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Bionomics and distribution of the stag beetle, *Lucanus cervus* (L.) across Europe*

DEBORAH J. HARVEY,[1] ALAN C. GANGE,[1] COLIN J. HAWES[1] and MARKUS RINK[2] [1]School of Biological Sciences, Royal Holloway, University of London, Egham, Surrey, UK and [2]Bad Bertricher Str. 4, 56859 Alf, Germany

Abstract. 1. The European stag beetle, *Lucanus cervus*, is thought to be widely distributed across its range, but a detailed description of its occurrence is lacking.

2. Researchers in 41 countries were contacted and information sought on various life history characteristics of the insect. Data on adult body size were collected from seven countries.

3. Habitat associations differ between the United Kingdom and mainland Europe. Larvae are most commonly associated with oak, but the duration of the larval stage and the number of instars varies by up to 100% across Europe.

4. Adult size also varies; beetles from Spain, Germany, and the Netherlands are larger than those from Belgium or the UK. In the former countries, populations are composed mainly of large individuals, while in the UK, the majority of individuals are relatively small. Allometric relations between mandible size and total body length differ in Germany compared with the rest of Europe.

5. Distribution maps of the insect, split into records pre- and post-1970, from 24 countries are presented. While these inevitably suffer from recorder bias, they indicate that in only two countries, Croatia and Slovakia, does the insect seem to be increasing in range.

6. Our data suggest that the insect may be in decline across Europe, most likely due to habitat loss, and that conservation plans need to be produced that focus on the biology of the insect in the local area.

Key words. European distribution, habitat associations, life history characteristics, *Lucanus cervus*, predation, size variation.

*List of authors who contributed to this study: Michele Abdehalden, Nida Al Fulaij, Therese Asp, Alberto Ballerio, Luca Bartolozzi, Hervé Brustel, Roger Cammaerts, Giuseppe Maria Carpaneto, Bjorn Cederberg, Karel Chobot, Fabio Cianferoni, Alain Drumont, Götz Ellwanger, Sónia Ferreira, José Manuel Grosso-Silva, Borislav Gueorguiev, William Harvey, Paul Hendriks, Petru Istrate, Nicklas Jansson, Lucija Šerić Jelaska, Eduard Jendek, Miloš Jović, Thierry Kervyn, Harald W.Krenn, Klaus Kretschmer, Anastasios Legakis, Suvad Lelo, Marco Moretti, Otto Merkl, Rodrigo Megia Palma, Zaharia Neculiseanu, Wolfgang Rabitsch, Santiago Merino Rodríguez, John T. Smit, Matthew Smith, Eva Sprecher-Uebersax, Dmitry Telnov, Arno Thomaes, Philip F. Thomsen, Piotr Tykarski, Al Vrezec, Sebastian Werner and Peter Zach

Correspondence: Alan C. Gange, School of Biological Sciences, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK. E-mail: a.gange@rhul.ac.uk

Introduction

The stag beetle, *Lucanus cervus* (L.), although absent in some countries (Bartolozzi & Sprecher-Uebersax, 2006), is distributed widely across Europe. However, from the conservation point of view, it is of concern that in many of the countries where it is present, it has endangered or protected status and has been included in Annex II of the EC Habitats Directive and is classed as a ‘European Protected Species’. It has International Union for Conservation of Nature (IUCN) status of near threatened in 2010 across Europe. Legislation giving the species protected status has been enacted throughout the EU. However, if European efforts to produce conservation plans for this insect are to be successful, it is essential that the occurrence of the species across Europe is established, its preferred habitat identified, and life history characteristics determined.

This paper attempts to identify the differences and similarities in the bionomics of the beetle across its European range, encompassing life history characteristics, habitat choice, and size variation. Pan-European distribution papers are few in the literature, a notable exception being Ranius *et al.* (2005) who studied another endangered beetle, *Osmoderma eremita*, and presented distribution, habitat requirements, and possible conservation measures. As with *O. eremita*, *L. cervus* presents many challenges for accurate determination of its status, as the larval phase is long and its subterranean nature does not lend itself to traditional sampling methods for such insects (Gange, 2005). Moreover, the adult stage is short lived and conventional traps are of little use for recording its abundance (Young, 2005). Here, the monitoring techniques currently used to determine the status of the beetle across Europe are reviewed.

In the UK, the distribution of the beetle is known to be mostly urban (Percy *et al.*, 2000; Smith, 2003) with the insect demonstrating a broad range of host plant association (Tullett, 1998; Hawes, 2009). This paper attempts to determine whether the urban distribution and host choice is mirrored across Europe, or whether continental habitat preferences differ, since this might necessitate different conservation strategies.

