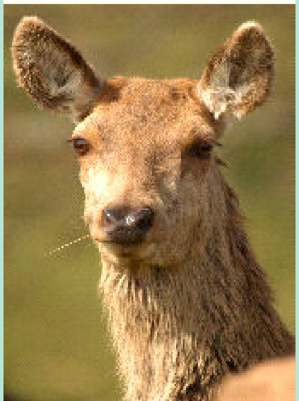
the deer initiative

Research Report 10/2



Predicting abundance and distribution of wild deer in England: supporting a vision for Natural England.

Rory Putman and Alastair Ward

August 2010

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1. Introduction

1.1 In order to develop future policy and inform management of the various different native and non-native species of deer within the UK, and their potential impacts (whether on agriculture, forestry, natural habitats, in spread of disease or in the context of public safety), it would be helpful to be able to predict, in some way, future patterns of distribution and abundance.

1.2 High deer densities can be associated with negative impacts on human interests, including the conservation status of sensitive woodland environments (Fuller and Gill 2001). Such impacts may be further exaggerated in the short-term through increased development pressures across the urban and rural landscapes. In the medium to long-term the effects of climate change are likely to become more obvious, and may include higher productivity of deer populations (Irvine *et al*., 2007). To facilitate decisions and approaches to the sustainable management of wild deer impacts it would be helpful to identify the conditions under which these impacts can be tolerated throughout British landscapes (Putman et al., Mammal Review *in press* (a)) and especially to determine more precisely deer distributions and abundances and the potential for changes in these.

1.3 It has been demonstrated that all species of wild deer have expanded their national ranges in recent years (Ward, 2005; Ward *et al*., 2008a) and are continuing to expand their distribution. Some foreknowledge of where deer populations are likely to continue to expand their range, or within that range, where they are likely to build up especially high densities, would help immeasurably to predict where and when management effort might need to be targeted to prevent, or reduce, the speed of range expansion and/or to reduce local densities.

1.4 Given, necessarily, limited resources it would make more efficient use of those resources if it were possible effectively to predict where there may in the future be local areas of high density and thus possible negative impacts. By the same token, it is equally important to predict areas where, even without human intervention/ management, deer populations would be unlikely ever to reach particularly high levels or impacts, and where therefore management can afford to “ignore” deer in those areas and focus attention on the places where there may be future problems.[1]

1.5 High deer densities are not necessarily and automatically linked to high impacts, nor are those impacts necessarily damaging; <u>impacts</u> are in effect ecologically neutral and may only be considered damage if they conflict with other land use objectives, previously identified (Reimoser and Putman, 2010; Putman et al., Mammal Review in press (b)).

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[1] In such analysis it is important however to note that even where deer may occur (now or in the future) at comparatively high density, this may not necessarily result in negative impacts, and high (or potentially high) density does not of itself constitute an issue. Indeed there may be areas where high densities of deer can be tolerated without any negative implications (and such high densities might be actively encouraged in such areas, for conservation or recreational benefits they may provide); conversely in other areas, negative impacts may be apparent even at comparatively low deer population density.

1.6 There are in addition many positive benefits which may be associated with deer presence – in terms of public amenity and public enjoyment, recreational stalking and actual financial gain from commercial stalking, as well as benefits in conservation terms (suppression of scrub in open habitats, maintenance of clearings and glades within woodlands etc.). It is thus important to establish a set of criteria against which to determine when intervention (or prophylactic management) may be appropriate and where circumstances do not warrant the costs of intervention.

1.7 Separate analysis of the critical threshold densities of deer above which damage to agriculture, forestry, amenity woodlands, conservation site and/or public safety may become of consequence has recently been published (Watson et al., 2010 Defra Thresholds report; Putman et al., Mammal Review in press (a)) and will not be further explored here, although much further work is required to define density thresholds at which deer impacts become intolerable for a wide variety of land use types and situations. This review is attached here as Appendix One.

1.8 Similarly, another review has recently been published (Putman and Watson, 2009; Putman et al., Mammal Review in press (b)) of methods available to assess directly deer impacts at the landscape, rather than site scale, and appropriate ways in which to interpret those data (as to whether or not intervention may be required). This review is also attached here as Appendix Two.

1.9 In this paper therefore we focus specifically on consideration of the distribution and abundance patterns of different species of deer in England and Wales and the potential to predict future distribution patterns. We review available information on historic and current distributions of the six species of deer free-living in England and Wales, and consider what factors would appear to affect (or at least be associated with) variations in local occupance. We then use those relationships to attempt to predict likely future changes in distribution and relative abundance of the different species of deer in England and Wales.

1.10 Specifically , and in relation to the original contract brief, we

- Quantify and map the local abundance of each species of deer across England (Sections 2 and 3 and Appendix Three)
- Identify habitat-specific factors associated with deer presence and rates of range expansion for each species (Sections 4 and 5 and Appendices Four and Five)
- Predict and map the likely future distributions of each species across England (Section 6)

1.11 In Appendix Five, our analyses focus specifically on identification of features of the landscape that have constrained or promoted the spread of each species of deer across Britain. We suggest that factors that appear to have constrained range spread in the past could hold potential for controlling the spread of deer in the future (Section 7).

1.12 Finally, we

- Identify data required to build a model or models to identify the conditions under which the impacts of deer can be tolerated and to assess how environmental features may be used to aid the management of deer populations.

In Appendix One we review the available literature in an attempt to derive critical thresholds of deer density above which some level of damage might occur to agriculture, forestry or conservation habitats, or where deer may pose a threat to public safety . In Section 8 and Appendix Six we offer a model structure to develop these ideas further in trying to identify what levels of impact may be considered broadly "tolerable"

2. Recent distribution and patterns of abundance of deer in England and Wales

2.1 Six species of deer are currently found in the wild state in Britain. Only two of these (the red deer *Cervus elaphus* and roe deer *Capreolus capreolus*) may be regarded as truly native; populations of all other species (fallow deer *Dama dama*, sika *Cervus nippon*, Chinese muntjac *Muntiacus reevesi* and Chinese water deer *Hydropotes inermis*) derive from ancient or more recent introductions by Man. Deer of at least one species now occur in over 86% of all 10 km x 10km grid squares of Scotland, England and Wales.

2.2 It is frequently stated, within scientific papers and policy documents concerning wild deer in Great Britain, that their numbers are increasing. However, no reliable national data are available to support these assertions and none have been through the process of formal peer review. By contrast, there is good information to suggest that national distributions, at least of the majority of these species, have expanded at an increasing rate in recent years, and that these distributional ranges continue to expand.

2.3 It is highly likely that numbers of deer have increased in association with these range expansions, as illustrated by game bag records for roe deer (Battersby, 2005) but these have yet to be reliably estimated or mapped.

<u>Red deer</u>

2.4 The British Isles presently hold the largest population of red deer in Europe, accounting for c. 30% of the total European population (Clutton-Brock and Albon, 1989). However, the current distribution of red deer in the British Isles is very uneven with most of the population occurring in Scotland, and comparatively few, much smaller populations scattered in England, Wales and the Republic of Ireland.

2.5 Red deer are present in most suitable habitat in mainland Scotland, with the exception of south east Scotland, and are also present on many of the Hebridean islands, and their range is still expanding into the few regions they do not currently occupy (Ward, 2005). The size of the Scottish population is not known with great precision and there is considerable debate about the actual number of red deer and the extent to which the population may be changing. [2] Our best estimates come from statistical modelling of population growth rates based on Deer Commission for Scotland counts of open hill land (Clutton-Brock et al., 2004), which suggest that open hill populations may have risen from 198,000 (± 35,000; 95% confidence interval) in 1967 to 351,000 (± 33,000) in 2000 (Clutton-Brock et al., 2004; T. Coulson, pers. comm.).

