



Reeves' muntjac populations continue to grow and spread across Great Britain and are invading continental Europe

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Abstract

The appropriate response for controlling an invasive non-native species depends on the extent to which its invasion has progressed, which can be revealed by information on its distribution and abundance. Reeves' muntjac is a native deer to China and Taiwan, but has been introduced and become well-established in Great Britain. Moreover, in recent years, reports and verified records in the wild from other European countries have become more frequent. We reviewed the status of Reeves' muntjac in Britain and evaluated its national range expansion from 2002 to 2016. While the British population appears to have tripled in size since 1995, the rate at which it has expanded its range seems to have peaked at approximately 12% per year between 2002 and 2005 and has since declined. We also consolidated observations on its international distribution, including a conservative evaluation of its presence in zoological collections. We predict that this species could expand its range to include every European country, although the availability of suitable landcover and climate is likely to vary substantially between countries. To prevent the significant impacts to conservation interests that have been observed in Great Britain from extending across Europe, national administrations should consider eradicating Reeves' muntjac while that is still feasible.

Keywords Invasive species · Population growth · Range expansion

Introduction

The Convention on Biological Diversity (<https://www.cbd.int/invasive/done.shtml> accessed 13 January 2020) and EU Regulation 1143/2014 on Invasive Alien Species (IAS) (Moore 2020) demand action against IAS since they can impact populations, species and the ecosystems in which they live. The options for controlling IAS include prevention of

arrival, rapid removal to prevent establishment, or eradication to reverse an invasion and ongoing control of well-established populations (Simberloff 2003). Which of these options is appropriate depends on the availability of resources for management, the type of invasion curve exhibited by the species in question (Shigesada and Kawasaki 2002) and the location of the species on the invasion curve (Carboneras et al. 2018). Understanding this latter criterion requires knowledge of an IAS' spatial distribution and abundance and change in these over time.

Reeves' muntjac (*Muntiacus reevesi*, henceforth referred to as muntjac) is native to China and Taiwan and an IAS to Europe, which is known to cause substantial impacts to woodlands and plants of conservation concern (Cooke 2020). It was placed on the original list of IAS of Union concern by the EU in February 2015. The core of its European range is central and southern England, and it expanded rapidly across England and Wales during the latter 30 years of the twentieth century (Ward 2005). Despite resulting from a very small founder population (Freeman et al. 2016), the species was estimated to number approximately 50,000 in Great Britain by 1995 (Harris et al. 1995). Cooke (2019) described attempts to introduce muntjac to several locations throughout Europe, few of

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which were successful. However, increasing reports in the scientific and popular press have indicated that this species has now become established in continental Europe (see below) and in Japan (Ohdachi et al. 2009). To decide whether to and how to respond to invasion by muntjac, administrations for affected countries could benefit from understanding the degree to which populations of muntjac can grow and spread, and their potential for spread across Europe in the future.

We sought to evaluate the continued spread of Reeves' muntjac across Great Britain since 2002 and to consolidate recent accounts of their presence throughout the rest of Europe. We also conducted a brief review of changes to their abundance in Britain since 1995 and speculated on their potential for spread across Europe if left unchecked. This included an evaluation of its maintenance in European zoological collections.

Method

We accessed the global distribution of muntjac from the IUCN red list of threatened species (<https://www.iucnredlist.org/species/42191/22166608>, accessed 22 May 2020). We assessed if this distribution was missing the presence of muntjac in any country from published literature (search term: Muntjac *country name* in Google Scholar, searched 22 May 2020). Based on these results we supplemented the global distribution with data from national biodiversity databases (Table 1).

The extent of muntjac kept lawfully in licenced collections was evaluated by searching the Zoological Information Management System (ZIMS: <https://www.species360.org/products-services/zoo-aquarium-animal-management-software-2/> searched 17 October 2019), a global database of 1100 zoological collections across 96 countries, for records of *Muntiacus reevesi*.