Lucanus cervus exhibits a wide variation in size, which is related to mating success (Harvey & Gange, 2006). Such variation is believed to be, at least in part, determined by the larval diet, so if habitat and larval pabulum varies, then size might vary across Europe too. Here we explore whether the body size of adults differs across mainland Europe and consider whether allometric relationships vary across the range. Specifically, we examine the relationship between mandible length and total body length in males, to determine whether it is linear, or whether there is non-linearity, shown by switch points, which might suggest polyphenism. Eberhard and Gutiérrez (1991) attribute such polyphenism to environment and genetic makeup, but Knell (2009) states that attributing a species to different morphs is more difficult than may appear. This is because it may be difficult to define switch points in the allometric relationships for different morphs and such a switch point may vary between different populations of the species. Investigating such switch points is important, because Clark (1967, 1977) suggested that, based on size, there may be two sub-species of *L. cervus*; the larger *L. cervus* facies *cervus* (L.) and smaller *L. cervus* facies *capreolus* (Fuessly). Using the Gini index and Lorenz asymmetry coefficient as measures of inequality (Damgaard & Weiner, 2000), size variability of the beetle is analysed across the range, where data are available. This has enabled us to determine if populations differ in the relative abundance of large and small individuals and whether there is any evidence of bimodality in size, both of which might be suggestive of a possible subspecies. Following the recent taxonomical and faunistic overviews of European beetle fauna (Bartolozzi & Sprecher-Uebersax, 2006), there are five European taxa of the genus *Lucanus: L. cervus cervus* (Linnaeus, 1758) with a wide distribution in Europe, *L. cervus turcicus* (Sturm, 1843) found in Romania, Bulgaria, Turkey, and Greece, *L. ibericus* (Motschulsky, 1845) in South-eastern Europe (Albania, Greece, Turkey, Ukraine), *L. tetraodon* (Thunberg, 1806) in France, Italy, Albania, and Greece, and *L.* (*Pseudolucanus*) *barbarossa* (Fabricius, 1801) in Spain and Portugal. In the present analysis, we considered only the taxon *L. cervus cervus* (Linnaeus, 1758). Outside Europe, *L. cervus* is also quoted from Israel, Lebanon, Syria, and Turkey.

One indication of an increased threat to a species is a decline in its range, as in most species, abundance, and range size are closely related (Holt *et al.*, 2002). However, abundance, defined as the sum of all organisms making up the population, across all life stages, is impossible to obtain for an insect like *L. cervus*, since the vast majority of the life cycle is spent in subterranean larval and pupal stages. Similarly, mapping areas using presence or absence data to determine the range of an insect may also give a distorted view of rarity, since it may fail to take into account areas that may not be suitable for habitation by the species. Many studies use presence in 10 km^2 to determine range size, for example Kennedy and Southwood (1984) and Percy *et al.* (2000), the latter being for the distribution of the stag beetle in the UK. However, even on a local scale such as in the UK, abundance studies within the range to date have been limited (Harvey *et al.*, 2011). Here an overall distribution of the beetle is given, demonstrating its widespread nature across Europe. Following the format of Ranius *et al.* (2005), countrywide distribution maps are provided, with data divided into pre- and post-1970, in an attempt to identify any decline in range.

The life cycle of the beetle is widely quoted in the literature as consisting of a prolonged larval phase, comprising three instars, the duration of which is quoted as varying between 1 and 6 years (Klausnitzer, 1995; Harvey & Gange, 2003). Subsequent pupation and eclosion occur in the soil, both of which are completed in late summer to early autumn (Harvey & Gange, 2003). The adult insects overwinter, and emerge in the following early summer. The adults die after a brief mating phase, lasting up to 3 months (Harvey, 2007). Here, we examine differences across Europe in the life cycle of the beetle, including temperature thresholds, where known, for crepuscular flight activity and details of oviposition.

Our overarching aim is to determine whether a single conservation programme is appropriate for the species across Europe, or whether differences in the life cycle may merit different conservation plans in different regions. The scale of this study is large, but we believe that conservation strategies need to be examined on regional scales, in order for the most effective targeting of limited resources for the preservation of the species.

Methods

Researchers in Albania, Andorra, Austria, Belarus, Belgium, Bosnia, Bulgaria, Croatia, Cyprus, Denmark, Estonia, Finland, France, Georgia, Germany, Greece, Hungary, Iceland, Ireland, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Malta, Norway, Poland, Portugal, Romania, Russia, San Marino, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, The Netherlands, Turkey, Ukraine, and United Kingdom were contacted and information requested on life cycle parameters, habitat associations, predators, size of adults, survey methods, and perceived status/threats. Not all data were available in all countries and those that were obtained are listed in Table 1.

Table 1. Summary of data obtained from European countries. A 'Y' indicates presence of information.

Country	Life cycle	Size data	Predation	Habitat	Status
Belarus				Y	Y
Belgium	Y	Y	Y	Y	Y
Bulgaria			Y	Y	Y
Denmark				Y	Y
France		Y		Y	Y
Germany	Y	Y	Y	Y	Y
Greece				Y	Y
Hungary				Y	Y
Italy			Y	Y	Y
Latvia				Y	Y
Moldova	Y			Y	Y
Netherlands	Y	Y	Y	Y	Y
Portugal	Y			Y	Y
Romania			Y	Y	Y
Slovakia				Y	Y
Slovenia	Y	Y		Y	Y
Spain		Y	Y	Y	Y
Sweden	Y		Y	Y	Y
Switzerland	Y		Y	Y	Y
UK	Y	Y	Y	Y	Y

Life cycle

Data were collected from nine countries (Table 1) and included place of oviposition, clutch size, duration of egg and larval stages, number of larval instars, pupation time, duration of pupal stage, time of adult emergence, duration of adult stage, threshold temperature for flight activity, and feeding behaviour of adults. The information on larval and pupal stages has been largely sourced from captive beetles, breeding in conditions designed to simulate their natural habitat, since such findings are incidental in the natural environment and often impossible to obtain.