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[2] In large part such debate stems from the fact that counting methodologies have changed over the years from counts on open hill ground, carried out largely by men on foot, to more recent estimates which are based in some areas by aerial count employing helicopters and digital cameras (Daniels, 2006). Thus, whether the difference in estimates is simply due to a difference in the methods or whether it reflects a genuine increase in numbers is actually not clear.

The number of red deer living in Scottish forestry has been put as high as 100,000 (Hunt, 2000, 2003) but this is pure speculation (Clutton-Brock et al., 2004).

2.6 In contrast to their more or less continuous distribution in Scotland, wild red deer are more patchily distributed in England (Ward, 2005). Numbers of red deer in England were estimated at 12,500 by Harris et al. (1995). Alternative estimates offered by Ward (2007) suggested a total population in England of between 16,000 and 20,000. Differences in estimates should not be taken as indicative of a trend in population numbers as they may reflect differences in methods used to estimate population size.

2.7 As noted, few red deer are recorded in Wales: Harris *et al.* (1995) estimated numbers at <50; Ward's more recent estimates also suggest relatively low populations at between 100-400. Numbers in Ireland are estimated at between 3,000 and 4,000 with <2,000 in Co. Donegal and <2,000 in Co. Kerry (T. Burkitt, pers. comm)

2.8 A few present day English populations of wild red deer are likely to have native ancestry. However, the vast majority of populations probably derive from relatively recent introductions, some of them documented. For example, the population in the Quantock Hills in Somerset was introduced specifically for hunting in 1860, and the population in the New Forest in Hampshire was re-established by introduction in the early 1960s (Putman and Langbein, 1999; Carne, 2000). Even populations which may contain native stock have probably experienced considerable 'subsidy' over the years with introductions of animals from other genetic origins or assimilation of animals escaping from nearby deer parks and captive collections. Deer of original native stock are only confirmed in parts of Ireland, Scotland and north-west England (Lowe and Gardiner, 1974).

2.9 Many populations are in addition currently suffering from hybridisation with the more recently introduced sika deer (*Cervus nippon*; Harrington, 1973, 1982; Lowe and Gardiner, 1975; Ratcliffe *et al.* 1992; Abernethy, 1994, 1998; Goodman *et al.*, 1999; Pemberton *et al.,* 2006; Diaz *et al*., 2006).

Roe deer

2.10 Roe deer are also native to the UK (although they do not occur in Ireland). Due to habitat loss and severe hunting pressure, however they became extinct throughout much of the country in the Middle Ages; by the beginning of the 18th century they are believed to have disappeared from England and Wales and to survive in Scotland only in a few relict populations in the north and west (Ritchie, 1920; Prior, 1968). An increase in woodlands during the eighteenth century led to a range expansion in Scotland, but populations in England stem largely from local introductions of stock translocated from Scotland or imported from continental Europe.

2.11 Roe of unknown origin were re-introduced to Milton Abbas, Dorset in 1800 by the early 1900s numbers were estimated in Dorset at 300-400 and there were also populations in the New Forest, Surrey and Sussex. The roe population of East Anglia is believed to originate from an introduction of German deer to the area between Brandon and Thetford in 1884 (Chapman *et al.* 1985), and the roe deer in the Lake District are thought to be of Austrian origin (Staines and Ratcliffe, 1991; Hewison and Staines, 2008). From these centres, roe deer have spread throughout much of eastern, northern and southern England during the course of this century. They are now absent only from areas in Kent, the Midlands and Wales (Ward, 2005).

2.12 Estimates of densities in woodland (based on dung group counts at 20 sites in Scotland; Latham *et al*, 1997) vary from 0.5 to 24.8 per km^2. Locally, densities of 75 deer per km^2 have been recorded in isolated woods in southern England but such estimates may in practice have included only part of the animals' ranges. Estimates for actual overall population size are more difficult to assess. Harris *et al.* (1995) offer estimates for roe in England and Wales at 150,000 with an additional 350,00 estimated to occur in Scotland.

2.13 More recent estimates by Ward (2007) suggested total populations of around 300,000 (range 275,000- 320,000) with perhaps 95,000 in England, 200,000 in Scotland and between 2,500 and 4,700 in Wales. As noted for red deer however, differences in estimates should not be taken as indicative of actual trend in population number, but more probably reflect differences in methods used to estimate population size.

Fallow deer

2.14 Fallow deer were present in the UK before the most recent glaciation, were made extinct by the glacial advance (c. 11,000 years BP) and re-introduced into parks and hunting reserves by the Normans in the 11th century (Chapman and Chapman, 1975; Langbein and Chapman, 2003; Langbein *et al*., 2008).

2.15 Populations in the wild state have become established through regular escapes from such enclosed park populations, or by release when parks were abandoned or broken up. However, as also noted by Liberg *et al* (2010; for Sweden), dispersion from original sites of release is notably slow. As a result their current distribution in the UK still owes much to this history of establishment around the sites of past or present deer parks. Fallow now occur in 29% of all recorded 10 km squares in England and Wales and locally in Scotland and in southern Ireland.

2.16 Population densities reported by Harris et al. (1995) ranged from between 18- 43 fallow per km^2. Even where accurate counts are available, it is rarely possible to relate these counts to the areas covered by the deer. In agricultural landscapes, densities are particularly hard to estimate, since they can vary tremendously with no apparent environmental cause, although levels of human disturbance and intensity of culling may be more important here than environmental quality *per se*. Further, populations are often heavily managed, so that density is maintained at a level that is not related to carrying capacity.

2.17 Harris *et al.* (1995) estimated overall population number in the region of 100,000, although they noted that such estimates were not particularly robust. Using different methodologies, Ward (2007) estimated numbers of fallow deer at between 144,000 and 184,000, with the bulk of the population occurring in England (127,500 - 156,500). Established feral populations of fallow have been reported to tend to expand slowly, with many remaining localised near to the deer parks from which they escaped (Chapman, 1975; Pemberton and Smith, 1985), however the results of a study of range expansion in British deer contradict these claims, showing significant expansion in fallow deer ranges since 1972 (Ward, 2005).

Sika

2.18 From their native Asia, sika have been widely introduced to a number of countries around the world - to much of Europe, including Austria, Denmark, the Czech Republic, France, Germany, Poland and Switzerland, as well as to the British Isles.

2.19 Sika were first introduced to Britain in 1860 when the Zoological Society of London was presented with specimens of both *C. n. nippon* and *C. n. hortulorum*; in the same year Viscount Powerscourt introduced Japanese sika into his deer park at Enniskerry in Co. Wicklow, Ireland. Numerous further introductions were made up until the 1930s - but in practice few of these later introductions came directly from Asia. Indeed only two populations, at Dawyck in Peebles-shire (extant) and Pixton Park in Devon (now extinct), are known for certain to derive from later introductions directly from Japan (Ratcliffe, 1987), although the origins of some other populations such as those in the New Forest of Hampshire are not recorded. It is clear, however, that many later introductions were of animals originally bred at Powerscourt Park where hybridisation between red and sika deer is known to have taken place (Powerscourt, 1884; see more below) and thus that many of the introductions to new sites may have involved animals already of hybrid status. For simplicity however, we will in this paper continue to refer to them as sika, on the basis that we use this term to refer only to phenotypic character, with no presumption of underlying genetic makeup.

2.20 Sika are now widely distributed on the Scottish mainland with some 14,000 km^2 colonised by the species (Putman, 2008). The main centres of population are in Peebles-shire, Argyll, Inverness-shire, Ross and Cromarty and Sutherland; all show dramatic recent expansion in range (Ward, 2005). Within mainland Britain as a whole, sika expanded their range at 5.3% per year between 1972 and 2002 (Ward, 2005) and a more recent analysis suggests a 7.3% per year expansion in range between 2002 and 2007 (Ward *al*., 2008a); these figures are dominated by the Scottish spread. There is little doubt that commercial conifer forestry is the preferred habitat of sika in Scotland and has greatly assisted their expansion (Livingstone, 2001).

