies in particular are at threat from local extinction through stochastic events where this habitat is not connected via suitable habitat to other water bodies (Riley and others 2018). Smaller populations may remain viable if they are spatially connected to other populations over short distances to allow dispersal and recolonisation of vacant habitats. Connectivity, both in terms of habitat suitability and distance, appears to heavily influence dispersal to new territories and lack of connectivity between suitable habitats may act as a significant barrier to movement between colonies within metapopulations. The collective impacts of development, land use change and climate change will likely increase habitat fragmentation.

Increasing habitat fragmentation and isolation of colonies leads to inbreeding and genetic bottlenecks. The loss of genetic diversity can lead to an increase in unfavourable genetic disorders caused by recessive genes.

The drivers of change act not only alone, but in combination, to continue to reduce Water Vole populations. For example, modelling on the River Windrush in Oxfordshire suggests that Mink predation may double the probability of extinction over that arising from fragmentation alone (Rushton and others 2000).

The UK Climate Change Risk Assessment (Adaptation Sub-Committee 2017) identifies several now-unavoidable changes in weather and sea level. By 2050, it is predicted that average summer rainfall will be 11% less and severe heatwaves will occur every other year, on average. Winter rainfall and heavy rainfall events will be 5% and 10% greater respectively. Sea level rise is predicted to be +3 cm to +37 cm from present levels by 2060. Whilst warmer average temperatures further north could promote breeding success, the increasing frequency of extreme weather events such as drought and flooding, together with total loss of habitats in some areas close to the coast, will put additional strain on increasingly fragile sub- and metapopulations through negative impacts on the availability and connectivity of suitable riparian and wetland habitat. This is likely to further isolate populations. In Mediterranean countries, declines are thought to be due to

increasing aridity of the region, leading to increasingly fragmented populations. This situation may be mirrored in England due to increasingly warmer and drier summers.

## **Natural range and distribution**

An extension in the range and distribution of Water Voles is required so that the species can occupy its former range, reversing the historical loss of the species' range and distribution, and to ensure resilience to climate change.

Opportunities for Water Voles to expand from their current range will be key to ensure they can adapt to climate change. As habitats in the south of England become drier and less favourable, inter-connected, high-quality, suitable habitat will be essential to allow natural dispersal within metapopulations and migration northwards.

The favourable natural range and distribution is taken as 1,163 hectads, that is all hectads with potential suitable habitat to support Water Vole populations. The slightly higher figure for hectads with presence records (Figure 4) is not considered to be the favourable value because these records relate to presence and may not relate to sustainable populations of Water Vole such as in the periphery of their range.

## **Population**

Based on current trends, current drivers of change, and potential future drivers of change, it is considered likely that the England population of Water Vole will continue to decline, unless significant change is implemented to substantially, meaningfully and permanently reverse the conditions causing decline.

A significant increase in population is necessary to restore populations to a level which may be viable and self-sustaining in the longer term and to occupy the favourable range and distribution.

Numbers of Water Voles vary according to habitat type and size, season and geographical location. Importantly, numbers within a population may decline as much as 80% over the winter period. Alongside this, counting numbers of individual Water Voles is extremely difficult to do effectively. Standard surveys rely on calculating density estimates from counting the number of latrines (Deane and others 2016). The number of latrines found per 100m of bankside habitat translates into a high, medium or low population density. It is not possible to make robust estimates of numbers of individuals from latrine counts. Latrines provide relative indices of activity, commonly used for the purpose of assessing impacts or designing mitigation.

Note the above is based on linear habitats, there is no agreed method for calculating density within wetland habitat areas, which are an important stronghold for Water Vole populations.

Given the above, the population metric is based on relative density across suitable habitat (see appendix 1 and habitat metric below) instead of number of individuals:

A favourable Water Vole population in England consists of viable colonies distributed across 184,224 km of suitable linear riparian habitat in England.

- A viable Water Vole colony is defined as where Water Voles are present at medium or high relative density over a 2km stretch or more as measured by number of latrines.
- Each colony must have functional connectivity to other Water Vole populations colony within 2km.

Each wetland habitat area with suitable habitat and more than 1 ha in area should have presence data recorded over two consecutive summer seasons and connectivity within 2km to other wetland or linear riparian habitat.

Given the inherent difficulty in effectively surveying wetland habitat areas, sustained presence is deemed as the most effective way of calculating favourable population. A minimum of one ha is considered to be the minimum area required to support a viable population, but this again will depend on habitat suitability.

The Water Vole Conservation Handbook (Strachan and others 2011) and Water Vole Mitigation Handbook (Dean and others 2016) both mention minimum viable population (MVP) figures for Water Voles, although the underpinning work to this is unknown. The documents mention that the MVP is currently unclear, though it is likely to be in excess of 100 individuals at peak breeding season (30-50 individuals at the beginning of the season occupying approx. 1.5-2km of habitat). An approximation of the overall population as 2.5 Water Voles per 100m of suitable habitat (derived from the median number of individuals (40) per 2km of linear habitat (large enough to support a self-sustaining population). This falls within the lower estimates given in the literature for population density (but it is not always known at what time of year they were calculated).

If the figure of 184,224 km suitable habitat (Appendix 1) is divided into 2km stretches, the data suggest there could be 92,112 'populations' in England. If each population consisted of 50 individuals, then the population might be expected to be 3,684,480 individuals. This is very high potential and assumes every part of the suitable habitat is occupied, which is unlikely to be the case all of the time (bearing in mind habitat is stated as suitable, not necessarily optimal). More realistically, should half of the habitat should be occupied at the beginning of the season, this provides space for the metapopulations to spread and function. This would equate to 46,056 populations or 1,842,240 individuals. Note this does not cover populations in wetland habitat areas, due to the difficulty in surveying and monitoring these habitats.

Ideally, optimal relative densities of Water Voles across different areas of England and within different habitats should be known and account accordingly for density estimates to determine what might be favourable for that area and habitat in local FCS strategies.

## Habitat for the species

Strategic restoration of connected, naturally functioning ecosystems will be crucial for the re-establishment of Water Vole populations to their former range and distribution across England. By allowing natural movement in response to life cycle needs as well as dynamic environmental conditions, metapopulations will become more resilient (Mainstone and others 2016).

Modelling completed by the Mammal Society for Natural England (see Appendix 1) concluded that there are 184,224 km of riparian habitat with climate, hydrology and terrain that is suitable for Water Vole. This is considered the minimum length of suitable linear habitat necessary to support the proposed favourable population of Water Vole.

The creation of more extensive wetland habitats is likely to reduce the impacts of Mink predation that are more prevalent in linear habitats. These more complex habitats will feasibly be more resilient to climate change, particularly in headwaters, and may also benefit multiple riparian and other species. However, if these measures are to deliver the greatest benefits not just to Water Vole conservation but to the recovery of nature more generally, fundamental constraints which impact river and wetland ecology (such as nutrient pollution and physical modifications) will also require action at source, so that these interventions can achieve their full potential. There is no accurate method for determining wetland habitat area in England due to the variation within habitats defined as 'wetland' and also due to the dynamic and potentially transitional nature of such habitats. It is not therefore possible to provide a figure within this definition of how much more wetland habitat would be needed to support a favourable population of Water Voles.

**Confidence:** Moderate

## 3.4 Constraints to expansion or restoration

The presence of Mink, lack of connectivity between populations (due to multiple drivers) and spread of other invasive non-native species (which affect habitat quality and availability and foodwebs at the local level), are all currently limiting the ability of Water Vole populations to expand and thrive. However, if Mink are eradicated in Great Britain (necessary to prevent recolonisation in England from Mink populations in other nations), and habitats are restored, enhanced and reconnected, there is no ecological reason why Water Voles cannot fully recover and be present in all suitable watercourses and bodies in England. Glossop and Morse (2024a) compared the area covered by regional key areas with the last iteration of the NWVDMP report (McGuire and Morse 2020) and found that the area covered had increased by 5.1%. Eleven new regional key areas were identified, while only nine were lost and more had increased in size than decreased. This is despite an overall reduction in range within England. Although the expansion in regional key areas and overall reduction in range are contradictory, the authors suggest that it may indicate that successful conservation strategies are allowing Water Voles to thrive in their strongholds, while they continue to struggle in areas of lower conservation priority.

Mink control programmes, such as Waterlife Recovery East, are showing significant potential to control or even eliminate Mink at a local and regional scale, with Water Vole populations responding well (25% re-occupancy of former sites in Essex (McGuire and Morse 2020)). Mink recolonisation remains a high risk though unless control effort can be maintained in the long-term or be carried out systematically across Great Britain (Glossop and Morse 2024a). This has been prohibitively cost- and/or labour-intensive in the past. Recent technologies and techniques such as smart traps, and larger-scale schemes which reduce recolonisation risk, may make wide-scale mink control more feasible in the future.