Habitat choice and status

Researchers were asked to identify the habitat within which the insect was found and the species of tree acting as a host for wild-collected larvae. 'Habitat' comprised sites where larvae have been identified, as well as those provided by monitors in surveys requesting information from the general public. Both species of tree and location were determined. Differences in host associations between mainland Europe and the United Kingdom were examined using the Chi Squared test.

Predators

Predation data were compiled from researchers, literature reviews, and monitor surveys, to determine whether there is a common predator in the larval and adult stage. The agent of predation was determined by the nature of the remains found, since predators of the beetle attack it in a distinctive fashion (Harvey, 2007).

Size variation

Measurements of wild caught adult beetles were obtained from the UK (1008 males, 599 females), Belgium (86 ♂, 71 ♀), Netherlands (130 ♂, 49 ♀), Germany (256 ♂, 202 ♀), Slovenia (33 ♂), Spain (280 ♂), and France (192 ♂). Only specimens caught post-2000 were used, in an attempt to provide as fair a comparison as possible, using standardised data. Museum collections were excluded because these bias the analyses, by concentrating on extremes in the insect (Harvey & Gange, 2006).

Total body length was used as the measure of size, following Harvey and Gange (2006). This included mandible length in the male, but the mandible length was also measured separately to allow for examination of the allometric relations between body size and armature size (Knell, 2009). Linear regression was used to evaluate these relationships and differences between slopes and intercepts examined with heterogeneity of regression test. Mean size of males and females was calculated and, following a Kolmogorov–Smirnov test to check for the normality of the data, a one-factor analysis of variance (ANOVA) was carried out to determine whether size differed across the European populations measured. The Tukey HSD test was used to separate means post ANOVA. Frequency histograms of body size were plotted to see whether there is any evidence of bimodality across the range, which might indicate presence of sub-species. The Gini and Lorenz asymmetry coefficients (Damgaard & Weiner, 2000) were calculated, as the former provides a measure of the size variability in populations, while the latter indicates which size classes (e.g. the larger or smaller individuals) contribute most to the total amount of inequality in the population. The use of these indices for measuring variability in insect size is explained in Harvey and Gange (2006). Confidence intervals for the Gini coefficient were obtained with a bootstrap procedure (Dixon *et al.*, 1987).

Distribution maps

A distribution map of *L. cervus* in Europe was produced by combining information available at national level. Within each country, information was collated from collections, entomological literature, and field observations. Data sources and providers for each country are listed in Table 2.

The information presented is as complete as possible, but inevitably some deficiencies exist. In some cases, data could not be ratified by entomologists (Austria and Lithuania) while in other countries, no comprehensive database is available (Albania, Bosnia-Herzegovina, Croatia, France, Romania, Serbia, and Ukraine). Doubtful data or data from introduced specimens were omitted.

Survey effort differed between countries. Four categories could be distinguished (Table 2): (1) 'High', when historical data were compiled from the literature, major collections or databases were consulted and one or more recent national surveys have

Table 2. Countries and data sources for the European distribution map of *L. cervus*.