2.21 Some authors have estimated that there are about 10,000 individuals in Scotland (Harris et al., 1995; Abernethy, 1998; Putman, 2008), but since the population estimation is very difficult in commercial forestry, this is little more than an educated guess. The fact that 6,000 sika were shot in Scotland in 2006-2007 (DCS, 2007) suggests that the population is substantially higher.

2.22 As described for red deer, populations of sika in England are much more discrete and localised (Ward, 2005), with numbers estimated at between 1,500 and 2,000 (Harris et al., 1995; Ward, 2007). English populations are found in the New Forest of Hampshire, south-east Dorset, Lancashire and the Lake District, with some smaller ones in Northamptonshire, Bedfordshire, and near the Oxfordshire, Buckinghamshire borders (Putman, 2000). There is some indication of a spread of the south Dorset population westwards into Devon and Somerset.

Muntjac

2.23 Following the original introduction to Woburn Park in 1894, Chinese muntjac are now established in most of southern England as far north as North and West Yorkshire, Derbyshire, Lincolnshire and Nottinghamshire, including some urban areas. In addition, there are scattered records outside this range, including Cheshire, Cumbria, County Durham, and Northumberland and in parts of north Wales and most of the counties adjoining the south Wales coast. The pattern of range expansion and current distribution of muntjac suggests multiple introductions and probably continuous translocations to different parts of England thereafter (Chapman et al, 1994; Ward, 2005).

2.24 Harris *et al.* (1995) estimated a total population size in England of about 40,000 with current numbers in Wales <250. Numbers are however likely to be still increasing ; Ward's (2007) estimates for the number of muntjac in England and Wales was of some 100,000 (range 91,600 - 116,700) and Ward (2005) estimates an annual rate of expansion of distribution at around 8.2%.

Chinese water deer

2.25 The Chinese water deer was first introduced into Britain at Woburn Park in 1896, from where thirty-two individuals were transferred to Whipsnade Zoo in 1929/1930. Leading up to the Second World War large populations built up in these areas. During and after the war, some escapes and deliberate releases occurred and the deer was first reported in the wild in Buckinghamshire in 1945 (Cooke, 1998).

2.26 Current wild populations are established in Bedfordshire, Cambridgeshire, Norfolk and Suffolk with a discontinuous distribution (Cooke and Farrell, 2008). Large populations centre around Woburn, Whipsnade, the Cambridgeshire Fens, and the Norfolk Broads; some small feral populations have established in Suffolk but died out in Hampshire, Northamptonshire and Shropshire (Cooke, 1998). Some sightings have more recently been reported in the Thames Valley.

2.27 The low numbers and impermanence of many feral populations have been taken to suggest that conditions are not ideal for the establishment of this species, and that numbers are likely to remain low (Harris *et al.,* 1995). However more recent analyses suggest the potential for expansion may be considerably greater than estimated. Recent population estimates by Cooke (Non-native Species Risk Assessments) were more than double the 1,500 animals estimated by Ward in 2007, and their reported range has expanded by 22.2% between 2003 and 2007 (Ward et al. 2008).

Overall numbers

2.28 Leicester (2006) recently summarised national estimates of abundance provided by a number of different sources for all species (Table 1.)

Table 1. Estimates of national deer abundance in England from several sources (Leicester 2006).

	Harris *et al*. (1995)	**BASC (1995)**	**Munro (2002)**	**The Deer Initiative (2003)**
Red	12,500	96,000	N/A	56,000
Roe	150,000	188,000	228,000	324,296
Fallow	95,000	93,000	104,500	262,332
Sika	2,500	10,500	3,300	16,800
Muntjac	40,000 + 12,000 juveniles	28,500	100,000	123,720
CWD	650	1,300	N/A	5,000
Total	**312,650**	**417,550**		**788,148**

2.29 All estimates except those by Harris *et al*. (1995) were extrapolated from known deaths (cull data and, in the case of Leicester 2006, deer-vehicle collisions), thus relying on the unsubstantiated assumption that a known proportion of the population was killed during each survey period. However, one of the benefits of this approach is that it is not habitat-type specific, so that all habitat-types in which deer are culled may have been represented in these estimates.

2.30 Abundance estimates presented by Harris *et al*. (1995) and those of Ward and Etherington (below; and Appendix Three) were extrapolated from estimates of woodland density estimates.

3. Current patterns of abundance of deer in England

3.1 Here we attempt to update these general descriptions to provide an indication of current distribution and abundance of four species of deer (red, roe, fallow and muntjac across England. No consideration is offered within this new analysis to Japanese sika or Chinese water deer since their distributions are very limited in England, with few local density estimates, making the accuracy and precision of extrapolations highly uncertain. Moreover, since CWD do not rely on woodlands as most other British deer species do, and since no clear environmental associations have been quantified for them, our approach was unlikely to produce reliable abundance estimates for CWD. Full details of this analysis are provided in Appendix Three (Ward and Etherington, 2010); we offer here a summary of methods and main conclusions.

Methods

3.2 Presence data for red deer, fallow deer, roe deer (*Capreolus capreolus*) and Reeves'or Chinese muntjac (*Muntiacus reevesi*), collected from 1973 to 2002 on a 10-km grid across Britain (Ward 2005), were supplemented with more recent distribution data gathered from the membership of the British Deer Society during their national deer survey. Deer presence was rescaled to 5km cells. The total number of individuals of a deer species within an occupied 5km cell was estimated by multiplying a local woodland density estimate by the total area of woodland within the cell. This was repeated for each species and every cell in England and Wales. Woodland area was extracted from Land Cover Map 2000 (Centre for Ecology and Hydrology, UK).

3.3 Deer density estimates collected between 2000 and 2007 were received from a number of individuals (9), estates (3), and Government bodies including Forest Research and the 15 English and Welsh Forestry Commission districts (Table 2). In extrapolation to other areas, density estimates were applied from the same geographical region or the nearest region for which an estimate was available to each cell within that region.[3]

[3] It should be emphasised that during Ward and Etherington's analysis, habitat structure was summarised from Landcover Map 2000, and deer density estimates originated from the late 1990's to early 2000's. Consequently, estimates approximate the abundance of deer in woodland during the year 2000.

Table 2. Minimum-maximum deer density estimates used to estimate the total number of each deer species in England. The simple average density estimate is presented in parentheses and was used to map abundance in 5 km grid cells.

	Deer density (km^{-2})			
Region	**Red**	**Roe**	**Fallow**	**Muntjac**
East	0.8-15.2 [6.9]	3.0-64.0 [16.7]	1.3-181.4 [53.9]	3.7-144.4 [45.5]
Central	3.0-36.5 [19.8]	1.1-23.6 [8.1]	2.2-132.0 [35.3]	6.0-87.2 [32.7]
Northeast	1.6-35.3 [11.0]	6.8-14.5 [10.6]	4.2-20.5 [11.7] [2]	1.3-26.0 [13.0] [1]
Northwest	1.6-35.3 [11.0]	0.75-48.8 [7.7]	4.2-20.5 [11.7] [2]	1.3-26.0 [13.0] [1]
Southeast	0.5-7.4 [5.3]	1.1-26.1 [11.8]	4.2-20.5 [11.7]	1.3-26.0 [13.0]
Southwest	0.8-18.8 [7.9]	0.5-9.9 [5.2]	1.9-16.2 [11.6]	1.3-26.0 [13.0] [1]

[1]Estimates of muntjac density were not available for these regions, so estimates from southeast England were used.
[2]Estimates of fallow deer density were not available for these regions, so estimates from southeast England were used.