Evidence from pilot studies combining habitat restoration with Mink eradication suggests Water Vole populations can respond positively and rapidly under these circumstances, emphasising the significance of Mink on Water Vole population expansion. However, if the numbers of Water Voles are very low they may not respond as quickly, or at all, particularly in upland areas (Gow 2021, pers. comm.).

Water Voles have been found to respond positively in areas re-wetted as result of Beaver damming creating more extensive, rather than linear, wetland habitats, even in the presence of Mink (Puttock and others 2023). Managed realignment of coastal regions may also support recolonisation by Water Voles by providing new areas of reedbed or other wetland habitat. Currently, large areas of habitat classified as Coastal and Floodplain Grazing Marsh (CFGM) are utilised by Water Voles which are primarily restricted to ditch networks and make limited use of the wider habitat, which is typically agricultural. The opportunity to create more complex and diverse wetland habitats at CFGM sites as part of realignment schemes is significant and will allow both expansion of range (into territories not currently suitable) and increased abundance where sparsely-occupied CFGM sites are replaced by wetland mosaic habitat with much greater potential to support Water Vole populations.

Where Water Vole numbers are low, reintroduction (following targeted Mink control and habitat restoration where necessary), may be necessary if there are no other Water Vole populations in proximity to allow natural recolonisation, due to the risk to long-term genetic health of small, isolated populations. Reintroduction may also be necessary to support colony expansion for small populations where this would otherwise result in a reduced genetic pool and inbreeding issues.

Water Vole reintroductions and translocations have been used as mechanisms to restore or safeguard populations since the late 1990's. However, the success of such interventions is variable, and further work is required to ascertain best practice techniques (M Dean and M Gelling, pers. comm. 2024). Translocations are an inherently stressful process for any free-living wild animal. Animals are exposed to many unfamiliar or unnatural conditions of confinement, given unfamiliar food, may undergo invasive procedures (handling, general anaesthesia, sampling), and have to adapt to a new unfamiliar environment at destination. Disease risk analysis, management and health surveillance are therefore crucial elements of many translocation programmes.

We do not currently have a true understanding of the risks from disease to Water Vole and other rodent populations or risks to individuals from stress associated with capture and transport from reintroductions. Stress can alter the susceptibility of Water Voles to stress-associated diseases and careful stress management is an essential component of a disease risk management and post-release health surveillance protocol. Poor husbandry of captive Voles could risk the spread of extant disease, or exotic parasites, which could endanger current Water Vole populations (Donald and Sainsbury 2023). Exotic parasites can have negative population level effects and potentially lead to extinction, as seen in the case of Red Squirrel populations from squirrel pox virus, and chytrid fungus to amphibian populations (Sainsbury and others 2008; Scheele and others 2019; Sainsbury and Vaughan-Higgins 2012). Population level effects can take many decades to be detected and so a negative impact may not be revealed for some time (Sainsbury and others 2008). Understanding of risk could be improved via a disease surveillance programme, and follow-up health monitoring of reintroduced Water Voles (Donald and Sainsbury n.d.).

The genetic divergence of Scottish Water Voles to those in England and Wales has implications for conservation in relation to captive breeding, reintroduction and translocation. To avoid the loss of evolutionary heritage and the potential for complications such as outbreeding depression, reintroductions and translocations have sought to avoid movement between populations in Scotland with those in England and Wales, and vice versa (Strachan and others 2011). However, genetic assessment of Voles in the north of England has found the Scottish haplotype, groups of DNA variations inherited as a set, is present in Northumbria and as far south as the Humber (Brace and others 2016), which may indicate natural mixing through dispersal and/or be a remnant of past reintroductions. Further evidence of the introduction of divergent lineages has also been found in south-east England (Baker and others 2020). Understanding of the genetic composition of regional populations is therefore important when considering reintroducing Water Voles from different watersheds (Baker and others 2020).

Consideration could be given to the potential benefits to both long-term survival of the species and the wider ecosystem of reintroducing Water Voles to fossorial habitats. Such habitats could provide greater resilience to climate change as riparian habitats become more prone to both flood and drought. Management of grassland sites for fossorial Voles need not be incompatible with conservation measures for other species, and many of the keystone functions recognised in riparian habitats could reasonably apply in grasslands for example, grazing and soil aeration resulting in greater botanical diversity. Interim guidance for the management of grassland sites for Water Voles has recently been published for the extant 'Easterhouse population' (Stewart and others 2020) and could form the basis of measures to prepare and manage potential receptor sites in England. However, further research is needed to identify what factor(s) may determine fossorial behaviour.

**Confidence:** Moderate

## 4. Conclusions

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### 4.1 Favourable range and distribution

The range and distribution of Water Voles will be favourable when populations occupy suitable habitat throughout their historical range. This equates to 1,163 hectads, almost 80% of hectads in England.

### 4.2 Favourable population

A significant increase in population is necessary to restore sustainable populations to the favourable range and distribution. A favourable Water Vole population in England consists of viable colonies distributed across 184,000 km (figure rounded) of suitable linear riparian habitat in England.

- A viable Water Vole colony is defined as where Water Voles are present at medium or high relative density over a 2km stretch or more as measured by number of latrines.
- Each colony must have functional connectivity to other Water Vole populations colony within 2km.

Each wetland habitat area with suitable habitat and more than 1 ha in area should have presence data recorded over two consecutive summer seasons and connectivity within 2km to other wetland or linear riparian habitat.

### 4.3 Favourable supporting habitat

The favourable population will require at least 184,000 km (figure rounded) of suitable riparian habitat to support sustainable populations.

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# Appendix 1: Species distribution model of Water Vole (*Arvicola amphibius*) in England

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## Author

Dr Frazer Guy Coomber – Mammal Society, 2022

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Ordnance Survey for background mapping in images.

## Executive summary

The Water Vole is one of the fastest declining mammals in Britain. National surveys undertaken in 1989-1990 and 1996-1998 identified a 78% loss in occupancy. The recent mammal review suggests a further 50% decrease between 1998-2016. This has led to the Water Vole being classified as Endangered in Britain. England was identified to contain 58.5% of the population and 52.5% of the suitable riparian habitat for this species but it is still classified as Endangered in this country.

This report aims to use species distribution models with available Water Vole records and environmental habitat predictors to identify suitable habitat that can support Water Vole populations in England. The model was created at a 1 km resolution across the extent of England.

Water Vole records were available across 13,362 1 km grid squares for the extent of England, this represents around 10% of the total available grids. There were also 43 environmental variable datasets available that covered climatic, hydrological, habitat, and terrain aspects of England.

There were 22 environmental predictor variables that passed collinearity checking. The variables of temperature seasonality, amount of available waterway and spring solar radiation levels were found to be the most important contributors to the model. The environmental relationships identified that Water Vole habitat is most suitable where there is a clear seasonal difference in temperature but stable diurnal temperatures, warm weather during the wettest periods but cooler, in the most part, when it is driest and solar

radiation levels are in the middle ranges. Suitable habitats for Water Voles include riparian, freshwater, and wetland habitats with terrain and flow regimes that have slow flowing water. Low woodland, both broadleaved and coniferous, and improved grassland percentage coverage was most favourable, indicating that woodland and monospecific habitats are less suitable. Built-up areas were shown to be suitable habitat for this species, but suitability was lowest at the extremes of percentage cover.

Utilising these environmental relationships and their importance contributions, the model successfully predicted habitat suitability indices across the extent of England. The distribution of the suitability indices was not uniform and distinct areas of high and low suitability were identified. For example, Cornwall and Devon were pronounced areas of low suitability and areas like the Wash and the Peak District had pronounced areas of high suitability. The model was found to perform adequately based on an Area Under the Curve statistic score of 0.648 but excellently based on the Boyce Continuous Index score of 0.953.

Using maximum sensitivity and specificity the habitat suitability score of 0.575 was estimated to be the threshold at which to divide habitats into binary classifications of suitable and unsuitable. Using this threshold, 55,338 (43.2%) 1 km grids in England were identified that should be classified as suitable habitat. The total length of waterways within these grids was calculated and indicates that 184,224 km of waterways across England are in areas with climate, hydrology and terrain suitable for supporting Water Vole populations. Moreover, 1,163 (77.9%) of the 1,493 hectads and 4,092 (74.5%) of the 3,049 catchments contained to some degree suitable habitat identified in the 1 km grids.

These results can be used to provide a Favourable Conservation Status assessment for Water Voles. Indicating the range and distribution Water Voles should occupy in England if they were to occupy all of the suitable habitat. The values above should be considered as a minimum goal to be occupied by Water Voles if they are to be considered thriving in their natural environment. The exception to this rule should be the total length of waterways occupied as this is likely an overestimation. The fact that these waterways are in areas environmentally suitable for Water Voles does not mean the entire waterway will be suitable for Water Voles. Fine scale habitat features, such as bank angles and vegetation are likely to be more important in defining if the waterways are suitable for Water Voles.