Country	Survey effort	Data sources
Albania	Very low	Hungarian Natural History Museum (Otto Merkl)
Andorra	Low	GTLI database (Marcos Méndez)
Austria	Middle	Compilation by Wolfgang Paill and Christian Mairhuber (Legorsky, 2007)
Belgium	Middle	Compilation by Roger Cammaerts, Arno Thomaes and Thierry Kervyn
Bosnia-Herzegovina	Very low	Hungarian Natural History Museum (Otto Merkl) + Royal Belgian Institute of Natural Sciences (Alain Drumont and Arno Thomaes)
Bulgaria	Low	Compilation by Borislav Gueorguiev + data by Nicolas Gouix and Hervé Brustel
Croatia	Middle	Compilation by Lucija Seric-Jelaska + Hungarian Natural History Museum (Otto Merkl) + Al Vrezec personal data + Royal Belgian Institute of Natural Sciences (Alain Drumond and Arno Thomaes)
Czech Republic	Middle	Agency for Nature Conservation and Landscape Protection of the Czech Republic 2007 + Luca Bartolozzi personal data + Strojny (1970)
Denmark	Middle	Compilation by Philip Francis Thomsen
France	Low	GBIF database† + Gangloff (1991) + National Natural History Museum Luxembourg (Marc Meyer) + GTLI database + INBO + Royal Belgian Institute of Natural Sciences (Alain Drumont and Arno Thomaes) + Personal data by different entomologists‡ + Lacroix (1968) + Moretto (1977) + Dajoz (1965)
Germany	Middle	Federal Agency for Nature Conservation (Götz Ellwanger) + Markus Rink personal data + Personal data by Nicolas Gouix and Hervé Brustel
Greece	Low	Compilation by Anastasios Legakis + Luca Bartolozzi personal data + Royal Belgian Institute of Natural Sciences (Alain Drumont and Arno Thomaes) + Personal data by Nicolas Gouix and Hervé Brustel
Hungary	Low	Compilation by Otto Merkl (Hungarian Natural History Museum) + Royal Belgian Institute of Natural Sciences (Alain Drumond and Arno Thomaes) + Museo Zoologico de 'La Especola' (Luca Bartolozzi) + Personal data by Nicolas Gouix and Hervé Brustel, and Roger Cammaerts
Italy	Middle	Checklist and distribution of the Italian fauna (Bartolozzi & Maggini, 2006) + data by Fabio Cianferoni + Austrian ZOOBODAT + Personal data by Nicolas Gouix and Hervé Brustel, and Roger Cammaerts
Latvia	Middle	Compilation by Dmitry Telnov + Strojny (1970)
Lithuania	Low	Pileckis and Monsevičius (1995)
Luxembourg	Low	National Natural History Museum Luxembourg (Marc Meyer and Arno Thomaes) + Royal Belgian Institute of Natural Sciences (Alain Drumont and Arno Thomaes)
Moldova	Middle	Compilation by Zaharia Neculiseanu
The Netherlands	Middle	Compilation by John T. Smit
Poland	Middle	Compilation by Piotr Tykarski, based on Strojny (1970), Kubisz (2004), Żmihorski & Barańska (2006), Kuśka & Szczepański (2007) and Bunalski & Przewoźny (2008).
Portugal	Middle	Compilation by Jose Manuel Grosso Silva
Romania	Low	Compilation by Petru Istrate + Hungarian Natural History Museum (Otto Merkl)
Serbia	Very low	John T. Smit personal data + Al Vrezec personal data + Museum of Helsinki (Luca Bartolozzi)
Slovakia	Middle	Complilation by Eduard Jendek
Slovenia	Middle	Compilation by Al Vrezec + Royal Belgian Institute of Natural Sciences (Alain Drumont and Arno Thomaes)
Spain	Middle	GTLI database (Marcos Méndez)
Sweden	Middle	Artdatabanken database (Björn Cederberg)
Switzerland	Middle	CSCF database 2009
Ukraine	Low	Compilation by Vasiliy Kostyushin + Strojny (1970) + Personal data by John T. Smit, V. A. Korneyev and S. Korneyev, and Roger Cammaerts
United Kingdom	High	PTES (1998, 2002 and 2006–2007 surveys) + NBN Trust database§ + Clark (1966)

†Includes data from the Museum d'Histoire Naturelle de Paris and the Museum of Nature and Human Activities, Hyogo Pref., Japan.
‡Mickaël Blanc, Laurent Bernard, Hervé Brustel, Camille Garin, Nicolas Guix, Nicolas Moulin.
§Includes data from the following databases: UK Biodiversity Action Plan Invertebrate Data for Wales (Countryside Council for Wales), Invertebrate Site Register – England (Natural England), BRERC January 2008 (Bristol Regional Environmental Records Centre), Dorset SSSI Species Records 1952–2004 (Natural England and Dorset Environmental Records Centre), Welsh Invertebrate Database (Countryside Council for Wales), RHS monitoring of native and naturalised plants and animals at its gardens and surrounding areas (Royal Horticultural Society).

been performed. (2) 'Medium', when a comprehensive review of literature sources, major entomological collections, and databases has been carried out and good contact with amateur entomologists exists. (3) 'Low', when information was available only from some literature sources, or from one or a few major collections or databases, or from brief contact with amateur entomologists. (4) 'Very low', when only miscellaneous records were available.

All maps presented are Universal Transverse Mercator (UTM) dot maps at 10×10 km resolution. Information was provided in grid mapping format or in latitude and longitude coordinates and converted to UTM coordinates using a DMAP Excel macro provided by Alan Morton (http://www.dmap.co.uk/utmworld.htm). When the information was provided as dot maps representing localities (Latvia, Lithuania, Poland) or patches of habitat occupied (Czech Republic), data were converted to UTM coordinates by overlaying that map with an UTM grid map. In cases where a list of localities was provided (Moldova), UTM coordinates were obtained by using an UTM coordinates finder available at http://www.tutiempo.net.

Where possible, in each country, distribution data have been divided into squares occupied prior to 1970, after 1970 only or both before and after 1970, in an attempt to determine any evidence of decline. This date was chosen since it marks a point when many European countries began to worry about the conservation status of *L. cervus*. Where data were ambiguous, only one of the dates of occupancy (before or after 1970) have been coded, which may give a slight underestimation of range change. Data from Denmark were coded separately, as *L. cervus* is believed to have gone extinct in 1970 (van Helsdingen *et al*., 1995).