3.4 Deer density estimates in Table 2 may be compared with those presented by earlier authors, summarised in section 2 above.

3.5 In order to estimate the total number of deer in England along with the associated error, the range of regional density estimates for each species was sampled by Monte Carlo simulation and multiplied by the area of woodland present in each occupied grid cell. The density range was defined by the minimum and maximum densities recorded, and these were modelled with a uniform distribution.

3.6 That is, any density within the range had an equal probability of selection during each repetition of the Monte Carlo simulation. We chose this distribution since there were so few density estimates for each species within each region, and no indication of the most common densities found across England. Simulations for each species were run 5000 times. The outputs from the simulations were the median estimated total number of deer of each species in England, and the 95th and 100th percentiles of estimates. Monte Carlo simulations were run in Crystal Ball 2000, standard edition v5.1 (Decisioneering, Denver, Colorado).

<u>Results</u>

3.7 Density estimates for each deer species and areas of woodland within 5 km cells varied considerably within and between regions in England and Wales. This resulted in a highly varied pattern of predicted abundance (Fig. 1). Deer were estimated to be particularly abundant in parts of East Anglia (all four species), central England (fallow deer and muntjac), Cumbria and southern England (red deer) and the northwest and southeast of England (roe deer) (Fig. 1).

3.8 Simple addition of the values in each 5km grid square in England based on local densities within woodlands produced absolute estimates of 195,533 fallow deer, 149,760 muntjac, 143,920 roe deer and 26,737 red deer. Monte Carlo simulations yielded subtly different estimates, with very tight error terms (Table 3).

Table 3. National estimates of the total number of deer in England.

	Red	**Roe**	**Fallow**	**Muntjac**
Median	62,144	166,483	285,376	244,470
0%	58,668	159,865	267,909	233,138
2.5%	60,212	162,713	276,215	237,157
97.5%	64,134	170,459	294,960	251,848
100%	66,223	174,004	302,705	259,918

3.9 Abundance estimates presented by Harris *et al*. (1995) and those in the current study (Ward and Etherington 2010; Appendix Three) were extrapolated from woodland density estimates, so that other habitat-types were not represented. Consequently, these are likely to underestimate the total abundance of deer in England, and the zero percentiles should be considered minimum likely numbers.

3.10 For those species not considered in these new analyses, Harris *et al*. (1995) estimated English populations of sika to number 2,500 in 1995 and, using a similar approach, Ward (2007) estimated them to number 2,600 in 2004. Harris *et al*. (1995) estimated Chinese water deer to number 650 during 1995; Ward (2007) estimated them at 1,500 during 2004, while more recently, Arnold Cooke estimated that the national population had more than doubled to 4,000 (A. Cooke, *pers.comm*.).

3.11 While estimates of total national abundance, particularly when compared over time, may be useful for informing national and regional policies relating to deer, they cannot be used to guide local impact management efforts. For this purpose, what is more relevant (in terms of impact, and management of that impact) is that

i) in some areas (quite large areas!) they occur in comparatively low abundance
ii) in other areas they occur at higher, but still relatively moderate abundances and still have relatively little impact upon the environment
iii) while in other areas again they have built up to relatively high numbers.

3.12 In some of these areas, where deer do occur at high density, they may have a significant impact. But even then, this is not necessarily a problem. As we have already emphasised, impacts, however high, only translate to "damage" if the impact recorded conflicts with (human-based) value judgements for what is appropriate, and where recorded impacts conflict in some way with primary land-use objectives.

3.13 Thus in practice, we may argue that the total number of deer of any species in England is at least to some degree somewhat academic, at least from a management perspective. What actually matters is that in some areas they occur at relatively high density, and in some of those areas (and only some) the impact is considered in conflict with other management objectives for those particular areas. Perhaps more useful than any estimate of overall numbers is a focus on that particular subset of areas where especially high densities are noted (Figure 1) and areas where the deer are having "unacceptable" impacts.

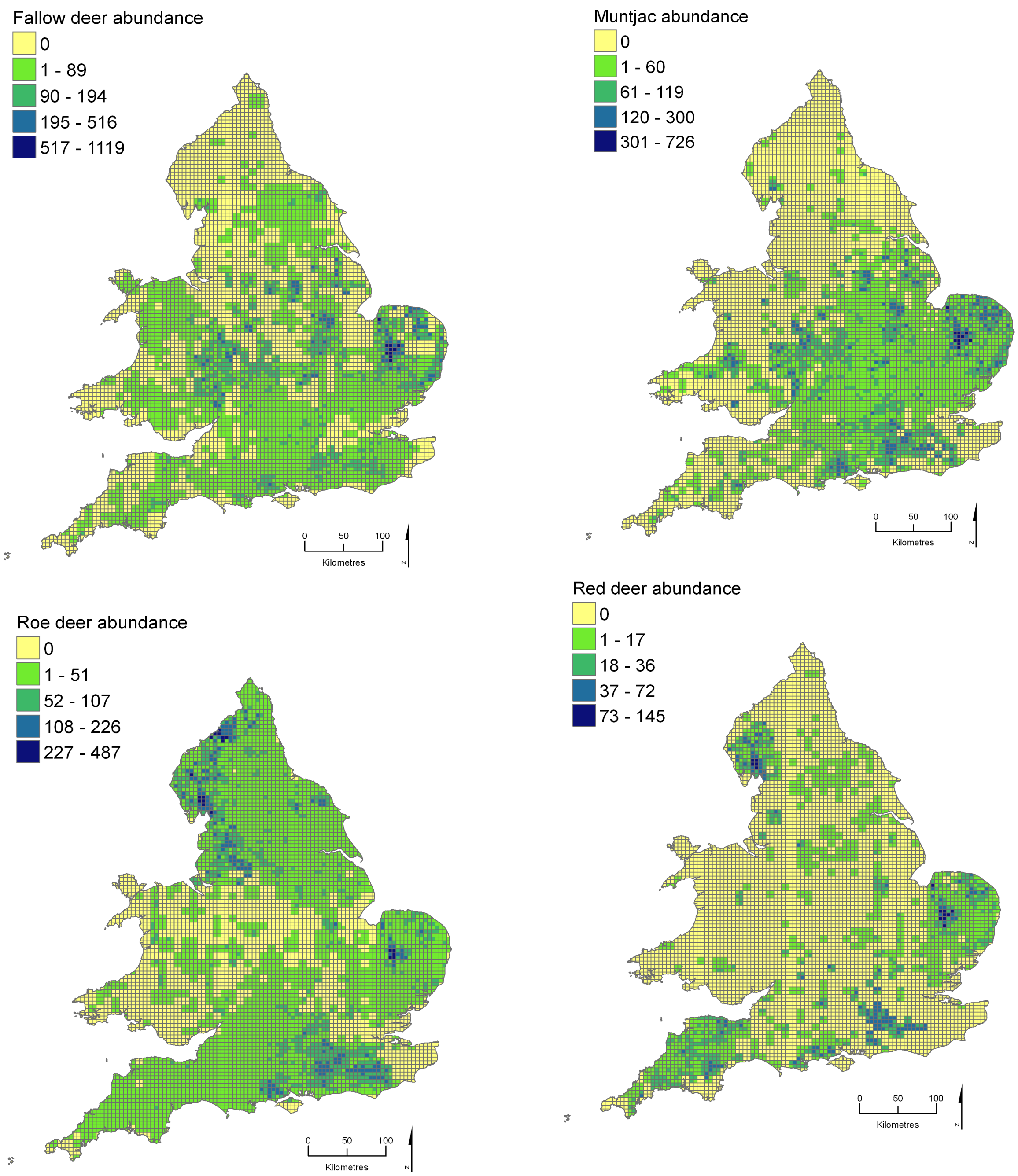

Figure 1. Abundance maps of four species of deer in England and Wales.