## List of abbreviations

AIC – Akaike Information Criterion

AUC – Area Under (the Receiver Operating) Curve

CBI – Continuous Boyce Index

FCS – Favourable Conservation Status

HSI – Habitat Suitability Index

LCM – Land Cover Map

MTSS – Maximum Training Sensitivity plus Specificity

SCS – Species Conservation Strategy

SDM – Species Distribution Model

## Glossary

AIC – a score used to select the best fitting model, a decrease in AIC between models utilising the same dataset indicates an improved model fit.

AUC – a score to present a model's predictive power with values of 0.5 indicating that predictions are no better than random to 1 which relates to a perfect prediction.

Biological records – Presence-only species points defining the position, time and species of where an individual or group of animals was reported.

CBI – an index that relates to how much the model predictions deviate from randomness with a higher index, which ranges from -1 to 1, indicating an increasing reliability of presence-only predictions.

Environmental variable – the climatic, terrain, hydrological and habitat descriptor variables used to present the spatial distribution of environmental gradients.

Monad – a 1 by 1 km British National Grid

Hectad – a 10 by 10 km British National Grid

## 1. Introduction

Whilst the Water Vole (*Arvicola amphibius*) remains widely distributed across Britain it continues to experience one of the most rapid declines of all mammal species recorded in the UK (Strachan 2004). This decline is attributed to the loss and degradation of semi-natural habitats through intensification and change of land management (Strachan and others 2011; Barreto and others 1998). Following the Second World War, policies for agricultural intensification resulted in the riparian engineering works to improve land drainage thereby destroying key wetland habitats and reducing the quality, diversity, extent, and connectivity of remaining features (Strachan and Jefferies 1993; Strachan and others 2011; Barreto and others 1998). The decline of Water Voles is further exacerbated by acute predation from the invasive American Mink (*Neogale vison* formerly *Neovison vison*). American Mink were originally introduced to the UK to be farmed for fur in the late 1920s, although it was not until the 1950s that escaped individuals became established along waterways (Dunstone 1993). The expansion of American Mink has seen local

extinctions and fragmentation of Water Vole populations (Woodroffe and others 1990; Rushton and others 2000; Aars and others 2001).

This has confined Water Voles to coastal areas, isolated headwaters and ponds, tributaries of main rivers and three-dimensional wetland habitats (Brzeziński and others 2019; Carter and Bright 2003; Essex Wildlife Trust 2021). National Water Vole surveys undertaken between 1989-1990 and 1996-1998 identified a 78% loss of Water Vole occupancy from historical sites (Strachan and Jefferies 1993; Jefferies 2003). The most recent mammal review suggests a further 50% decrease of Water Vole occupancy across Britain between 1998-2016 (Mathews and others 2018). Owing to this decline, the Water Vole is now listed as Endangered on the Red List of British Mammals (Mathews and Harrower 2020). The most recent mammal review also identified that 58.5% of the population and 52.5% of the suitable riparian habitat for this species in Britain occurs in England (Mathews and others 2018). Despite the majority of this species' population and habitat residing in England it is still classified as Endangered in this country (Mathews and Harrower 2020).

Before 2008 the Water Vole was indirectly protected by the Wildlife and Countryside Act 1981 through the protection of their habitat in England and Wales. After 2008 Water Voles were granted full protection under Section 9 of Schedule 5 by also making it an offence to intentionally kill, injure, or disturb this species and providing legal obligations for UK statutory nature conservation bodies to protect this species ([www.legislation.gov.uk](http://www.legislation.gov.uk)). The Environment Act 2021, an act to make provisions about targets, plans and policies for improving the natural environment, has directed the development of Species Conservation Strategies (SCS). SCSs will act as information sources to drive species conservation through different parties to create a combined, focused plans that prioritises actions for a species' conservation.

To help inform SCSs the presentation of the Favourable Conservation Status (FCS) – the situation in which a species is thought to be thriving throughout its natural range – needs to be addressed so that guidance towards long-term goals can be provided (JNCC 2018; Mousley and Van Vliet 2021). FCS needs to be definable, specific, and measurable so that actions made towards favourable status can be measured against achievable goals.

Species Distribution Models (SDM) – also known as habitat suitability models – are computer algorithms that link environmental factors to species occurrences (Elith and Leathwick 2009). They can be used to describe a species' biotic interactions and to predict a species distribution, including extrapolating to un-surveyed areas (Elith and Leathwick, 2009). These models have been used extensively in ecological studies across many different species.

## 1.1 Aim

This report aims to use species distribution models with available Water Vole records and environmental habitat predictors to identify suitable habitat that is capable of supporting Water Vole populations in England. This information will be used to provide a measure of

Favourable Conservation Status, as the amount and distribution of habitat across England. Thus, presenting an identified and measurable goal on the potential area that Water Voles should occupy in this country if they were thriving in their natural environment.

## 2. Methods

### 2.1 Species information

Presence-only biological records, defined as species occurrence points for Water Vole and other riparian species (American Mink, European Otter (*Lutra lutra*), Brown Rats (*Rattus norvegicus*) and Black Rats (*Rattus rattus*)) were sourced from the Mammal Society's database of mammalian biological records (Mathews and others 2018; Barreto and others 1998; Crawley and others 2020). This database includes all mammalian species records from across the British Isles and includes records from the 1960s up to the beginning of 2017.

All biological records of Water Voles and riparian species were reviewed for inclusion into the analyses, based on the availability, extent, and resolution of spatial and temporal information. For example, any records with missing location information or a spatial resolution coarser than 1 km were removed. Records with missing temporal information, or a temporal resolution greater than a year, were also removed. Records beyond the extent of the survey area were also removed. Given that records were sourced from a variety of repositories it was possible that duplicated information exist so records with identical latitude, longitude, species, and year information were removed before analysis.

### 2.2 Environmental Data

A total of 43 environmental datasets were collated for consideration in the modelling process. Information on where these datasets were sourced, their finest available spatial resolution, and any copyrights or relevant citations are presented in Table 1.

The selection of hydrological, habitat and terrain variables were based both on the availability and biological relevance of datasets. It is widely acknowledged that Water Vole densities fluctuate and that environmental factors, such as upland and lowland habitats (Walsh and Hall 2005), vegetation type and cover (Lawton and Woodroffe 1991, Bonesi and others 2002), linear and wetland habitats (Strachan and others 2011), and stream order (Telfer and others 2001) can influence occupancy. In addition, available climatic variables were also considered as they are known to play an important role in the distribution of species (Schwager and Berg 2021).

The habitat information used to build the model was the 1990 Land Cover Map (Rowland and others 2020) to best represent the median time across the records used. However, the 2021 Land Cover Map was used to predict the model to best represent the current habitats across England (Marston and others 2022). The Land Cover Map data at 25 m resolution was compiled into the 1 km grids as the percentage cover in that grid of the target class habitat. However, due to a large number of target classes (21) a number were

compiled into their aggregate classes. This included neutral, calcareous, and acid grasslands into semi-natural grasslands, heather and heather grasslands into heath, littoral and saltwater into coastal and urban and suburban into built-up. The length of available waterway was created by calculating the total length of the linear master waterways vector layer within each 1 km<sup>2</sup> grid. This was conducted in QGIS (QGIS.org 2022), using the sum line lengths in polygon tool from the “fTools” toolbox. The terrain rugosity within each 1 km<sup>2</sup> was represented by the standard deviations of the Digital Elevation Model at its finest resolution. The variable of aspect was not considered for any future modelling due to the cyclic nature of this data.

**Table 1** The environmental spatial datasets compiled for this project, with information on the source (NE – Natural England, UKCEH – UK Centre of Ecology and Hydrology, EEA – European Environmental Agency), availability (Open source – Ordnance Survey (OS) or under licence – L), highest available spatial resolution, and any relevant citations or copyright. © Natural England 2025; This table is published under the [Open Government Licence v3.0](#) for public sector information.

Dataset		OS/L	Highest available Resolution	Source	Citation or Copyright
Hydrological	ww_length.asc	L	Vector	NE	OS MasterMap® © Crown Copyright and database rights 2025. Ordnance Survey AC0000851168.
	q2.asc	L	25 m2	NE	(Graham et al., 2020)
	q80.asc	L	25 m2	NE	(Graham et al., 2020)
	LCM_Bog.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Broadleaved_woodland.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Built_up.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Coastal.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Coniferous_Woodland.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Freshwater.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.