We received muntjac distribution data for the UK from the British Deer Society constituting observation records from national surveys completed during 2007, 2011 and 2016. During these surveys, volunteers recording presence-only for each deer species. We plotted records at a resolution of 10 km² on the British National Grid projection, with earlier records layered on top of later records to illustrate range expansion over time. Range expansion between survey periods was calculated as a compound annual rate as described by Ward (2005).

We used landcover variables significantly associated with the presence of muntjac in Great Britain (identified from Acevedo et al. 2010) to map the minimum extent of Europe that might be suitable for muntjac occupation. These variables were matched as closely as possible to those in the CORINE Land Cover inventory for 2018 (<https://land.copernicus.eu/pan-europe/corine-land-cover>, accessed 22 May 2020) and

plotted at a resolution of 25 ha. The variables were woodland, grassland and agriculture with natural vegetation. Mountain ranges, which were identified as unsuitable for muntjac occupation by Acevedo et al. (2010), were identified from the EEA Geospatial Data Catalogue (<https://sdi.eea.europa.eu/catalogue/srv/eng/catalog.search#/home>, accessed 22 May 2020) and excluded from the dataset.

Results

The natural range of Reeves' muntjac is subtropical eastern China and Taiwan (Fig. 1) and possibly extends to tropical southern China. However, records from this latter region might be misidentifications of *M. muntjak* (Timmins and Chan 2016). The species was first liberated into the wild in England in 1901 (Chapman et al. 1994; Chapman 2020) and with many later releases has become widespread and abundant in England and increasingly in Wales, but not in Scotland (see below). More recently, it has been introduced to the island of Ireland, France, Belgium, the Netherlands, Denmark, Germany and Japan (Fig. 1, Table 1), where it is known to be breeding. The species is kept in licenced zoological collections across Europe and throughout the world and is highly likely to be kept in unlicensed collections too. The ZIMS database listed 99 institutions holding 355 individuals throughout Europe, 5 institutions holding 67 individuals in Asia and 40 institutions holding 105 individuals in North America during October 2019 (Table 2).

Carden et al. (2011) explained that muntjac were first reported in the Republic of Ireland in 2007, and Dick et al. (2010) confirmed the first verified report in Northern Ireland in 2009. The pattern of records is consistent with multiple release sites in counties Wicklow and Kildare in the Republic of Ireland and in the counties Down, Armagh, Fermanagh and Londonderry in Northern Ireland. There may have been other introductions in counties Wexford, Longford, Leitrim, Sligo, Roscommon and Donegal (Carden et al. 2011; Dick et al. 2010). The National Biodiversity Centre, Republic of Ireland (<https://maps.biodiversityireland.ie/Species/119475> accessed 19 June 2020) listed 133 records of muntjac sightings within 35 10-km squares since 2008.

Muntjac were introduced to France in 1891 at a number of locations, probably including Chambord, the largest enclosed park in Europe, and Rambouillet (Liger and Richard 1983). However, these introductions failed to establish (Baiwy et al. 2013) and muntjac were considered extinct in France at the time of the IUCN red list of threatened species entry for this species (Timmins and Chan 2016). However, records from the Indre et Loire, Loire et Cher and Indre regions of western central France continue to be reported, and probably have their source in a privately held collection that has included muntjac

Table 1 Global records of invasive non-native Reeves’ muntjac occurrence in the wild

Country	Muntjac status	Source
Austria	Unconfirmed reports only	F. Marshall, K. Schmidt. pers. com.
Belgium	Established Rare but growing	www.waarnemingen.be
Denmark	Established, localised No current evidence of growth	https://www.netnatur.dk/muntjac-yngler-nu-i-danmark/ https://www.tv2nord.dk/laeso/borgere-jagter-uonsket-hjortear-den-skal-skydes
France	Established, localised No current evidence of growth	https://inpn.mnhn.fr/ Terlin (2017)
Germany	Status uncertain No current evidence of establishment or growth	Hofmann (2018)
Great Britain	Established Widespread and abundant	British Deer Society and https://species.nbnatlas.org
The Netherlands	Established Rare but growing	www.waarneming.nl
Island of Ireland	Established Rare but growing	Carden et al. (2011); https://maps.biodiversityireland.ie/
Japan	Established	Ohdachi et al. (2009)

since 2000 (Terlin 2017). Occasional records have been reported from other parts of France, but these have mostly been

of single males only (Terlin 2017), so are unlikely to constitute established populations.