4. Factors associated with distribution patterns of different deer species in England.

4.1 If we can actually determine those environmental factors which are associated with distribution patterns of individual species of deer and if we may presume that some of these relationships are causal, we may be able to use a knowledge of the distribution of those same variables to predict likely trends in future distribution of deer within England.

4.2 Using the favourability function described by Real *et al*. (2006a) Acevedo et al. (2010; Appendix Four) have attempted to determine the ecological determinants of deer species distributions in Great Britain, by definition, focusing on those factors that were positively associated with a species' presence.

4.3 The effects of many climatic, human and ecological variables on abundance and distribution of ungulate species have been described (e.g. Hewison *et al*., 2001; Acevedo *et al*., 2006; Acevedo and Cassinello, 2009). From these, Acevedo et al. selected twenty-six variables, grouped into five main factors: spatial (SPA), climate (CLI), topography (TOP), human disturbance (HUM) and habitat structure (HAB), (Table 4). These variables were chosen on the basis of their potential predictive power, and were assumed to be at least correlated with more proximal causal factors. Analyses also considered the possible negative interaction of actual or potential competition between deer species (Last category in Table 4).

Table 4. Variables used in the analyses. See Appendix Four for details and data sources.

Factors	Codes	Variables
Topography	RgAlt	Range of altitude (m)
	Malt	Mean altitude (m above sea level)
	MxAlt	Max altitude (m above sea level)
	Mslop	Mean slope (º)
	MxSlop	Max slope (º)
Human disturbance	Urban	Built-up areas and gardens (m^2)
	DmainR	Distance to main road (m)
	DprimR	Distance to primary road (m)
Habitat structure	Arable	Arable horticulture (km^2)
	Forest	Forest and woodland (km^2)
	Littoral	Littoral zone (km^2)
	Sea	Sea (km^2)
	Mountain	Mountain/Upland (km^2)
	Pasture	Pasture (km^2)
	Water	Standing water/canals (km^2)
	Diversity	Shannon index
Inter-specific factors	RedP	Red deer present
	RoeP	Roe deer present
	FallowP	Fallow deer present
	SikaP	Sika present
	MuntP	Muntjac present
	CWDP	Chinese water deer present

4.4 Since the species-environment relationships were not known *a priori*, an inductive approach was employed to estimate the macro-ecological requirements of the species from the locations in which they occurred (Stoms *et al*., 1992; Corsi *et al*., 2000). Acevedo et al. modelled both presence and absence, assuming that a lack of recorded observation within a cell equated to absence, for each of the six deer species separately. In reality, confirmation of absence can be extremely difficult, and is rarely recorded (Lobo, 2008). However, since considerable effort went into recording species' presence, it was considered likely that the majority of cases of absence equate to the absence of the species at that location. They considered modelling absence as important as modelling presence, since the absence of a species from an area may be due to ecological, historical, or anthropogenic reasons, all of which are relevant to predicting future distributions (Real *et al*., 2008).

4.5 From these analyses (Appendix Four) Acevedo et al. infer that, in descending order the top five (maximum) variables associated with deer presence were:

- Roe deer: Precipitation during the wettest month, maximum temperature during the warmest month, area of broad-leaved woodland, area of mountain/upland, area of arable/horticultural land.
- Red deer: Area of mountain/upland, area of broad-leaved woodland, precipitation during the wettest month, latitude.
- Fallow deer: Area of broad-leaved woodland, latitude, area of arable/horticultural land, area of coniferous woodland, area of mountain/upland.
- Sika: Area of mountain/upland, area of coniferous woodland, area of broad-leaved woodland, precipitation during the wettest month, latitude.
- Muntjac: Area of arable/horticultural land, temperature seasonality (i.e. variability in temperature over time), area of broad-leaved woodland, area of standing water/canals, area of coniferous woodland.
- Chinese water deer: Latitude, temperature seasonality (i.e. variability in temperature over time), area of coniferous woodland, area of arable/horticultural land.

The top five (maximum) variables associated with deer absence were:

- Roe deer: Minimum temperature during the coldest month, distance to primary road, maximum altitude, temperature seasonality (i.e. variability in temperature over time), built-up area.
- Red deer: Longitude, area of pastoral land, built-up area, minimum temperature during the coldest month.
- Fallow deer: Built-up area, minimum temperature during the coldest month.
- Sika: Longitude, built-up area, area of arable/horticultural land.
- Muntjac: Distance to primary road, area of mountain/upland.
- Chinese water deer: (none)

4.5 Acevedo et al. estimate that roe deer and red deer are geographically similar in their relationships with the introduced deer species. Thus, areas predicted to be exclusively favourable for roe deer and red deer, in comparison with muntjac and Chinese water deer, were detected in the north of Scotland. In contrast, we would expect that these introduced species could constrain the spread of red deer and may exclude roe deer, particularly in the southeast. If resources are or become limited, the introduced species could have adaptive advantages in many south-eastern areas since these appear to be environmentally closer to their optimal requirements, particularly for muntjac (Fig. 2 of Appendix Four).

4.6 Observations on local-scale dietary overlap between roe deer and muntjac support this hypothesis (Hemami, 2003; Hemami *et al*., 2005). Nevertheless, Acevedo et al. predict coexistence in Thetford Forest where Hemami *et al*., 2005 found competition at finer scales. Acevedo et al. interpret this as suggesting that when environmental favourability is high for both species, muntjac may displace roe deer in areas where the former attains high densities. A similar situation has been observed in Italy, where fallow deer reduced the habitat suitability for roe deer (Focardi *et al*., 2006).

4.7 Acevedo et al.'s results also suggest that sika may be weak competitors of roe deer and red deer since in grid cells where they were coincident, favourability always remained below that of these native species (Appendix Four: Figs. 3 and 4). Consequently, we would not expect sika to displace roe deer or red deer.

4.8 Favourability for fallow deer was closely correlated with those for the Chinese water deer and muntjac (Appendix Four: Fig. 5). In general terms these results suggest that fallow deer may out-compete the latter two introduced species.

4.9 The approach presented by Acevedo et al. to describe biogeographical relationships between deer species in Great Britain is novel. They propose that it can be used to assess, from a biogeographical perspective, factors that may be associated with likely future increase in distribution or abundance of different deer species as well as relative competitive ability between species. Although the results of this analysis do not conclusively demonstrate competitive exclusion, they provide directional hypotheses that can be tested in experimental field and laboratory studies (Anderson *et al*., 2002).

4.10 Habitat structure variables did not perform well for roe deer, which is an adaptable, pioneering species, known to be capable of exploiting a wide variety of habitat types. For this species distribution was more closely related to topographic and particularly climatic factors. In contrast, some of the most highly ranked variables for red deer were habitat structure factors. In particular red deer presence was associated with mountain and upland environments and broad-leaved woodland, but their absence was associated with pastoral land and built-up areas. The positive association with upland habitats is probably a historical artefact, resulting from the red deer's long-standing cultivation in the Scottish Highlands for sporting purposes (Macmillan and Phillip, 2008). Nevertheless, relative to most other deer species, red deer do persist well in these barren environments, although with lower body condition and productivity (Clutton-Brock *et al*., 1982), whereas most other species cannot.

4.11 Habitat structure variables also performed better than did climatic variables for fallow, muntjac and Chinese water deer. Having originated from the Mediterranean region, it should be unsurprising that fallow deer presence was associated with decreasing latitude and their absence with cold temperatures. They are also known to prosper in a landscape mosaic of arable farmland and woodland, particularly broadleaved woodland (Chapman and Chapman, 1975), so it was reassuring that these same factors were associated with their presence in the models.