	LCM_Heath.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Improved_grassland.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Inland_rock.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Saltmarsh.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	LCM_Semi_improved_grassland.asc	L	25 m2	UKCEH	(Rowland et al., 2020) Based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © UKCEH. Contains Ordnance Survey data © Crown Copyright 2007, Licence number AC0000824257.
	Tree_Density.asc	L	10 m2	EEA	(Copernicus Land Monitoring Service (2018) ) <b>Generated using European Union's Copernicus Land Monitoring Service information</b>
<b>Bioclimatic</b>	Max_Temp_Warmest_Month.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
	Mean_Diurnal_Range.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
	Mean_Temp_Coldest_Quarter.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)

Mean_Temp_Driest_Quarter.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Mean_Temp_Wettest_Quarter.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Min_Temp_Coldest_Month.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Precipitation_Coldest_Quarter.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Precipitation_Driest_Quarter.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Precipitation_Seasonality.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Precipitation_Warmest_Quarter.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Precipitation_Wettest_Month.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Precipitation_Wettest_Quarter.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Temp_Annual_Range.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Temp_Seasonality.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Annual_Mean_Temp.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
Annual_Precipitation.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
av_autumn_srad.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
av_spring_srad.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
av_summer_srad.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)
av_winter_srad.asc	OS	1 km2	WC	(Fick and Hijmans, 2017)

Terrain	Esdras	OS	25 m2	EEA	(European Commission, 2012)
	Elevation.asc	OS	25 m2	EEA	(European Commission, 2012)
	Slope.asc	OS	25 m2	EEA	(European Commission, 2012)

It is often required by modelling software for spatial and environmental datasets to be prepared and input as specific formats and/or at identical resolutions and extents. Therefore, all sourced environmental data were pre-processed in R version 4.1.1 (R Core Team 2021) within the RStudio development environment version 2021.09.0.351 (RStudio Team 2021) using the following packages: “raster” (version 3.5-2: Hijmans 2021), “sp” (version 1.4-6: Pebesma and Bivand, 2005), “usdm” (version 1.1-18: Naimi and others 2014), and “gstat” (versions 2.0-8: Pebesma 2004).

Each environmental dataset available in a raster format was resampled to create an ASCII formatted raster with identical extents (England: 82000, 657000, 4000, 659000), spatial projections (EPSG: 27700 – BNG projection), and 1 km<sup>2</sup> spatial resolution.

The presence of correlated predictor variables can hide significant effects or change the direction of identified trends making statistical interpretation difficult to impossible (Zuur and others 2010). Environmental variables were checked for multicollinearity, high intercorrelations amongst the independent variables, using the Variance Inflation Factor (VIF) within the “usdm” package (version 1.1-18 Naimi and others 2014). For the model any variables that were found to have a VIF greater than a threshold value of three were removed using the VIFstep command. This threshold is based on the recommendations of Zuur and others (2010). The correlation coefficients were also calculated between all available environmental variables.

## 2.3 Species Distribution Models

The vast majority of the data available for Water Voles, and other riparian species, was of presence-only records. Although presence-absence survey data does exist there were very few absence records available in the accessible dataset, in comparison to the proportion of presence records. Therefore, Water Vole habitat suitability was considered to be identified through a presence-only SDM technique.

To identify the suitable habitat for Water Voles in England, SDMs were conducted using the “dismo” package (version 1.3-5: Hijmans 2021) in R (R Core Team 2021) using the R Studio environment (RStudio Team 2021). The SDM considered for this project to identify suitable habitat, equivalent to the probability of occurrence, was Maxent (Phillips and others 2006). Maxent — Maximum Entropy modelling — is an SDM that predicts the probable distribution of a species using presence-only records. This is calculated by finding the maximum entropy (closest to uniform) distribution probability within a set of

constraints set out by available species sample points and environmental variables (Phillips and others 2009). Alternative SDM approaches were considered but, Maxent is one of the most widely used techniques and is repeatedly among the best performing predictive modelling techniques for estimating species distributions from presence-only records (Aguirre-Gutiérrez and others 2013; Elith and others 2006; Wisz and others 2008).

The species presence records used in the SDM were all the combined species presence-only records available. The models were fitted at a spatial scale of 1 km<sup>2</sup>. The results of this model should therefore present the total available habitat for Water Voles based on the environmental conditions favoured by Water Voles and therefore can be used to inform FCS.

Presence-only SDMs can be heavily spatially biased, due to the uneven coverage of sampling effort (Kramer-Schadt and others 2013; Syfert and others 2013), and this can greatly affect the model outputs (Phillips and others 2009). To take this potential bias into account a bias file was created using observations of all riparian species as a proxy for sampling effort.

Presence records of other riparian species were chosen for the bias file based on the fact that these species have been shown to be co-recorded as a survey assemblage (Coomer and others 2021). Co-recorded species are likely to be observed using the same methods and share similar sampling bias (Phillips and others 2009). To create this bias file, 1 km resolution grids were compiled with all other riparian species records available. Any grid with at least one reported riparian species presence was classified as 1 and those without as 'NA'. The model then utilised pseudo-absences drawn only from areas where riparian species had been recorded but no Water Vole records. The number of absences was set to be roughly equal in number to the available presence data.

To identify the best setting for the model the parameters of the regularization multipliers (RM) and the feature classes (FC) were tuned using the ENMevaluate function from the "ENMeval" package (Kass and others 2021). The FCs determine the potential shape of the marginal response curves and all combinations of FC types (L, linear; H, hinge; Q; quadratic; P, product; T, threshold) were tested. The RM determines the penalty associated with variable inclusion, with higher RM values imposing stronger penalties on more complex models. The RM was tested in increments of 0.5, from 0.5 to 4. The best RM and FC settings were selected for a proposed candidate model based on the lowest Akaike Information Criterion (AIC: Akaike 1973) score. This score is good for selecting between models that utilise the same data but cannot be used to compare models that use different data. A final model was then created using the optimal settings identified to produce model predictions and response relationships.

A four-fold cross validation technique was used to investigate the model's predictive performance. The presence records were split into four geographically partitioned blocks using the ENMevaluate function from the "ENMeval" package (Kass and others 2021), with three subgroups being used to train the model, and the remaining subgroup being used to test the model's predictions. This was repeated four times, using a different

subgroup for testing each time, and average AIC scores of model performance being used to select the best settings for each candidate model. It should be noted that ideally the model outputs should be compared against a new independent sample of data.

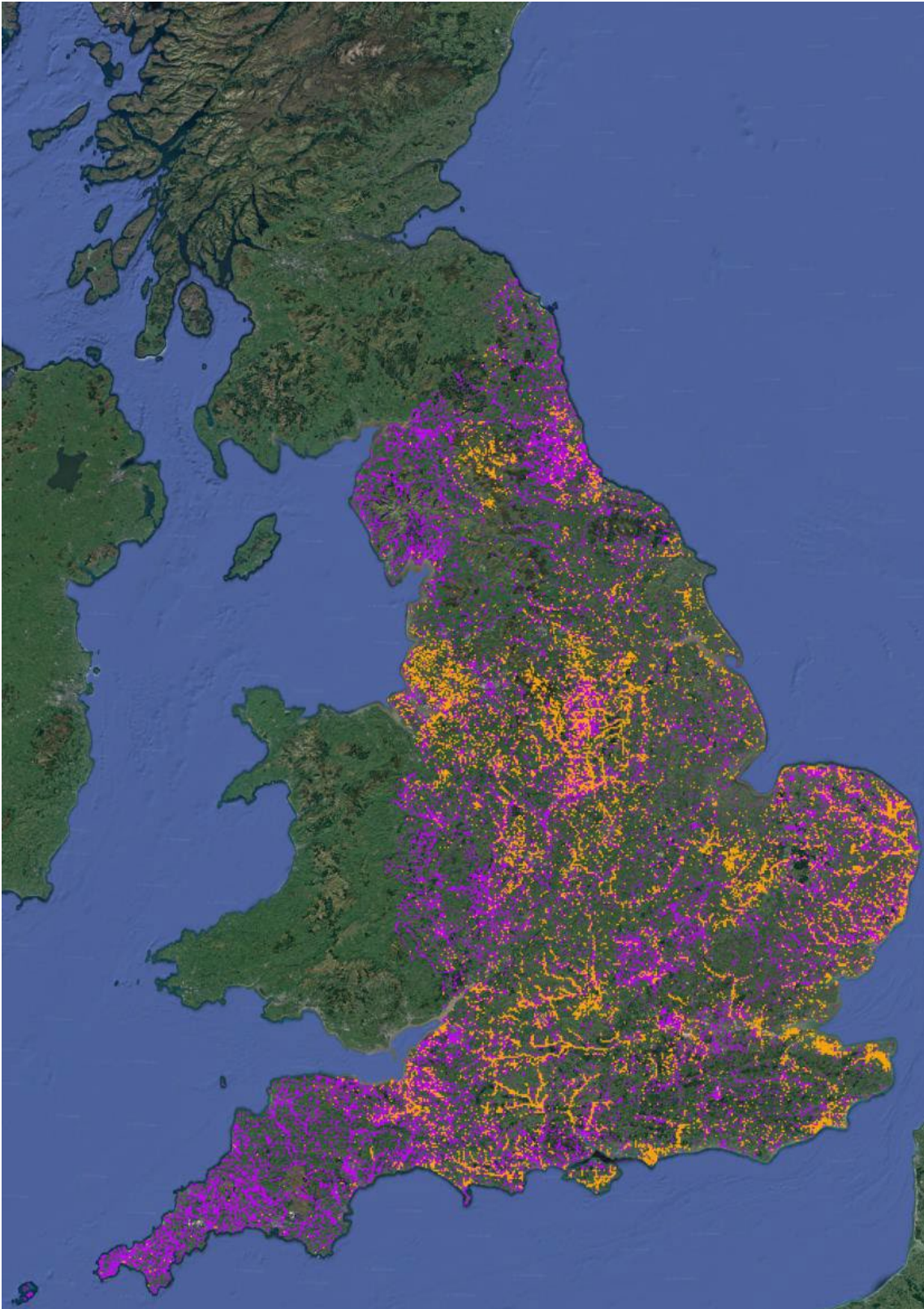
To identify the predictive power of the model and evaluate its performance the Area Under the Receiver Operating Characteristic Curve (AUC) statistic (Melo 2013) was used. The AUC score is a measure of how well a model ranks sites according to its suitability for the species. It measures the probability that the model will rank the conditions at a randomly chosen presence point above the absence points. An AUC value of 0.5 indicates that the model's predictions of habitat suitability are no better than random, whereas the greater the value above 0.5, the greater the model's predictive accuracy (Melo 2013). The Continuous Boyce Index (CBI: Hirzel and others 2006) is another predictive measure that was considered and only requires presences. The index relates to how much the model predictions deviate from randomness with a higher index, which ranges from -1 to 1, indicating at increasing reliability of presence-only predictions.