Table 2 Licenced zoological collections holding Reeves’ muntjac and listed in the ZIMS database

Country	Number of institutions	Number of males	Number of females	Number of births in previous 12 months	Total number of adult muntjac
Austria	1	1	0	0	1
Belgium	2	4	3	0	7
Czechia	6	12	13	0	25
Denmark	3	4	11	0	15
Estonia	1	1	0	0	1
France	26	44	50	4	94
Germany	19	25	44	1	69
Hungary	2	4	6	4	10
Lithuania	1	3	3	0	6
Italy	3	6	0	0	6
Netherlands	9	14	21	0	35
Poland	7	11	23	5	34
Portugal	1	2	4	0	6
Romania	1	2	0	0	2
Slovakia	2	2	4	0	6
Spain	4	9	8	0	17
Switzerland	1	0	1	0	1
UK	9	9	9	0	18
Ukraine	1	1	1	0	2
Israel	1	1	1	0	2
Turkey	2	3	3	1	6
Russia	2	0	2	0	2
China	1	20	39	0	59
North America	40	49	56	2	105

Baiwy et al. (2013) stated muntjac were ‘not established’ in Belgium in 2013, but reported isolated sightings increasing from 2005. Since 2008, reports have become more frequent, particularly near the cities of Brugge, Mol-Neerpelt, Braschaat and Hasselt. The authors did not discount the possibility of immigration from populations in the Netherlands. The website www.waarnemingen.be (www.waarnemingen.be/species/7700 accessed 10 June 2020) listed 385 observations involving 448 individual muntjac sightings since 2010, principally in the regions of East Flanders and Antwerp. Since 2010, muntjac have been reported from 56 10-km squares out of a total of 375 squares, four of which were in Wallonia and the remainder in Flanders and Brussels. Currently, a population genomic study is seeking to establish the extent to which the different populations share common ancestries and whether they are related to seized individuals from illegal private collections.

Muntjac were first recorded in the Netherlands during 1997–1998 in the provinces of Gelderland and Overijssel (Hollander 2015). Hollander (2015) reported that the population in Gelderland still persisted around the Veluwe, but that other observations across the Netherlands were infrequent. Since 2000, the trade and possession of any species of muntjac has been forbidden in the Netherlands and zoos must be licensed to keep them (Hollander 2013). Nevertheless, some road deaths have been reported each year and illegal ownership is suspected (M. La Haye, pers. com). In the province of Noord-Brabant, initial reports were recorded in 2005, and a mother and fawn were observed during 2013, but breeding in the wild could not be confirmed (Hollander 2015). The south of Noord-Brabant province borders Belgium, and migration from there into the Netherlands was not ruled out by Hollander (2015). The [waarneming.nl](http://www.waarneming.nl) website (<https://www.waarneming.nl/species/7700/> accessed 10 June 2020) listed 42 observations and 36 photographs of muntjac since June 2019, covering the provinces of Gelderland, Limburg and Noord-Brabant.

Confirmed records of muntjac in Denmark were not discovered in the scientific literature during our searches, but two online newspaper articles (Table 1) recorded the species as breeding in central Jutland during 2015 and at least one individual, which probably escaped from a farm known to breed muntjac on Læsø island during 2019.