Results and discussion

Life cycle

Life history characteristics of the insect are given in Table 3. In most cases, there is little variation across Europe, with the exception of the larval stage. Even though larvae were kept in standard conditions, it is evident that the number of instars (3–5) and length of this stage (3–6 years) can vary by up to 100%. In both cases, the lower value was reported from the Netherlands, while the higher value came from the UK.

Table 3. Bionomics of *L. cervus* across Europe (n = 9 countries for each parameter).

Life history characteristic	Mean ± SE	Range
Clutch size	24 ± 3.1	15–36
Egg duration (days)	29 ± 4.1	21–45
Larval stage duration (year)	4 ± 0.58	3–6
Number of larval instars	3 ± 0.4	3–5
Pupal stage duration (days)	44.2 ± 6.9	28–60
Adult male active period (weeks)	8.4 ± 0.75	6–10
Adult female active period (weeks)	12 ± 1.03	8–14
Threshold temperature for flight (°C)	14.32 ± 1.04	11–18

All researchers reported oviposition in the soil, near rotting wood. Pupation time also seems to be standard, occurring in late July. Adult males emerge about a week before the females, with most appearing in late May. Males have occasionally been noted as early as April, while in cooler climates such as Sweden and those with a wet spring, such as Switzerland, appearance is delayed. Across Europe, there are scattered records of adults (particularly males) feeding at sap runs on tree trunks, yet this behaviour has never been recorded in the UK.

Habitat choice

The habitat preference across mainland Europe is concentrated in urban and oak woodland areas. However, there is a marked difference in habitat association between Europe and the UK (χ^2 = 85.2, d.f. = 8; Fig. 1). The species exhibits a largely urban distribution in the UK, while in Europe it is associated with more densely wooded areas, either at the edges of forests or in parkland. However, all researchers stated that a critical part of the habitat is its openness to make both flight easier and allow the insect warming time before flight.

Larval host associations across Europe (excluding the UK) are depicted in Fig. 2. Here, it can be seen that over 50% of all records come from the genus *Quercus* (this includes several different species, but most records are from *Q. robur*). These data are quite different to those of the UK, published by Percy *et al.* (2000) and Hawes (2009). In Britain, the species has been recorded from 60 different hosts, and although the most prevalent was oak, it formed only 9%–19% of records. Furthermore, within urban areas, both within mainland Europe and the UK, it appears that the larva does not necessarily require subterranean wood, being found in, among other things, railway sleepers, bark chippings, fence posts, and compost heaps. The use of fence posts suggests that tree size is not necessarily relevant, with small (approximate diameter 20 cm) pieces of timber providing habitats for small numbers of larvae. However, what is unclear is whether such small wood sources are able to provide long-term habitat, where there are similar posts in an area, or at least corridors for dispersal or whether such populations will inevitably die out. Across Europe the altitude at which the beetle is found varies from 5 to 50 m above mean sea level (Suffolk, UK) up to 1700 m in Bulgaria.

Predation

An assessment of predation of adults across Europe shows that magpies (*Pica pica*) and other corvids inflict the majority of predation, with foxes (*Vulpes vulpes*) the next most common predator (Fig. 3). Hall (1969) and Franciscolo (1997) also quote common shrew (*Sorex aranaeus*) and kestrel (*Falco tinnunculus*) among predators. The major predators of the larvae are wild boar (*Sus scrofa*) and badger (*Meles meles*). However, the largest perceived threat to the beetle across Europe is believed, by most researchers working with the species, to be man, with the loss of

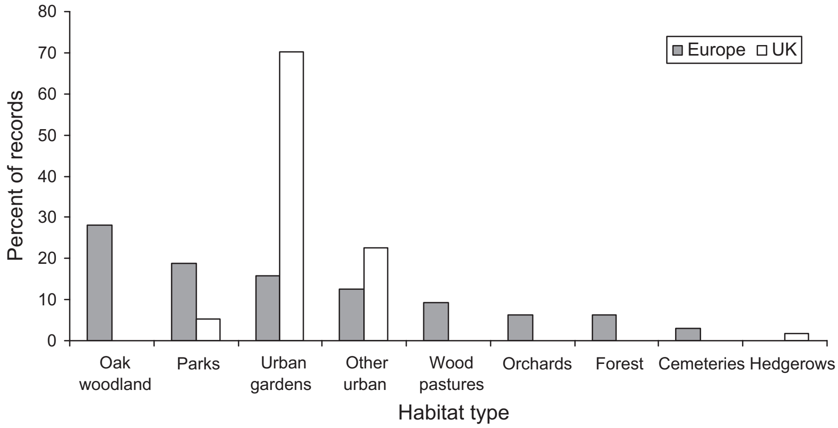

Fig. 1. Habitat associations of the stag beetle in mainland Europe and the United Kingdom. Data are expressed as the percentage of all records over 19 countries (see Table 1) or of all records in the United Kingdom.