Environmental predictor variable permutation importance was assessed using a jack-knife test to reveal the percentage contribution of each variable to the models (Elith and others 2011). The output provided by Maxent included response curves showing the strength and direction of species-variable relationships, accounting for that variable's interactions with other variables in the model.

The outputs of the model range from 0-1, representing the probability of occupancy, and can be approximately interpreted as the Habitat Suitability Index (HSI) for each grid cell (0 = unsuitable, 1 = highly suitable). It is generally preferable to use the raw outputs of SDMs rather than a binary division of cells into suitable or unsuitable (Guillera-Arroita and others 2015). This is because the latter is a coarse interpretation of species occurrence probabilities and reduces the information content compared with using the full range of values provided by the SDM (Guillera-Arroita and others 2015). However, it can be helpful to visualise locations of high suitability, and to assess their size and connectivity. A binary conversion was therefore undertaken to identify suitable habitat to inform FCS. The threshold used for inclusion was based on a stringent Maximum Training Sensitivity plus Specificity (MTSS) approach, which maximizes the sum of sensitivity and specificity obtained from the error matrix (Fielding and Bell 1997) for the training data. The MTSS threshold balances errors of omission and commission and has found a high degree of support when evaluated against other threshold methods across a range of prevalence values (Liu and others 2005; Jiménez-Valverde and Lobo 2007). Cells with Maxent output values greater than or equal to the MTSS threshold were classified as suitable habitats.

## 3. Results

### 3.1. Species occurrence data



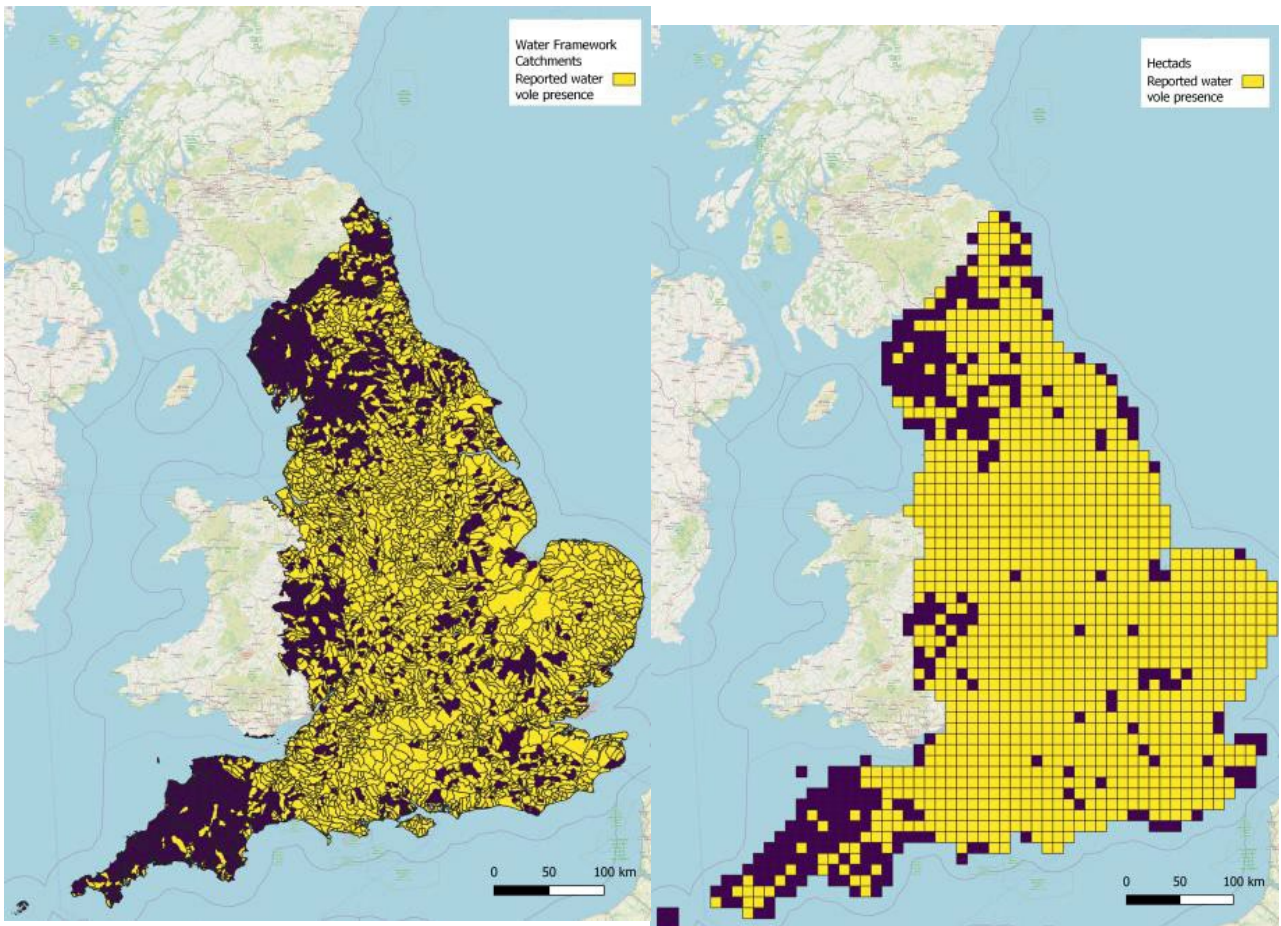
**Figure 1** The species points available used to build the model, presented as 1 km ordnance survey grid square presences. Orange represents Water Vole presences superimposed over all

other riparian species presences (that is, where pseudo-absences were drawn from). © Environment Agency copyright and/or database right 2022. All rights reserved. Contains OS data © Crown copyright and database right 2025; This map is published under the [Open Government Licence v3.0](#) for public sector information.

The number of observations available from the Mammal Society's database of mammalian biological records included 121,819 records of Water Voles and 240,948 records of all other riparian species combined. These records were distributed across 13,362 1 km<sup>2</sup> grids for Water Voles and 25,940 1 km<sup>2</sup> grids for the other riparian species across the survey extent of England (Figure 1). Once records were filtered for inclusion into the modelling process a total of 12,770 non-duplicated Water Vole presences were incorporated into a Maxent model.

The number of 1 km<sup>2</sup> grids found to have had at least one record of a Water Vole is about 10% of all the available grids across England. The compilation of all Water Vole records into water framework directive catchments © Environment Agency identified that 2,451 (59.9%) have had a Water Vole recorded in them at some point in England (Figure 2a). Similarly, the number of hectads across England that have had at least one record of Water Voles is 1,202 (80.5%: Figure 2b).

These observations are available across national extents. The available Water Vole records appear to be well distributed across the country but some areas such as the North West and South West of England have spatial gaps. It is also apparent that choice of scale and geographical unit has an effect on the amount of area occupied.



**Figure 2** The number and distribution of a) water framework catchments and b) hectads across England that have had reported Water Vole presences across the available dataset. © Environment Agency copyright and/or database right 2022. All rights reserved. These maps are published under the [Open Government Licence v3.0](https://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/) for public sector information.

## 3.2 Species Distribution Model

### 3.2.1 Environmental Habitat Predictors

There were 22 environmental variables that remained after collinearity checks. The environmental predictor variables of temperature seasonality, length of waterway and average spring solar radiation were found to be important contributors (Table 2).