After the first free-living sightings of muntjac in Germany in 2004, Nehring and Skowronek (2017) reported records from eight widely scattered areas within five states, mostly of single deer, and some of which were subsequently eradicated. Later reports have been widely scattered within Rheinland-Pfalz, including Bad Kreuznach, Kusel, Birkenfeld, Mayen and near the towns of Trier and Koblenz (Hofmann 2018). A muntjac skull was found in a forest near Hildesheim, Lower Saxony a few years ago (U. Kierdorf, pers. comm.).

In Austria some muntjac were taken in the latter part of last century to a private deer park at Altenfelden in the Oberosterreich (F. Marshall, pers. com.). Some 90 km to the south-east of Altenfelden around 2018, there were unconfirmed reports close to Mondsee, not far from where muntjac had been held privately.

The range of muntjac in England has continued to expand since 2002 (Ward 2005). The annual compound rate of range expansion accelerated from its 1972–2002 rate (8.57%) to nearly 12% per year by 2007 but has since declined to 2–3% (Table 3). The invaded area of England and Wales grew substantially between 1972 and 2002, with a pattern consistent with movement by human agency and expansion of their core range (Chapman et al. 1994; Ward 2005; Chapman 2020). During that period, muntjac expanded their range into East Anglia, Lincolnshire, all four counties of Yorkshire and into South Wales, and isolated reports were received throughout western England and the Midlands. Records from isolated parts of Scotland were not verified (Ward 2005). Since 2002, new records of muntjac observations have in-filled the core range in central England and have expanded to cover the central south coast (Fig. 2). Expansion in the south west of England and Wales seems to have been much slower, with greater patterns of expansion into Wales across the border with England, and markedly into Cheshire and Lancashire in the north west of England. Records continue to be reported in the north east of England, although an extensive search for muntjac in county Durham revealed no tangible evidence of their persistence (I. Smales, pers. comm.). At the time of the 2016 survey, muntjac were present in 39.8% of the 2653 10-km squares throughout mainland Great Britain (excluding the Outer Hebrides, Orkney and Shetland islands), including 61.3% of the 1715 10-km squares of England and Wales.

The pattern of range expansion across Britain has been consistent with those identified previously: gradual in-filling of the range within the core area of central England, gradual expansion at range edges and frequent new reports from locations at considerable distance from core populations (Fig. 2).

The pattern of suitable landcover for muntjac is highly variable across Europe (Fig. 3). Every Western European country has some landcover likely suitable for muntjac occupancy, and most countries have abundant landcover that may be suitable. Moreover, there appear to be many potentially suitable corridors that could facilitate expansion from the populations in France, Belgium, the Netherlands and Denmark to the Russian border and the eastern Mediterranean.

Discussion

The change in the rate of muntjac range expansion in Great Britain likely relates to their position on the idealised invasion curve (Carboneras et al. 2018). As muntjac have in-filled the



Fig. 1 The global distribution of free-living Reeves’ muntjac to the year 2020 (distribution in Japan not shown). Adapted from Timmins and Chan (2016)

core range in central England and reached the south and east coasts, the ability to expand their range has been limited to the remaining northerly and westerly directions. Moreover, the suitability of land for muntjac is not uniform across the country, potentially becoming less favourable in more northern and western regions (Croft et al. 2019). However, predictions of land favourability for muntjac in Britain have necessarily been based on data recorded across their national range at the time of the study in question and included no information on landcover within their native range. We assumed that landcover in China was likely too different to that of Europe for its inclusion in our predictions of potential spread across