4.12 Muntjac presence was also associated with area of woodland, in common with other British deer except CWD, but their association with arable/horticultural land may be an artefact of their current preponderance in the east of the country, where this habitat type is more common than it is in the west. Presence of muntjac (and CWD) was also associated with high variability in temperature, which, along with negative associations with latitude and area of upland/mountain, perhaps implies limited ability for successful colonisation of the far north of Britain. However, since no factors were identified as significantly associated with CWD absence (probably due to their very limited current distribution), we cannot confidently predict, from these results, areas that they are unlikely to colonise in the future.

4.13 For sika, habitat structure variables also performed well at predicting both absence and presence, but presence of sika was also associated with precipitation during the wettest month. This, and further associations with mountain/ upland may be an artefact of the fact that their current distribution is concentrated towards northern and western areas of Britain, which experience higher annual rainfall than do the east and south. However, sika presence was associated with both broadleaved and coniferous woodland and we predict that this species has considerable potential for range expansion into the east and south of the country.

4.14 From an applied perspective, significant variables that were ranked highly have potential for managing the future spread of deer. Clearly, the important climate, spatial and topographical features cannot be easily or purposively manipulated, but their effects could be included in plans to manage the spread of deer. For example, the minimum temperature of the coldest month was associated with roe deer absence, so resources for controlling their spread may be better focused outside areas predicted to suffer particularly cold periods. By contrast, arable or horticultural land was associated with the presence of muntjac, so changes in land use resulting in reduction of this land cover type may result in a reduction in their spread. (see also below, Section 7).

4.15 Where environmental requirements are similar for sympatric species this can offer some advantages from a management perspective. For example, improving habitat suitability for one species should also benefit the other and *vice versa*. This characteristic is desirable when both species should be conserved (Acevedo *et al*., 2007a) or controlled (Real *et al*., 2008), but it may be problematic when there are opposite interests for two or more ecologically similar species, such as when one species is native and should be conserved while the other is introduced and may be selected for control or eradication.

4.16 Clearly, application of significant factors for management purposes may be particularly challenging, and should be contingent on independent *post hoc* validation of the model outputs. Nevertheless, identification of significant factors represents the first step towards establishing their utility, which then require innovation for their effective exploitation.

5. Identification of landscape features that might influence the spread of different deer species.

5.1 Given these associations between distribution and various environmental variables (including potential competitive interactions between the deer species themselves), can we now identify factors that could be used to control the spread of each species across England?

5.2 Ward et al. (2010; Appendix Five) have used landscape variables to model the rates of national range expansion of each deer species from 1972-2002, before validating the estimated relationships by assessing the fit of the models to comparable data from 2003 - 2007. They focused on variables that were negatively associated with species' presence in order to identify features that may be exploited to control their spread.

5.3 The expansion of each species' range was modelled as the presence or absence of a species within each cell throughout GB from 1972 to 2002. Presence was defined by the occurrence of at least one observation of a species within a cell within the survey period. Determining absence was more complicated since it is not reasonable to expect each species to be able to expand into every cell within GB with equal probability due to proximity, so unoccupied cells at great distances from occupied cells are unlikely to represent choice. Consequently, the maximum distance that each species had expanded from any cell and in any direction between 1972 and 2002 was taken to define a radius encompassing all cells that could have been expected to become occupied within the survey period. A buffer zone with this species-specific radius was placed around each cell occupied by that species during 1972. Cells within these buffer zones that had not become occupied by 2002 were used as records of absence.

5.4 The models developed on recorded changes in distribution from 1972 – 2002 were validated by predicting the distribution of each species by 2007 and comparing these with BDS distribution records from 2003 to 2007.

5.5 In order to reduce the number of independent variables entered into the final models one of each pair of independent variables that were co-linear ($r_s > 0.6$) was excluded. Remaining independent variables were fitted against presence/absence data for each species in turn within logistic regression models following a backwards stepwise procedure, with variables dropped from the model if not achieving P<0.1 at each step.

5.6 Variables significantly associated with the presence/absence of each species of deer at the final step of each model are shown in Table 5 below (Appendix Five Table 3). (Where *P* is quoted as 0.000, *P*<0.001.) The significance in the current context is the sign attributed to each variable (whether the distribution of any particular deer species is positively (+) or negatively (-) associated with each independent variable).

Table 5. Variables significantly associated with the presence/absence of each species of deer at the final step of each model.

Species	Variable	*β*	S.E.	Wald	d.f.	*P*	Exp(*β*)
Red	RoeP(1)	-1.454	0.126	133.530	1	0.000	0.234
	SikaP(1)	-.620	0.178	12.193	1	0.000	0.538
	Forest	.020	0.005	14.923	1	0.000	1.021
	Littoral	-.158	0.066	5.787	1	0.016	0.854
	Mountain	.035	0.003	122.496	1	0.000	1.036
	Pasture	-.018	0.003	43.614	1	0.000	0.983
	Sea	.255	0.082	9.591	1	0.002	1.290
	Urban	-.068	0.010	42.815	1	0.000	0.934
	Water	.145	0.039	14.029	1	0.000	1.157
	FallowP(1)	-.240	0.128	3.509	1	0.061	0.786
	Constant	.419	0.243	2.967	1	0.085	1.521
Roe	MuntjacP(1)	-.660	0.119	30.778	1	0.000	0.517
	RedP(1)	-1.444	0.126	130.544	1	0.000	0.236
	SikaP(1)	-1.406	0.238	34.932	1	0.000	0.245
	Forest	.041	0.006	44.918	1	0.000	1.042

	Mountain	.017	0.003	32.727	1	0.000	1.018
	Pasture	.005	0.002	5.692	1	0.017	1.005
	Sea	-.172	0.084	4.174	1	0.041	0.842
	Urban	-.010	0.005	5.005	1	0.025	0.990
	Water	-.114	0.028	16.080	1	0.000	0.892
	Diversity	.028	0.009	10.253	1	0.001	1.029
	Constant	2.187	0.318	47.344	1	0.000	8.913
Fallow	MuntjacP(1)	-1.882	0.129	214.042	1	0.000	0.152
	RedP(1)	-.237	0.131	3.249	1	0.071	0.789
	Forest	.044	0.005	63.962	1	0.000	1.045
	Mountain	-.021	0.004	22.206	1	0.000	0.979
	Pastoral	.016	0.003	35.635	1	0.000	1.016
	Diversity	.024	0.011	4.995	1	0.025	1.024
	CWDP(1)	-1.143	0.348	10.809	1	0.001	0.319
	Constant	.136	0.414	.108	1	0.742	1.146
Sika	MuntjacP(1)	.735	0.293	6.281	1	0.012	2.086
	RedP(1)	-.555	0.180	9.505	1	0.002	0.574
	Forest	.035	0.006	32.528	1	0.000	1.036
	Littoral	-.397	0.233	2.921	1	0.087	0.672
	Mountain	.030	0.003	83.159	1	0.000	1.031
	Sea	.240	0.113	4.507	1	0.034	1.271
	Urban	-.049	0.018	7.712	1	0.005	0.952
	Water	.099	0.028	12.782	1	0.000	1.104
	Diversity	.095	0.015	38.789	1	0.000	1.100
	RoeP(1)	-1.346	0.243	30.793	1	0.000	0.260

5.7 The quality of the models, in terms of their ability to accurately describe the data used to construct them, was generally good, but varied between species.
The muntjac model correctly predicted absence on 93% of occasions, and presence on 44% of occasions (Appendix Five). The red deer model was also good at correctly predicting absence (86% of occasions), and at correctly predicting presence (60% of occasions). Roe and fallow models performed fairly well, but the roe model was better than the fallow model at predicting presence (correctly on 80% and 43% of occasions respectively), and fallow absence was better predicted than roe absence (correctly on 90% and 59% of occasions respectively). The sika and Chinese water deer models weakly estimated presence, with 36% and 11% predicted correctly, but with 96% and 99% of absence predicted correctly.