**Table 2** The environmental predictor relative contributions and permutation importance. © Natural England 2025; This table is published under the [Open Government Licence v3.0](#) for public sector information.

Variable	Percent contribution	Permutation importance
Temp_Seasonality	44.6	32.4
ww_length	20.8	24.1
av_spring_srad	20.8	17.4
Mean_Temp_Wettest_Quarter	3.1	7.1
LCM_Improved_grassland	2.2	1.3
q2	1.4	4.0
LCM_Coniferous_woodland	1.3	1.1
Mean_Temp_Driest_Quarter	1.1	4.0
LCM_Built_up	1.0	2.3
q80	0.8	3.2
Slope	0.8	0.3
LCM_Fen_Marsh_Swamp	0.6	0.3
Isothermality	0.4	0.7
LCM_Broadleaved_woodland	0.3	0.1
LCM_Coastal	0.2	0.3
LCM_Semi_improved_grassland	0.2	0.4
DEM_SD	0.1	0.2
LCM_Inland_rock	0.1	0.2
LCM_Bog	0.0	0.2
LCM_Heath	0.0	0.2
LCM_Saltmarsh	0.0	0.0
LCM_Freshwater	0.0	0.0

The climatic predictors had a relationship that generally indicated that Water Vole habitat is most suitable where there is a clear seasonal difference in temperature but stable diurnal temperatures, warm weather during the wettest periods but cooler, in the most part, when it is driest. Temperature seasonality, the amount of temperature variation over a yearly range based on standard deviation, was found to be the most important environmental predictor (Table 2). The relationship generally indicates that increased seasonality, greater temperature variability between months, is related to increased habitat suitability for Water Voles. However, this variable is correlated to the maximum temperature of the warmest month and inversely related to several precipitation climatic

variables. So, this relationship could also indicate that Water Vole suitability could also be related to the higher temperatures of the warmest month or decreased amount of precipitation.

The average spring solar radiation was found to be an important predictor with Water Vole habitat suitability being highest in the middle range of roughly 12,250 to 13,600 kJ m<sup>-2</sup> day<sup>-1</sup>, with suitability dropping off substantially outside of these limits at the lower and higher end. However, this variable was also correlated to several other environmental variables that were excluded from the model due to high variance inflation. These variables included the other season solar radiations, mean temperatures and also temperatures during the coldest quarter. This indicates that the effect of spring solar radiation could also be linked to radiation from other months or the effect it has on temperature.

The number of waterways available within each grid is expected to improve habitat suitability as Water Voles are a riparian species. This is also true when it comes to the presence of freshwater habitat and other wet habitats such as fens, marshes, swamps, bogs, saltmarshes and coastal. The flow exceedance values for Q2 (high flow) and Q80 (low flow) indicate that as high flow exceedance increases the habitat suitability decreases, the effect of low flow exceedance was more pronounced. However, this generally indicates that slower flowing water is more suitable than faster and areas with higher exceedance values are generally less suitable. This is further confirmed by the identified relationship between a sharply decreasing suitability with increasing slope or terrain rugosity, both of which are likely to affect the general flow rate of any waterways.

The habitat suitability was inversely related to the percentage of coniferous woodland, broadleaved woodland and improved grassland, with coniferous woodland percentage increase displaying the most dramatic decrease in suitability. Semi-improved grassland, heath, and inland rock showed a weak positive, almost binary, relationship to Water Vole habitat suitability. The general habitat consensus is that monospecific habitats are not favourable but a mixture of grasslands and woodlands, with the presence, irrespective of percentage coverage, of some habitats being weakly favourable.

The relationship between built-up areas is parabolic being low at low percentages and also low at high percentage coverage. This indicates that built-up areas do represent suitable habitat for Water Voles unless it is highly built-up, with an area coverage greater than 75%.

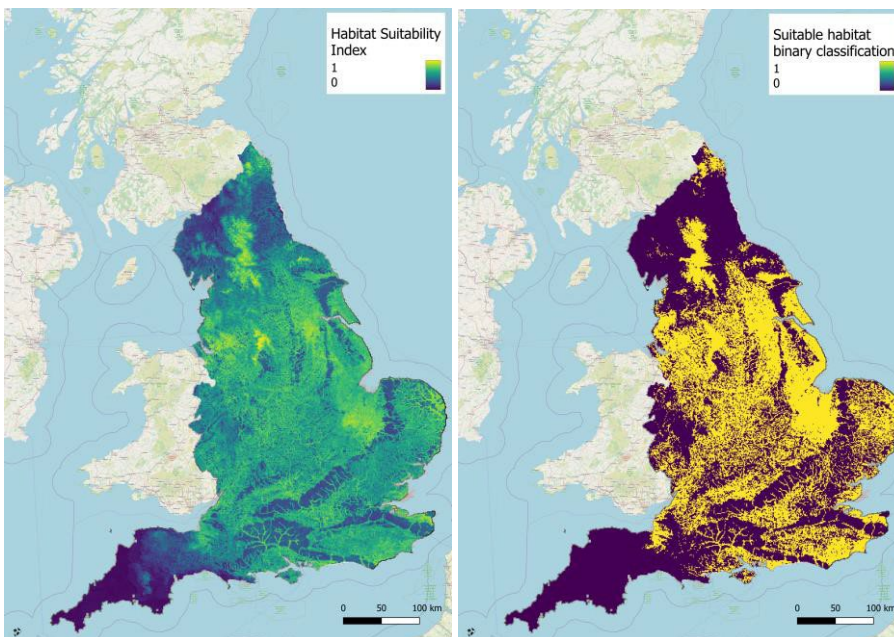
### **3.2.2 Spatial Predictions of Water Vole Habitat Suitability**

The model predictions based on the environmental predictor datasets identified a large proportion of England to have suitable habitat for Water Voles. The distribution is not uniform with areas such as the Wash, Peak District National Park, Weald, Pennines, and Yorkshire Dales having large areas of suitable habitat, for example. Conversely areas such as the North Wessex Downs, Chiltern and Mendip Hills show areas with less suitable habitat. The counties of Cumbria, Devon, Cornwall, and south-west Northumberland also show more pronounced areas of unsuitable habitat.

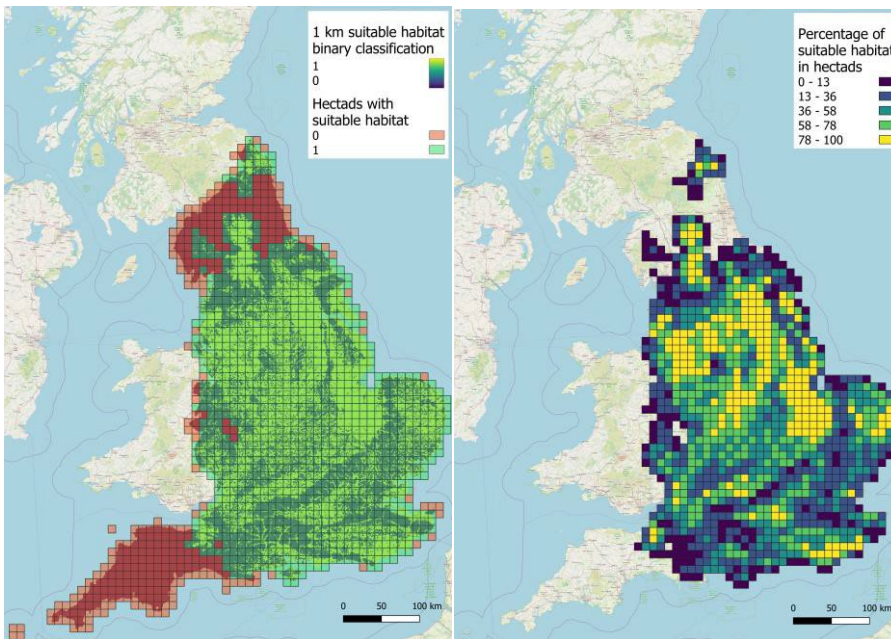
The predictive power of the model was shown to be adequate based on an AUC score of 0.648, but very good with a CBI score of 0.953. Using equal sensitivity and specificity the habitat suitability score of 0.575 was estimated to be the threshold at which to divide habitats into suitable and unsuitable. Using this threshold, the division into suitable and unsuitable 1 km<sup>2</sup> grid squares indicated that 55,338 grids should be classified as suitable (Figure 3b). This indicates that at a resolution of 1 km 43.2% of England has suitable habitat that could support Water Vole populations. Calculating the total length of waterways within these 1 km grids indicates that 184,224 km of waterways across England reside in areas with climate, hydrology and terrain suitable for supporting Water Vole populations.