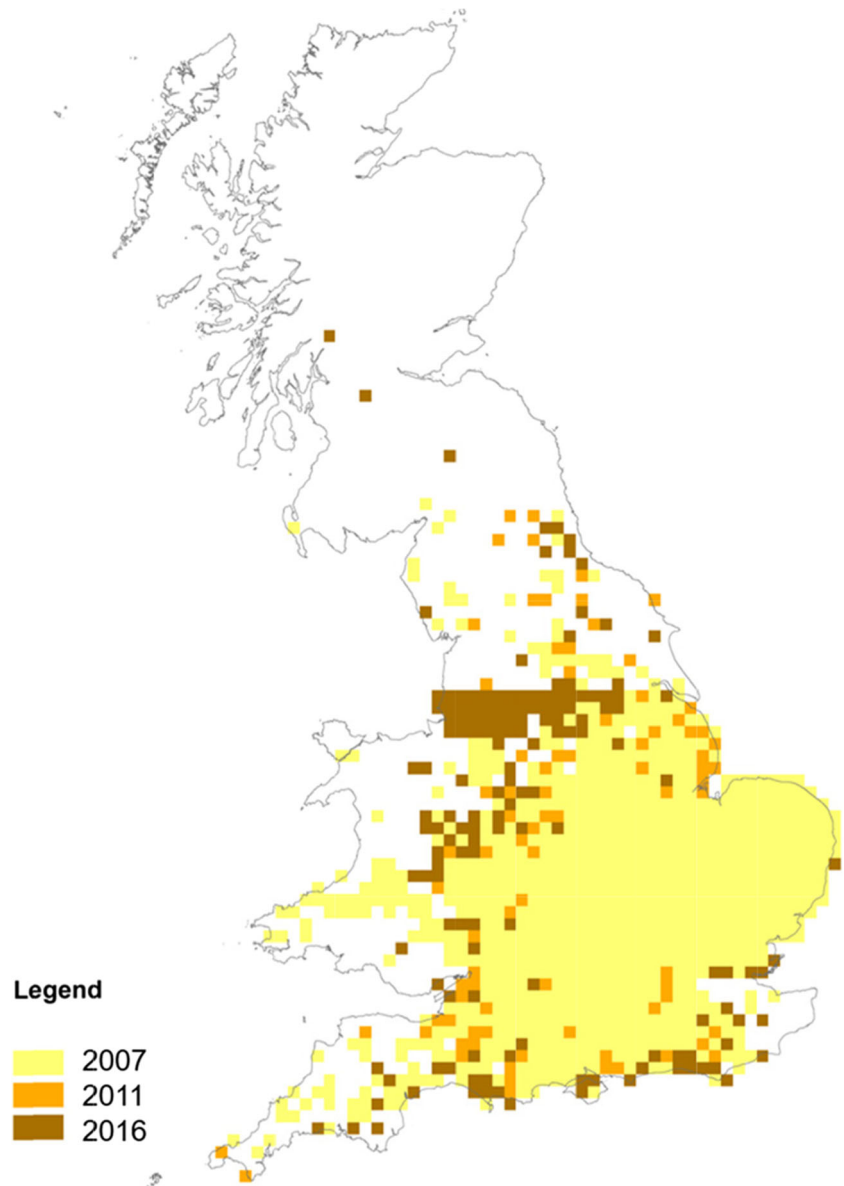
Europe, although this assumption has yet to be tested. It is perhaps noteworthy that Croft et al. (2019) predicted a greater area of favourability for muntjac in northern Britain than did Acevedo et al. (2010), and that there were many subtle differences in predicted future distributions and likely maximum range edges between the two studies. The maximum geographical range extent of muntjac in Britain may be greater and distributed differently than currently predicted (Croft et al. 2019). The reliability of predictions of future range extent in Britain could be improved with more reliable distribution data than are currently available. This could be achieved by ensuring that records of deer observations are valid and correctly identified, that every 10-km square across the country is surveyed and that a species’ absence is recorded following extensive searching revealing no evidence of presence.