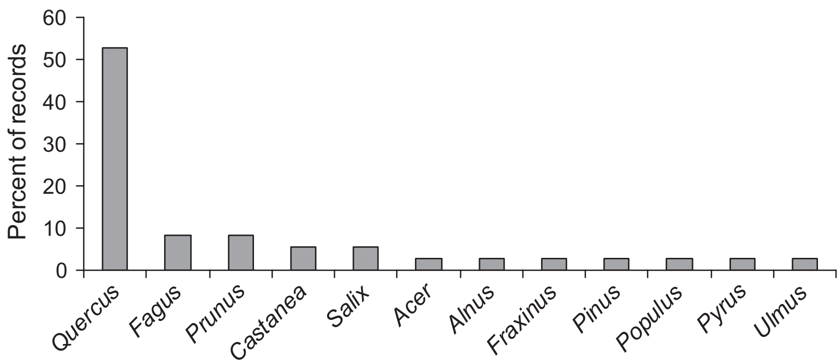

Fig. 2. Host associations of the stag beetle in mainland Europe and the United Kingdom. Legend as in Fig. 1.

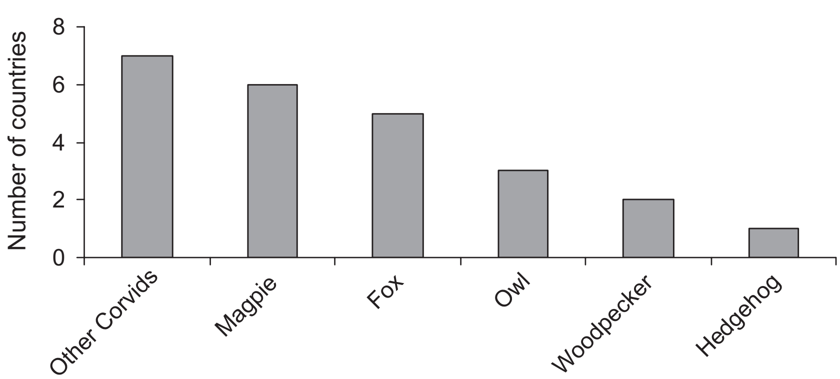

Fig. 3. Frequency of predators of the stag beetle, expressed as a percentage of all records across Europe (United Kingdom and mainland Europe combined).

habitat in urban areas and forest management techniques being the main factor in the decline of numbers.

Body size and size variation

Figure 4 depicts the size distributions of adult males in seven countries. There was no clear evidence of bimodality in any of the samples and the only country with data not fitting a normal distribution was Spain (Kolmogorov–Smirnov test, $P < 0.001$).

In all countries, males are larger than females. The mean size of beetles varies significantly across Europe ($F_{6,1313} = 36.1$, $P < 0.001$), with Spanish males larger than those in any other country (Fig. 5a). Those from the Netherlands were smaller than Spanish individuals, but larger than those from all other countries except Germany. Males in Belgium, France, Slovenia, and the UK were of similar size. The range in male size for each country was: Belgium, 31–72 mm; France, 36–80 mm; Germany, 36–74 mm, Netherlands, 33–77 mm; Slovenia, 39–74 mm; Spain, 40–83 mm; and UK, 30–71 mm.

Fewer countries supplied female size data, but Fig. 5b shows that females also differ in size across Europe ($F_{3,404} = 18.6$, $P < 0.001$). German and Dutch females tend to be larger than

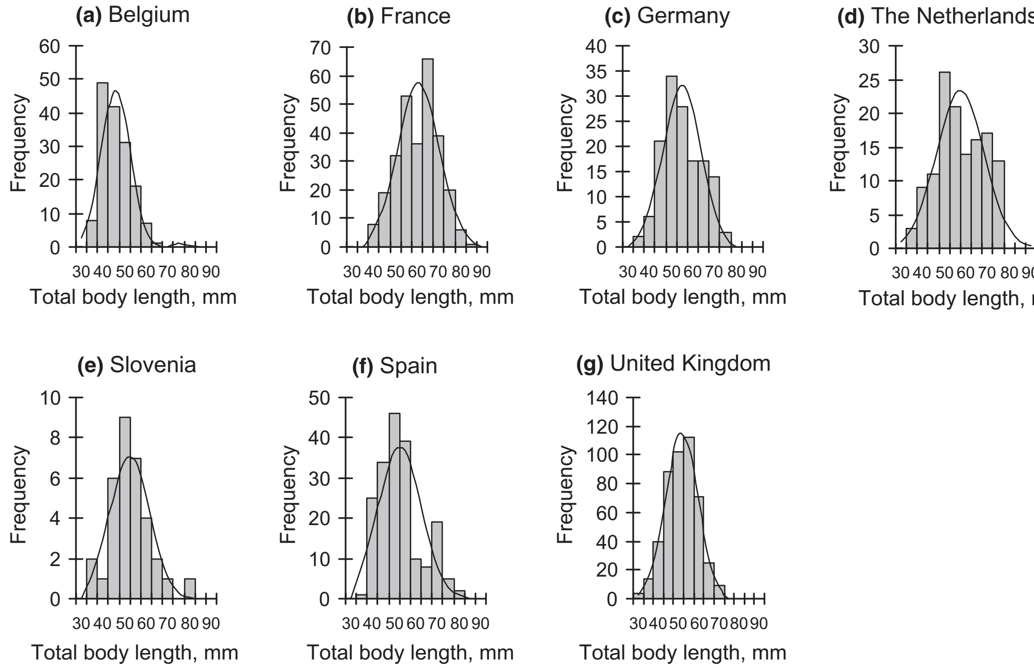

Fig. 4. Size distributions based on total body length of males from each country of adult male stag beetles in seven countries. The line represents the fitted normal distribution in each case.