5.8 The ability of these models to predict deer distribution from 2003 to 2007 varied slightly between species. The red deer model correctly predicted presence on 21% of occasions, and absence on 39%. The fallow deer model correctly predicted presence on 38% and absence on 11% of occasions. The sika model was particularly poor at correctly predicting presence (2% of occasions), but was much better at correctly predicting absence (79% of occasions). For muntjac, correct predictions of presence were made on 25% of occasions and absence on 27%. For Chinese water deer, the model correctly predicted presence on 14% and absence on 41% of occasions.
The roe deer model predicted absence very poorly (correct prediction on 2% of occasions), whereas its ability to correctly predict presence was very good (correct prediction on nearly 68% of occasions).

5.9 The models developed by Ward et al. identified landscape features that were associated with range expansion of the six species of deer throughout Great Britain.

Those relationships were employed to identify those factors that could be used to constrain range spread (see section 6).

5.10 As noted above, the actual predictive ability of the models was generally low to moderate, with models for red deer and muntjac moderately predicting both presence and absence correctly and those for Chinese water deer and fallow deer moderately predicting absence correctly. The roe deer model was particularly good at predicting presence but poor at predicting absence, and the sika model was the reverse.

5.11 No dataset for any species was perfectly balanced (i.e. a 50:50 and spatially even distribution of presence and absence records), but also, the categories chosen for the environmental variables were quite coarse perhaps describing the landscape features too imprecisely to strongly predict range expansion by deer. Inclusion of additional categories may have improved model performance, and indeed, r^2 values were all low to moderate, implying that some unmeasured factors might in addition have driven deer choices during the study period.

5.12 Moreover, as deer have expanded across the country their choices may have altered, perhaps due to new habitat types becoming available to them. As further distribution data become available it would be worthwhile to re-estimate relationships explored here in order to support or refute this latter hypothesis. It would also be beneficial to split some of the gross habitat-type categories into more precise ones, and to include additional spatial datasets, such as those on soil types. For example, 'Forest' could be split into 'Conifer' and 'Broadleaf', which may statistically interact with soil types (sika, for example, are considered to be predominant on acidic soils, Putman, 2000) to produce more powerful predictive models.

5.13 Nevertheless, many environmental factors were identified as significantly associated with the presence and absence of each deer species, and we cautiously suggest that careful interpretation of these relationships might hold potential for the prediction of future range spread of each species. Caution is warranted, however, because this was an exploratory analysis and not the result of a controlled experiment.

6. Application of the models to predict future trends in distribution and abundance.

6.1 As above, there is a need for further work to refine and improve the favourability and expansion rate models before they can be confidently applied to predict future changes in distribution and abundance of the six deer species. Indeed, extrapolation of the favourability models to predict future abundance would be a substantial additional but informative step.

6.2 The first step should be to validate the models using sequential deer distribution data on a five-yearly basis (the periodicity of British Deer Society distribution surveys). It should also be ascertained whether relative favourability variables correlate with relative abundance to evaluate whether favourability functions can be used to predict changes in abundance.

6.3 Sequential refinement of the models is advisable because climate change is predicted to have substantial impacts on deer distribution and abundance in the UK and across Europe (Irvine et al., 2007; see also Mysterud and Saether, 2010), and

land use change might cause some climatic and landscape variables to exceed beyond the limits defined within the current models.
We note however that the climate variables in Acevedo et al.'s models were summarised over a 50 year period, and so will have included most if not all weather scenarios likely to occur within the next few decades. Thus the relationships identified here should not change much, as evidenced by the moderate fit of the 1972-2002 models to the 2003-2007 data.

6.4 To an extent therefore, this paper represents a scoping study to illustrate the potential of these approaches, and further work is required for development of more robust predictions of future patterns of distribution, which could lead to predictions of changes in abundance.

7. Management options to contain future range expansion.

7.1 As part of the analysis of Ward et al (2010) in Appendix Five, variables selected for inclusion in the predictive models deliberately emphasised features that were negatively associated with range expansion, and which might thus provide hints of available options for controlling or containing future spread of each of the deer species.

7.2 Thus in Table 5, for example, area of urban land was weakly associated with the absence of red deer, so plans to contain or control their spread could exploit the presence of urban areas to define the geographical limits of management efforts.

7.3 Similar indications may be drawn from the predictive modelling of Appendix Five. These analyses specifically emphasise those landscape features that are estimated to have constrained the expansion of deer from 1972 to 2002. Those strongly negatively related to range expansion are summarised in Table 6, below and hold the greatest potential for exploitation to control the future spread of deer.

Table 6. Landscape features that are estimated to have constrained the expansion of deer from 1972 to 2002. Those strongly related to range expansion hold the greatest potential for exploitation to control the future spread of deer. Only features estimated to have a negative relationship with range expansion are reported.

Landscape feature	**Strength of relationship**		
	Weak	**Moderate**	**Strong**
Urban (m^2)	Red, Roe, Sika		
Forest and woodland (km^2)	Muntjac		
Littoral zone (km^2)	Red, Muntjac	Sika	CWD
Sea (km^2)	Roe, Muntjac		
Mountain/Upland (km^2)	Fallow, Muntjac		CWD
Pasture (km^2)	Red, CWD, Muntjac		
Standing water/canals (km^2)	Roe		
Red deer present	Fallow	Sika	Roe, CWD
Roe deer present		Red, Muntjac	Sika
Fallow deer present	Red	Muntjac	CWD
Sika present			Red, Roe
Muntjac present	Fallow		Roe
Chinese water deer present		Muntjac	Fallow

7.4 From the table it appears that that Chinese water deer have strongly avoided mountainous areas and the littoral zone, so these factors alone may contribute to plans to control the expansion of this species in England. In contrast, muntjac range expansion was only weakly negatively associated with forest, the littoral zone, the sea, mountainous areas and pasture, so in isolation, each of these factors are unlikely to strongly constrain their future spread, and it may be more appropriate to seek combinations of multiples of these to strengthen their effects. However, it is important to note that for Chinese water deer and sika at least, ranges remain quite restricted in Britain. The consequent limited sample size of presence records may have resulted in biased estimates of habitat associations simply because they may not yet have spread into areas containing other habitat types, and so their distributions cannot illustrate selection of these. We recommend repeating these analyses as more distribution data become available so that more robust models of spread can be derived.

8. Conclusions

8.1 In this report we have presented predictions of future range expansion and the likely future distributions of the six different deer species free-living within England. In Section 7 (and Appendix Five) we have presented and discussed some mechanisms which might help to contain or direct such spread (other than control efforts directly simply through targeted culling). However, none of the models developed in this report were designed to predict what may be future patterns of <u>abundance</u> within different parts of England since data adequate for this task are not currently available. **More crucially, as they stand the models cannot be used to determine what levels of abundance might be considered tolerable - or at least compatible with other nature conservation or land use objectives.**

8.2 As noted in paragraphs 1.5 –1.8 high deer densities are not necessarily and automatically linked to high impacts, nor are those impacts necessarily damaging; impacts are in effect ecologically neutral and may only be considered damage if they conflict in some way with some human interest (Reimoser and Putman, 2010; Putman et al., Mammal Review *in press* (b)). There are in addition many positive benefits which may be associated with deer presence – in terms of public amenity and public enjoyment, recreational stalking and actual economic gain from commercial stalking, as well as benefits in conservation terms (suppression of scrub in open habitats, maintenance of clearings and glades within woodlands etc.).
It is thus important to establish a set of criteria against which to determine when intervention (or prophylactic management) may be appropriate and where circumstances do not warrant the costs of intervention.