Table 3 The number of 10 × 10-km squares in which Reeves’ muntjac has been recorded during five survey periods by the British Deer Society, and the annual rate of change between survey periods that the increase in occupancy represents

Year	Muntjac		Source
	Presence	% change	
1972	40		Ward (2005)
2002	472	8.57	Ward (2005)
2007	816	11.57	BDS
2011	900	2.48	BDS
2016	1055	3.22	BDS

Harris et al. (1995) estimated approximately 50,000 muntjac in Britain, and 23 years later, Mathews et al. (2018) estimated 115,000–147,000, consistent with a tripling in abundance assuming the accuracy of both estimates. However, there are no robust, systematic nation-wide surveys of any deer species across Britain. Therefore these estimates constitute extrapolations from a limited number of case studies on muntjac density and predictive studies of range expansion (e.g. Acevedo et al. 2010; Croft et al. 2019), with a consequent risk of inflating error. Indeed, the consequences of extrapolating limited data with considerable uncertainty is exemplified by Croft et al. (2017) who applied a standardised approach for

Fig. 2 The distribution and range expansion of Reeves' muntjac in Great Britain between 2007 and 2016



combining information on mammal species abundance and range to estimate muntjac abundance. Their estimate was 1,962,152 to 5,046,501, which is likely far higher than reality. Croft et al. (2017) used density estimates from the few localities in England where the species has been surveyed and where muntjac exist at relatively high densities. Without robust, empirical evidence of muntjac density or population size from a representative sample of sites across Britain and without properly validated records of their distribution, all estimates of national population size remain highly uncertain and potentially biased. However, it is perhaps reassuring that predictions from the National Gamebag Census (Aebischer et al. 2011: a survey of animals shot on a large number of private estates around Britain) estimated growth of numbers of muntjac shot in Britain of 138% to 337% between 1995 to 2009. This estimate is consistent with the predicted change in

abundance between the estimates of Harris et al. (1995) and Mathews et al. (2018).

Most striking about the growth and spread of muntjac populations globally has been the repeated reports of observations far from and in isolation of their existing ranges (Figs. 1 and 2), which strongly suggests transport by human agency (Chapman et al. 1994). Muntjac are widely kept in licenced zoological collections across Europe (Table 2) and are likely to also continue to be kept in unlicensed private collections, which became illegal in EU member states following the implementation of EU Regulation 1143/2014. Amongst anecdotal reports and private comments received during this study was a high frequency of alleged links between zoological collections and the presence of free-living muntjac in their vicinity. The recent emergence of muntjac on the island of Ireland and across continental Europe can only have resulted