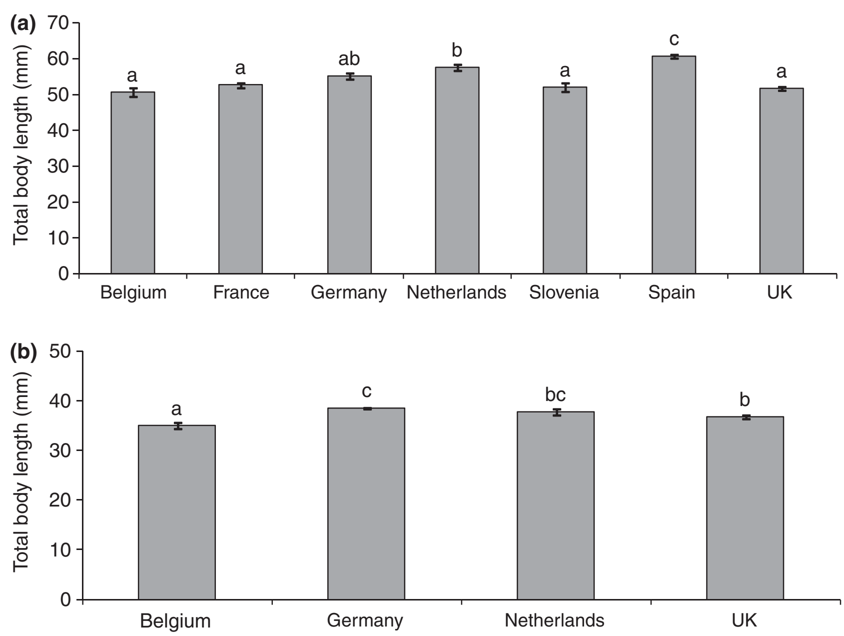

Fig. 5. Size (total body length) of adult male (a) and female (b) stag beetles across Europe. Bars represent means ± one SE. Bars that share the same letter do not differ at $P = 0.05$.

those from Belgium and the UK, in a similar pattern to that of their male counterparts. The range in female size in each country was: Belgium, 25–43 mm; Germany, 29–49 mm; Netherlands, 28–45 mm; and UK, 27–43 mm. Ratios of average male to female size were: Belgium, 1.44; Germany, 1.43; Netherlands, 1.52; and UK, 1.41.

Figure 6a shows that the male beetles in the UK have the smallest Gini coefficient, suggesting that variability is low in the UK population, and that the majority of beetles are small, shown by the low value of the Lorenz asymmetry coefficient (Fig. 6b). This contrasts directly with Belgian and Dutch populations, which are much more variable in size,

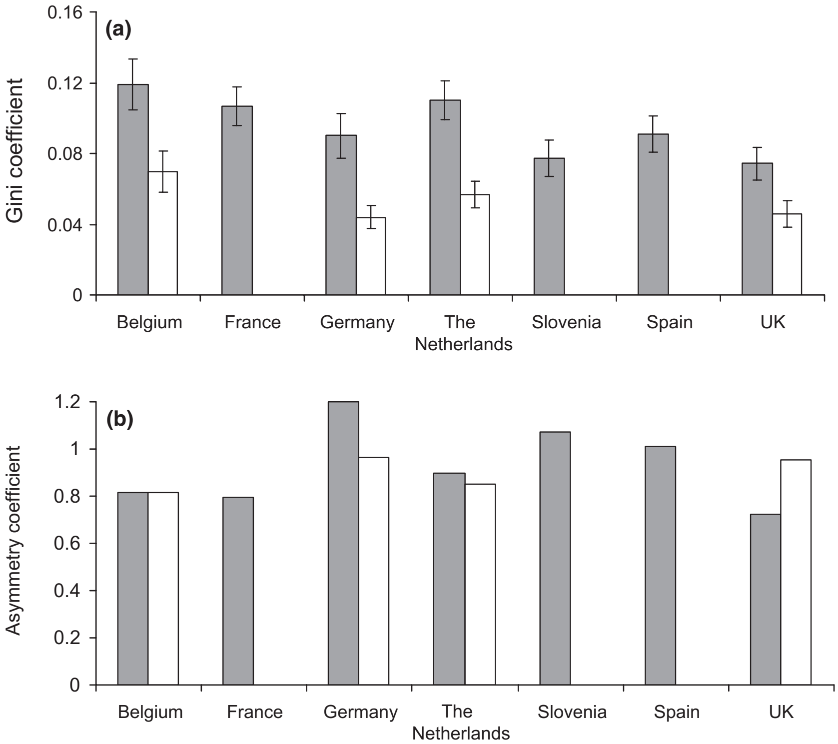

Fig. 6. (a) Size inequality (measured by Gini coefficient, with 95% CI) and (b) Lorenz asymmetry coefficients for male (shaded bars) and female (open bars) stag beetles across Europe.