The identified suitable habitat when compiled into hectads (10 by 10 km Ordnance Survey Grid Squares) indicated that 1,163 of the 1,493 (77.9%) hectads across England contained some degree of suitable habitat (Figure 4). Moreover, the percentage of suitable 1km habitat within each hectad was also calculated and this indicates that there are quite a few hectads with large proportions of suitable habitat (Figure 4).

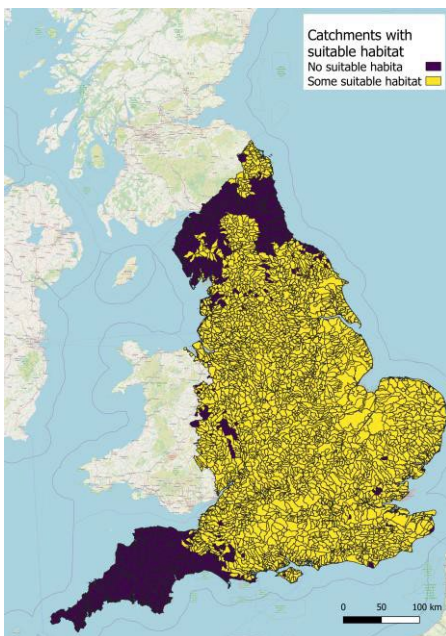
Furthermore, to represent more biologically relevant areas the number and percentage of water catchments were also calculated. Of the 4,092 catchments 3,049 fully contained or had at least some 1 km suitable habitat overlapping. This number represents 74.5% of all the catchments that are in England.



**Figure 3** a) the habitat suitability predictions, ranging from 0 for highly unsuitable to 1 for highly suitable habitat and b) the binary results using the sensitivity and specificity cut-off for Water Voles in England. © Environment Agency copyright and/or database right 2022. All rights reserved. Contains Ordnance Survey data © Crown copyright and database right 2025. These maps are published under the [Open Government Licence v3.0](https://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/) for public sector information.



**Figure 4** The identified hectads which a) contained at least some suitable habitat that could support Water Vole populations (green) and hectads which contained no suitable habitat (red) and b) the percentage of suitable habitat within each hectad. © Environment Agency copyright and/or database right 2025. All rights reserved. Contains Ordnance Survey data © Crown copyright and database right 2025. These maps are published under the [Open Government Licence v3.0](#) for public sector information.



**Figure 5** The catchments with suitable habitat. © Environment Agency copyright and/or database right 2022. All rights reserved. Contains Ordnance Survey data © Crown copyright and database right 2025. This map is published under the [Open Government Licence v3.0](#) for public sector information.

## 4. Discussion

### 4.1 General findings

The species distribution modelling using available records and broad scale environmental variables has successfully identified the habitat suitability for Water Voles across the extent of England. The relationship between environmental variables and habitat suitability has also been explored and the climatic, hydrological, habitat and terrain factors that drive habitat suitability have been identified. These relationships have been used to predict the spatial likelihood of suitable habitat for Water Voles across the national extent of England. The predicted habitat suitability across England has indicated that a large proportion of England is suitable habitat for Water Voles. This information can thus be used to provide support to identify FCS of habitat and indicate the amount of England that should be occupied by Water Voles. Thus, identifying a goal towards the understanding of whether Water Vole populations are thriving in their natural environment.

### 4.2 Defining favourable supporting habitat

The Maxent model predictions, at 1 km resolution and using the specificity and sensitivity cut-off, found that 55,338 km<sup>2</sup> (43.2%) of England had suitable environmental conditions capable of supporting Water Vole populations. This information could be used to help define the natural range and distribution of Water Voles as the environmental boundaries to this species potential distribution.

At the scale considered the area that has ever been occupied by Water Voles, based on all available records compiled into 1 km grids, was 13,362 km<sup>2</sup>. The difference in area between suitable habitat and previously occupied habitat could indicate: 1) the model has identified areas beyond those surveyed as suitable habitat for Water Voles; 2) Water Voles are below FCS as this value indicates that only 24.1% of the suitable habitat has ever been reported as occupied; and 3) that Water Voles are potentially under recorded in these areas.

The identified area of suitable habitat across England represents a measurable and definable goal. If Water Voles were to be recorded in at least 55,300 km squares across England they could be classified as thriving in their natural environment. This would indicate that they occupy at least all the areas where environmental conditions can support them. This value should be the minimum FCS threshold as it is possible that Water Vole populations can exist outside of the identified suitable habitat, occupying sub-suitable habitats. Although animal densities from these areas may be lower (Bonesi and others 2002). It can also be seen that there do exist species presence records beyond that identified as optimal by the model, once again supporting the fact that this FCS goal should be a minimum.

Given that the Water Vole is primarily a riparian species, although fossorial populations are known (Stewart and others 2017), the natural range for Water Voles could best be

described as the length of waterways capable of supporting populations. The total length of waterways that reside within the environmental conditions found to be suitable for supporting Water Voles was 184,224 km, or 62.7% of the total waterway network across England. This length of waterway is likely an exaggeration as it is unlikely that all waterways within a 1 km resolution grid will be suitable for Water Voles. Fine scale habitat details, such as riparian bank angles or vegetation cover, are likely to play more important roles in defining if a stretch of water is suitable over that of the broad-scale environmental factors.

The compilation of suitable habitat into larger scale resolutions or other biologically significant areas has an impact on the FCS. The suitable habitat at 1 km resolution when compiled into hectads identified that 1,163 (77.9%) contained at least some degree of suitable habitat. However, there are 1,202 (80.5%) hectads which have never been occupied by Water Voles. Furthermore, 4,092 (74.5%) of river catchments, a more biologically relevant spatial area given Water Vole riparian preference, contained some degree of suitable habitat and 2,451 (59.9%) have had reported Water Vole presences. Both of these results and areas proposed roughly coincide with the statement that roughly 80% of hectads in England should be occupied as a goal for FCS (Ali Moore pers. comm.). Moreover, the reported number of records within these areas provides an idea of the current or historical distribution of Water Voles and could be used to define the increased numbers that would be needed to become occupied in order to reach FCS.

The fact that the number of hectads with presence records is already slightly larger than the number that contains suitable habitat indicates that these values should be considered a minimum. As this fact gives weight to the point that Water Voles can exist in areas of sub-optimal habitat or suitable habitat not identified by the model.

All of the information above provides a definable and measurable goal towards FCS for Water Voles. As such this represents information that can be used to help steer a SCS to achieving this goal.

### **4.3 Environmental variable importance and relationships**

The environmental relationships identified in the model fit relatively well with what has previously been identified for Water Voles. These relationships, corroborated by previous studies, provide weight and validation of the techniques used to define the area of suitable habitat and the FCS goals. Although this work primarily looks at habitat suitability the index of habitat suitability is analogous to the probability that a species should occupy a particular area.

#### **4.3.1 Climate**

Temperature seasonality was found to be the most important predictor variable for Water Vole habitat suitability, with increasing seasonality leading to increased habitat suitability. Seasonality affects animals and plants both directly and indirectly (Williams and others 2017). The effect of seasonal environments affects small rodent population dynamics directly through the critical parameters of age at first reproduction and the length of the

breeding season (Tkadlec and Zejda 1998). It can also affect rodent populations indirectly through their food such as through the seasonal aspect of plant growth and development (Croft and others 2017).

Most temperate mammal species restrict their sexual activity to a part of the year where environmental conditions are most favourable (Vasantha 2016). Water Voles are seasonal breeders and although their seasonal regulation is predominantly photoperiod, factors such as temperature and food availability may have regulatory functions (Poissenot and others 2021). The effect of temperature seasonality is linked to higher temperatures in the summer months, and this may be good for Water Vole populations and breeding success. For instance, the increased summer temperatures may increase the availability of forage as temperature is the primary factor affecting the rate of plant development (Hatfield and Prueger 2015). This increased food availability may influence demographic rates and increased reproductive success and immigration in Water Voles (Moorhouse and others 2008). Although it could also lead to colder winter months, which could also have a converse effect on Water Voles. Water Voles are known to have high over winter mortality (Strachan and others 2011, Baker and others 2018), and seasonality linked to lower temperature during these months could have a detrimental effect on Water Vole populations. However, solar radiation is directly correlated to mean and minimum winter/coldest month temperatures and is spatially inverse to seasonality. So, this could indicate that it is the increased summer temperatures that is driving the habitat suitability of seasonality.

The inverse correlation between temperature seasonality and decreased precipitation may also be advantageous to Water Voles due to a reduction in flood risk events. There are examples where flooding has caused population mortality events (Moorhouse and others 2009) or caused a habitat to become unoccupied by water. However, there are also cases where flooding did not have a significant negative effect on local Water Vole populations (Richards and others 2014).

The fact that Water Vole habitat suitability increased as isothermality decreased, indicates that stable temperatures between night and day are important for this species. Water Voles have been shown to most active at dusk and dawn (Brzeziński and others 2019) and the seasonal and diurnal predictability is likely advantageous to Water Voles especially during peak biological time, such as breeding or feeding.