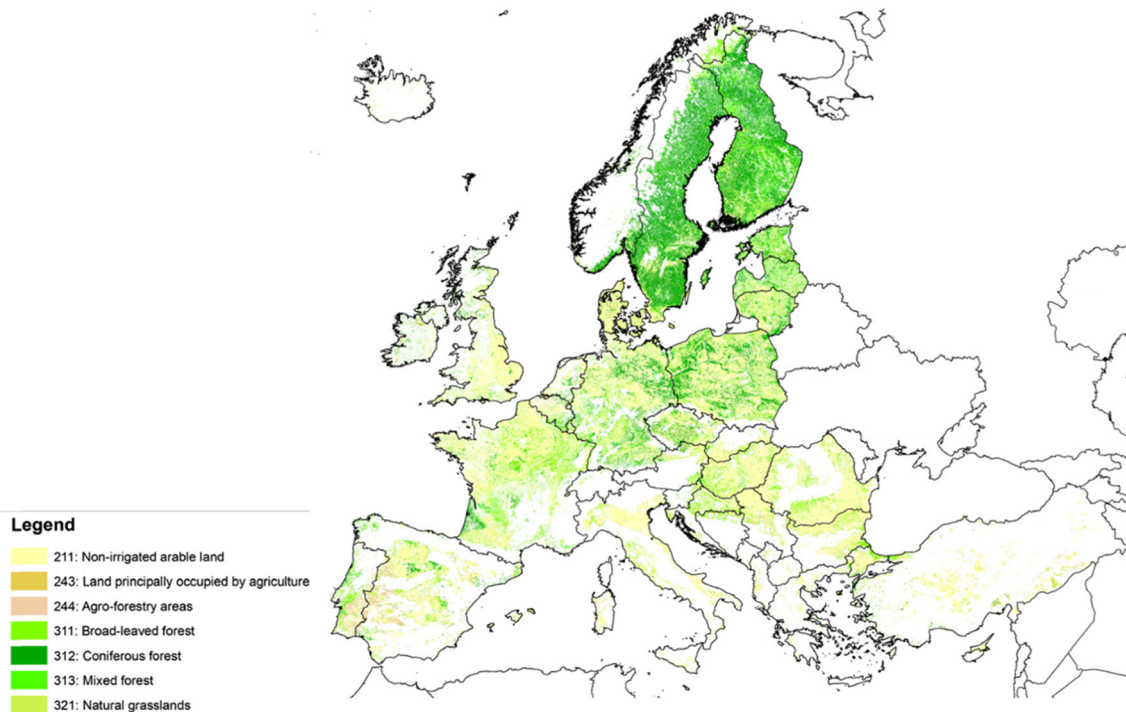


Fig. 3 Landcover in Western Europe likely to be suitable for occupation by Reeves' muntjac

from deliberate or accidental introductions. The pattern of their distributions in these and other countries, characterised by observations from discrete and distant locations, is consistent with the earlier pattern observed in Britain, and which has been strongly influenced by the repeated introduction of muntjac to new locations (Chapman 2020).

The fact that muntjac have been frequently and consistently reported in several locations within Europe is consistent either with the regular reintroduction of animals or to the establishment of the species. The potential consequences of establishing populations of muntjac on the European continent can perhaps be learnt from experience in Britain. Britain's population started from a very small founder population (Freeman et al. 2016) but has grown to cover a large proportion of England and probably numbers up to 147,000 (Mathews et al. 2018). During the 1970s, muntjac was considered an interesting yet benign addition to the British fauna by some government advisors (Anon pers. comm.). In the 1980s, calls to consider the impacts and management of the species were just starting to be made (Bray 1980). Their impacts to plants of conservation importance and woodlands in particular can be extremely severe (Cooke 2020), and it seems likely that they compete with native species, out-competing roe deer (*Capreolus capreolus*) under some circumstances (Chapman et al. 1993; Hemami et al. 2004; Acevedo et al. 2010). These and other considerations have motivated the Scottish Government to implement legislation to monitor their keeping in collections and to adopt a zero-tolerance policy towards their presence in the wild (<https://www.gov.scot/>

[publications/management-wild-deer-scotland/pages/22/](https://www.gov.scot/publications/management-wild-deer-scotland/pages/22/) accessed 10 June 2020). The lawful keeping of muntjac in Belgium is similarly being strictly enforced and their presence in the wild is being controlled. For free-living populations in England and Wales, the only option is for ongoing control to prevent or reduce growth and spread (see Moore 2020), the annual costs of which are likely to be significant (Ward and Lees 2011).

Fløjgaard et al. (2009) opined that there was no immediate risk of muntjac invading Denmark from Great Britain, but that the species might be introduced to serve hunting interests. Indeed, 10 years later, it was established and gaining favour amongst hunters (Table 1). This pattern appears to have also emerged in France, Belgium, the Netherlands, Ireland and Germany too. Perhaps, for muntjac, British history is repeating and will continue to repeat elsewhere in Europe. If left unchecked, the British experience suggests that populations will grow and spread, and people will likely continue to move them to new locations. Figure 3 illustrates the likely minimum range extent that muntjac could achieve across continental Europe, based on their presence in comparable landcover types in Britain. Muntjac might not persist, grow or spread particularly well where these landcover types correspond with areas that experience extremely low winter temperatures. Chapman et al. (1994) reported that the extremely cold and long winter experienced in Great Britain during 1962 to 1963 resulted in substantially elevated mortality of muntjac in the core of their English range. Moreover, Acevedo et al. (2010) found a higher likelihood of muntjac absence from more northerly parts