8.3 A separate review aimed at identification of some critical threshold densities of deer above which damage to agriculture, forestry, amenity woodlands, conservation sites and/or public safety may become of consequence, has recently been published elsewhere (Watson *et al*., 2010; Putman et al. Mammal Review *in press* (a); Appendix One to this report).

8.4 That review emphasises that there is no such thing as a “single” density threshold above which damage may be expected to occur. In examining available literature to elicit threshold densities at which impacts may be considered to become damaging, we should recognise that densities at which negative impacts occur will differ between contexts. Thus densities at which damage may occur to woodland ground flora may be different from the density at which damage may occur to agricultural crops, or at which bark-stripping damage may occur in commercial woodlands (e.g. Ratcliffe, 1989).

8.5 In addition, even within one given context, densities at which damage may occur may show enormous variability, depending on other environmental and social factors. Thus, pursuing the example above, damage to regenerating woodland may depend on site conditions (and the vigour of regeneration); availability of alternative forage; juxtaposition of regeneration sites and close cover etc. (Reimoser and Gossow, 1996; Kerr and Nowak, 1997; Reimoser and Putman, 2009). Ward *et al*. (2008) found that in plantation forests in northeast England although an index of local density was positively associated with the incidence of conifer leader browsing by roe deer, it was mediated by the availability of palatable understorey vegetation at the local scale. That is, for a given density index value leader browsing incidence was much higher in areas lacking in understorey vegetation than it was in areas with abundant vegetation. They inferred that the use of deer culling to control conifer leader browsing was likely to be far less efficient in vegetation poor areas and that a more co-ordinated approach, including environmental manipulation, may more appropriate.

8.6 Relationships are similarly complex between deer density and agricultural damage (see for example Putman & Kjellander, 2002), and between deer density and the frequency of deer-vehicle collisions, which is also affected by a range of other landscape features (e.g. Bashore *et al*., 1985; Finder *et al*., 1999; Hubbard *et al*., 2000; Malo *et al*., 2004; Seiler, 2004; Putman *et al.,* 2004).

8.7 In consequence, even in relation to one given context we should not expect to find a single fixed threshold above which negative impacts may become significant. This clear variability in the relationship between damage and density emphasises that we should not be seeking to establish simple densities at which management action is necessarily required. In practice, we should aim to establish trigger levels at which it may be appropriate to undertake more intensive monitoring to establish whether significant negative impacts are or are not occurring. This could be supported by the development of a predictive tool to identify potential problem hotspots that merit further surveillance to inform prescription of prophylactic or corrective management.

8.8 Because of the complex relationship between deer densities and actual impacts sustained in any given situation, we believe that density alone is unlikely to be a particularly good predictor of expected impact (see again Appendix One and Putman et al. in press). In addition it is clear that it is in practice difficult and labour-demanding reliably to assess true densities of any deer species. Thus we suggest that it may be better, in the long-term, to base assessment of management requirement on assessment (including prediction) of actual impacts of deer, alongside estimates of actual density. Densities and impacts would need to be monitored at all relevant scales and we would advocate the methodologies of Putman and Watson, 2009; Putman *et al.* Mammal Review *in press* (b) [Appendix Two, here] for assessments at the landscape scale.

8.9 Ward *et al*. (2008b) also strongly advocate this mixed approach, noting that population abundance (even in broad, relative terms), occupance, impacts and local conditions all ought to be assessed to inform management options when 'balance' is required (see also Morellet *et al*., 2007). With this landscape scale information the decision is not limited to 'shoot more/less', but can be used to tailor management (including non-lethal forms) to local conditions.

8.10 It is important, however, to recognise that deer management should not be targeted towards remedying any single area of concern or considered single-objective. Any management decision taken in any given context (to increase or reduce numbers of a given ungulate population, to influence their distribution, or simply to alter relative utilisation of different parts of their range) will by definition affect densities, affect range-use and thus of necessity have implications on other ecosystem processes of which ungulate populations are an integral part.

8.11 Of necessity therefore, effective management must consider all relevant ecosystem processes in which these ungulate populations may play a role, and must seek to develop integrated management systems which take account of *all* these effects and take due account of other, potentially competing land-use interests which are affected by the same populations of ungulates. Rather than adopting management approaches which seek to solve a single problem, or deliver a single objective, management must pay due heed to all aspects of the interactions between ungulate populations and their wider environment, to develop management strategies which take due account of all impacts and all needs, balancing conflicting or complementary interests in a much more **holistic** way.

8.12 Management of deer (and other ungulates) should not simply be about managing ***them*** in isolation, but needs to be considered (and integrated) within a wider framework of how they themselves, and their management relate to other land-management aims and objectives in more general terms. Monitoring and management must therefore attempt to take full account of all the effects of deer and their management (both positive and negative) in relation to all relevant land-use interests simultaneously, at a scale that is consistent with the range of the deer population in question (see also Kenward and Putman, in press).

8.13 Further, to some degree, the assessment of what is, or is not "significant" in terms of any recorded impact is necessarily itself a subjective judgement and will vary with varying levels of tolerance; those variable levels of tolerance will themselves be affected by the balance of perceived positive benefits from deer and negative impacts experienced in any given situation. What is accepted as tolerable is thus in effect defined by the values of stakeholders, which are also likely to vary between stakeholders and individual contexts.

8.14 Ward (Appendix Six) proposes that maximum impact thresholds ought to be identified which minimise costs and maximise benefits across the greatest number of stakeholders within a zone, although the size or value of each stake will also need to be taken into account. With maximum impact thresholds identified from stakeholder values across the zone, it should be possible to infer the maximum usage rate of each species that should result in impacts up to that threshold in each site throughout the zone. Summing these usage rates across all sites and fixing for a specified period of time will provide an estimate of the maximum number of each species of deer present that could be tolerated within the zone.

8.15 This approach not only provides a framework whereby maximum numbers of deer can be defined for a given zone (e.g. an area covered by a deer management group), but would also facilitate more strategic national planning. This would require the application of estimates and maps of national abundance for each species (as in Appendix Three), and national datasets on land cover and stakeholder distribution (national census, June agricultural census) in order to compare current and predicted deer abundance distributions with predicted maximum tolerable deer abundance distributions so that priority areas for monitoring and management can be identified.

9. Recommendations for further work

9.1 As discussed in earlier sections of this report the outputs of the models presented should be viewed as preliminary. The models themselves would benefit from re-estimation as new data are produced. The British Deer Society update their distribution records every five years and Centre for Ecology and Hydrology have updated their LandCover Map approximately every 10 years. Consequently, this 5-10 year periodicity would seem an appropriate scale at which to reconstruct and validate further models. The BDS should be providing their update sometime between 2010 and 2012 and LandCover map 2007 recently became available.

9.2 At a more basic level, the deer density estimates used to estimate local and national abundance of deer in woodlands (Appendix Three) came from as early as 2000. Moreover, there were no quality indicators for these data, and no measures of variability. Should further attempts be required to estimate the abundance of each species of deer in grid cells and nationally, it would be necessary to collate and/or collect a robust sample of density estimates using standard data collection techniques, stratified by land cover type and covering each region of the country. It would be advisable to produce estimates of variability from these data so that variability in total abundance estimates could be characterised appropriately in order to quantify whether changes over time are statistically significant or not.
Following this approach, total national abundance could be estimated and mapped more robustly than at Appendix Three, and, with sequential surveys, changes in local and national abundance could be quantified and then predicted.

9.3 The models and national abundance estimates presented in this report can provide useful baseline information on which to build Natural England's vision for wild deer in England. However, the development of this vision should also include consideration of the appropriate distribution of the densities of each deer species, which will be defined, to a greater extent, by maximum or minimum impact levels that local stakeholders find acceptable. Developing an understanding of the links between deer density, impact incidence (for a wide range of impact types) and stakeholder preferences for these impacts therefore constitutes a further and considerable research requirement.

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