Solar radiation was also found to be an important habitat suitability predictor for Water Voles with middle radiation levels found to be beneficial. The amount of solar radiation that reaches riparian habitats has important effects on both the aquatic and surrounding primary production that affects the composition and structure of riparian vegetation (Gregory and others 1991). Generally increased available solar radiation provides favourable conditions for riparian adjacent understory growth, and this provides food and escape from predators (Mate and others 2012, Lawton and Woodroffe 1991, Bonesi and others 2002). The increase of bank side vegetation has previously been identified to be a positive environmental predictor for Water Vole habitat suitability, at fine scales (Telfer and others 2001) and important for the presence of Water Voles (Priestly 2011). However, the

decrease in habitat suitability with high levels of solar radiation contradicts this and it is this relationship that makes the counties of Cornwall and Devon lower suitability areas. Excess solar radiation can have a negative effect on plants by causing overheating, desiccation, and photoinhibition (Barber and Andersson 1992, Long and Humphries 1994). This would be even more pronounced in riparian habitats where there is no shade from trees and other larger plants.

Solar radiation also provides increased energy, in the form of heat, when it strikes the water (Gregory and others 1991). Which is in keeping with the correlation found between solar radiation and the mean temperature across England and this should be kept in mind when interpreting this environmental relationship.

#### **4.3.2 Habitat**

Increasing percentage cover of trees, both broadleaved and coniferous, is associated with decreasing habitat suitability for Water Voles. This fits with what was previously found at fine scales where increasing percentage tree cover had a negative correlation with Water Vole habitat suitability (Telfer and others 2001). It is likely that this relationship is due to the effect that trees have on the understory structure, as trees were found to be inversely correlated to grasses and herbs (Bonesi and others 2002). This may be why Water Voles tend to avoid trees (Barreto and others 1998) and forests (Brzeziński and others 2019). Although low density of trees is advantageous to the species, potentially linked to shading from solar radiation extremes.

The amount of semi-improved grass was found to be advantageous but improved grassland was found to be detrimental to Water Vole habitat suitability. Grass coverage is critical for making a waterway suitable for Water Voles (Lawton and Woodroffe 1991) and it is expected that semi-improved or rough grasslands are beneficial to Water Vole habitats. Indeed, fossorial populations exist in semi-improved grassland habitats (Stewart and others 2017). However, improved grasslands are probably linked to agriculture and the identified relationship of decreases with this habitat coverage was also found by Nelli and others (2022). It was changes in farming practice that may have helped in the population decline of this species (Strachan and Jefferies 1993). It may be fine scale habitat features such as human disturbance or increased cattle poaching along waterways occurs in this habitat.

The preference of this species for heath habitats is supported by the presence of populations in Scotland in habitats that are predominately heather (Priestly 2011).

This project identified that middle percentage cover of built-up areas was suitable habitat for Water Voles. A large number of Water Vole records come from within cities and this urban habitat, especially waterways and green spaces within it, has been suggested as being important for this species (Leivesley and others 2021). Indeed, there are identified urban populations, for example, the fossorial population in Glasgow (Stewart and others 2017), and Water Voles are tolerant of moderate bank modifications and occupy a number of canals (Barreto and others 1998). It has also been shown in Poland that urban areas

could also act as a refuge from Mink predation (Brzeziński and others 2017). However, Water Vole habitat suitability was shown to decrease with increasing built-up percentage area coverage (Nelli and others 2022). This supports the findings of this project where suitability drops off with higher percentages of built-up habitat. However, the lower habitat suitability on low built-up area coverage could be an artifact of species recording and may be due to accessibility. Remote areas with little to no urban or suburban areas may be inaccessible to people and therefore species recording is also likely to be lower.

Freshwater habitats, including riparian, reedbeds, salt marshes, fens and bogs were all found to be suitable habitats for Water Voles. It is not surprising these habitats are important given the aquatic nature of this species, but these habitats can also act as refuges from predation by American Mink (Macpherson and Bright 2010; Carter and Bright 2003; Chen 2010; Richards and others 2014).

#### **4.3.3 Terrain and hydrology**

The identified terrain, of low slope and rugosity, plus the exceedance flow characteristics all suggest that slow flowing but not still streams and rivers are suitable habitat for Water Voles. This preference for slow flowing streams has been stated a number of times in the scientific literature (Priestly 2011; Bonesi and others 2002; Zejda and Zapletal 1969; Lambin and others 1998).

#### **4.4 Potential modelling considerations**

To identify a measurable and definable distribution of suitable habitat it was necessary to divide a continuous habitat suitability index into a binary classification. This was conducted by using a threshold cut off value. It is not recommended to split a continuous habitat suitability index into a binary outcome as detailed information is lost (Lobo and others 2008). However, in order to be able to define a measurable area of suitable habitat this is unfortunately required. In this project the area and distribution of suitable habitat for Water Voles is currently set based on a sensitivity and specificity threshold specified by the model. This threshold is a good point to place the cut off as it maximises the model's specificity and sensitivity,. However, changes to increase or decrease this threshold could be conducted to present a range of suitable distributions of habitat.

To be confident in the model output we have to assume that all records of Water Voles have been utilised in the data modelling procedure. This may not necessarily be the case as some records may not be available or accessible. Although the dataset used represents one of the most complete sources for mammalian observations, having been compiled to conduct the recent review and atlas of British mammals (Mathews and others 2018; Crawley and others 2020), it is possible that there may be further records that could help in defining FCS range and distribution. The Water Vole Database and Mapping Project (McGuire and Whitfield 2017), may represent a suitable dataset for this as it is a specifically riparian species database and could have further Water Vole records beyond the ones used in this study. This is especially true for recent records, as the current dataset only includes observations up to 2017. However, this may not have a dramatic

effect as Water Vole distribution has generally declined (Strachan 2004) and they are well monitored (McGuire and Whitfield 2017) so recent records are highly unlikely to come from areas beyond that of the data used in this project. Unless there is a case where Water Vole distribution has expanded beyond that of all the known historical areas! Other sources of biological records are such as those from Local Record Centres.

The use of habitat data from 1990 may have lost some of the detailed habitat interactions due to the large time frame of species records. Maxent uses spatially overlapping rasters to extract point source information from presences and pseudo-absences. As such the model has no way to incorporate information from a point source at different times, that is, habitat over decadal scales. The landscape of the UK is constantly changing and for this project the median LCM 1990 was used to be the median habitat classification across presence records that spanned decades. This may mean that a particular species presence record may be classified incorrectly and may hide some of the habitat relationships. The spatial predictions were made to 2021 habitats to provide the best estimate based on current habitat classifications. Modelling techniques such as Generalized Linear Models or Generalized Additive Models, could potentially take these changes into consideration if the habitat at time of species presence recording was extracted before the modelling process.

The model outputs are good in answering the national extent environmental conditions suitable for Water Voles. However, only using the general climatic, terrain and habitat scenarios suitable for Water Voles it is possible that a number of fine scale habitat features will be lost or not incorporated. Although, as was conducted previously (Coomber and others in press), if fine scale detail habitat requirement were to be investigated the low resolution national extent habitat suitability indices could be incorporated into fine scale SDM.

The fact that this modelling process was run at 1 km resolution may mean that some of the fine scale detail available was also lost during the dataset creation. A number of the environmental variables were available at resolutions greater than 1 km, for instance the Q2 and Q80 flow data. Compiling this into a maximum, mean or minimum value for a 1 km grid may granulate the environmental variable and thus hide some of the more detailed environmental presence relationships. To some degree the habitat data incorporated this by calculating the percentage cover within a grid.

#### **4.5 Spatial outcomes of predictions**

The large, pronounced area of unsuitable habitat in the counties of Cornwall and Devon appears to be driven by the importance and effects of seasonality and solar radiation environmental predictors. However, there are records of Water Voles from these areas but the number of records is quite low. The 1996-1998 Water Vole survey found only a couple of positive sites and the general occupancy of percentage sites surveyed from this region was the lowest across Britain (Jefferies 2003). Historical records from local mammal groups also indicate that Water Voles do occupy a number of sites in the south-west England, however, the proportion of hectads occupied are reported as low (Jefferies and

others 1989). Given the predicted habitat suitability the authors have spoken with local mammal groups from the area to ask them about their thoughts on the habitat suitability predictions. The Cornwall Mammal Group has indicated that there are some records from the area but they do not seriously disagree with the modelled habitat suitability (Dave Groves, pers. comm.).

Maxent can satisfactorily model observed data but may be limited where there are gaps especially across national extents (Croft and others 2017). So, this gap in suitable distribution across these counties could be an artifact of modelling inadequacies. Although the area does appear to be of generally lower habitat suitability, the presence of some historical records may mean that this area, despite being found to have a low overall habitat suitability, may potentially support Water Vole populations.

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