of Britain. However, global climates are forecast to change, with Europe likely to experience a general northward shift of bioclimatic zones by the end of this century under the International Panel of Climate Change's scenario A2 (Metzger et al. 2008). The more arid landscape of the Iberian Peninsula might continue to disfavour the establishment of muntjac if introduced and the Pyrenees probably constitutes a geographical barrier to natural spread. Indeed, Acevedo et al. (2010) found that the area of uplands and mountains was associated with the absence of records of muntjac in Britain, and Ward and Lees (2011) postulated that the uplands of the Scottish borders might prevent the natural invasion of Scotland by muntjac if they invade the far north of England.

Much of the Mediterranean region may become even less favourable for muntjac than at present as it warms and becomes drier. Conversely, many parts of Northern Europe, particularly those countries along the northwest Atlantic coast (northern France to Scandinavia), might become more favourable, especially where increased average temperatures and rainfall continue to promote strong growth of woodlands and forests. However, the precise response of muntjac to continental European environments is uncertain, because all European range modelling to date has only included landcover variables from Great Britain and not from other parts of the world inhabited by muntjac, including their native range, where conditions are different. Nevertheless, the genetic structure of muntjac populations in China provides clear evidence of responses of muntjac to climate change over the millennia (Sun et al. 2019), so we should expect them to respond by altering their global ranges in the future.

Whether large predators may impede the spread and growth of muntjac populations remains to be seen. The grey wolf (*Canis lupus*) has been growing and spreading across much of Europe in recent years (Herzog 2018) and can regulate roe deer (*Capreolus capreolus*) populations (Randon et al. 2020). Improved understanding of the responses of wolves to the increasing presence of muntjac and the response of muntjac populations to wolf presence and predation could offer insight into the nature of predator-mediated trophic cascades (Letnic and Ripple 2017) when impacted by an invading non-native species, and the potential role of native predatory mammals in regulating (or not regulating) invasive non-native mammals (see Sheehy and Lawton 2014).

Perhaps the introduction to and establishment of muntjac in continental Europe offer them a much greater likelihood of persistence in Europe under climate change than Great Britain, notwithstanding their responses to predators. Records from continental Europe are all consistent with the early stages of invasion, hence now is the most efficient and cost-effective time to implement eradication (Robertson et al. 2017) and to engage in a campaign of education and

enforcement to seek to minimise or eliminate the risk of muntjac being moved around the continent by people (Genovesi et al. 2015; Oele et al. 2015). Germany has demonstrated the feasibility of eradicating small groups and individual muntjac on several occasions (Nehring and Skowronek 2017), and The Republic of Ireland, Northern Ireland and Belgium, at least, are planning control options for this species. Ireland, France, Belgium, the Netherlands, Germany, Austria and Denmark have the opportunity to choose to adopt a zero-tolerance policy that is consistent with delivering the EU regulation on invasive species (Moore 2020) and with Article 8(h) of the Convention on Biological Diversity (<https://www.cbd.int/invasive/done.shtml> accessed 13 January 2020) and which England and Wales have lost.

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Author contribution Study conception and design were performed by Alastair Ward. Material preparation and data collation were performed by Alastair Ward, Suzanne Richardson and Joachim Mergeay. Data analysis was performed by Alastair Ward and Suzanne Richardson. The first draft of the manuscript was written by Alastair Ward. All authors commented on previous versions of the manuscript and read and approved the final manuscript.

Data Availability All data are available from the primary sources listed in the manuscript.

Code availability Not applicable.

Declarations

Ethics approval The University of Hull Research Ethics Committee approved this study. Approval number FEC_2020_137.

Consent to participate Not applicable.

Consent for publication All authors have consented to the publication of this manuscript.

Conflict of interest The British Deer Society paid travel expenses to Alastair Ward for attendance at a symposium on Reeves' muntjac held at Newcastle University, UK, in January 2020, from which this manuscript arose.

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