shown by the larger Gini coefficients. Furthermore, in Germany, Slovenia and Spain, the Lorenz coefficient for males is greater than 1.00, suggesting that the population of males is made up of mainly larger beetles, with few small individuals. Although it should be noted that sample size in Slovenia (33) was small, samples in Germany (202) and Spain (106) were large, suggesting a real biological difference in populations. In all populations measured, males are more variable than females in size, as indicated by the much greater values of the Gini coefficient.

Allometric relationships

Further evidence for differences between the populations of males is provided by a comparison of the allometric relationships between mandible length and total body length (Fig. 7). All relationships were highly significant, but both slopes ($F_{3,1068}$ = 59.1, P < 0.001) and intercepts ($F_{3,1068}$ = 71.9, P < 0.001) showed big differences between the countries. The slope and intercept for German beetles was much lower than that for all other countries, while the Spanish population showed the greatest values of these parameters. The slope and intercept of Spanish beetles were greater than those from the UK. In each of the individual relationships, the data were best fitted by a linear model and there was no evidence of a switch point, thereby corroborating the lack of evidence for bimodality in size of these populations.

Survey methods

Of the 20 countries supplying data (Table 1), eight (Belgium, Bulgaria, Moldova, Netherlands, Slovakia, Slovenia, Sweden, and the UK) have used volunteer surveys to determine beetle numbers. Lured traps have been trialled in the UK (Harvey *et al*., 2011), Slovenia (Vrezec *et al*., 2006, 2007) and France (Brustel & Clary, 2000) giving some information about the numbers or sex ratios of the beetle. In each country, different lures have been trialled, including ginger (Harvey *et al*., 2011),

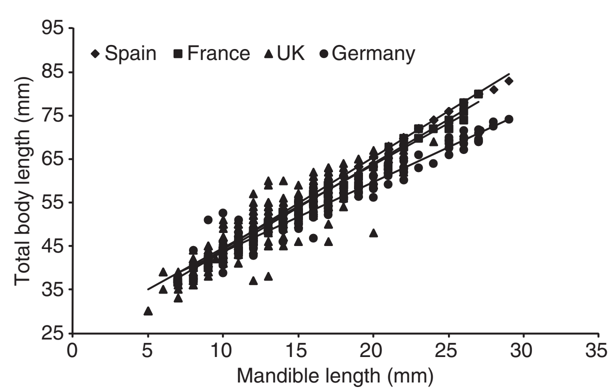

Fig. 7. Allometric relationships between mandible length and total body length of adult male stag beetles in four countries. Lines represent the fitted linear regression in each case.

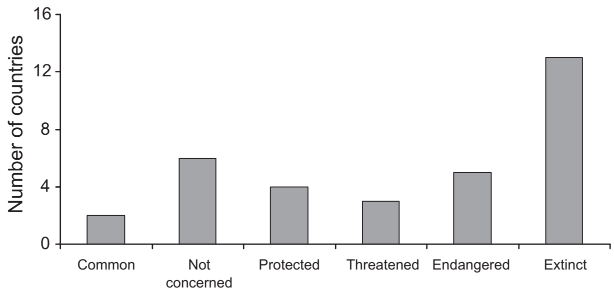

Fig. 8. The perceived status of the stag beetle across Europe, summarised as the number of countries placing it in each category.

banana, and beer (Brustel & Clary, 2000), vinegar, or alcohol-sugar mix (Vrezec & Kapla, 2007). All have trapped beetles, but in low numbers. In addition, Harvey *et al.* (2011) and Vrezec and Kapla (2007) used pitfall traps, where equal numbers of both sexes of beetle were trapped, and in Sweden, Jansson (unpubl.) produced a monitoring station where beetles were attracted to a platform lured with 'beetle porridge', a form of fermented wood.

Road kill monitoring has been used in four countries across Europe, namely the UK (Harvey *et al.*, 2011), Belgium (R. Cammaerts, unpubl.; A. Thomaes, unpubl.), the Netherlands (P. Hendriks, unpubl.), and Spain (Mendez, http://entomologia.rediris.es/gtli/espa/cuatro/H/mortal.htm). This method involves collecting corpses along predetermined transects and has been used to estimate abundance as well as giving data on presence or absence in an area (Harvey *et al.*, 2011).

Evening transects of flying beetles (Vrezec *et al.*, 2006, 2007) and radio telemetry have also been used, the latter to determine the dispersal distance of the insect and to determine the relative importance of males and females in dispersal (Rink & Sinsch, 2006). Predictive methods of distribution have been trialled in Sweden (T. Asp, unpubl.) utilising GIS techniques and Belgium (Thomaes *et al.*, 2008a, 2008b), coupled with monitor surveys to predict the areas in which stag beetles may be found.

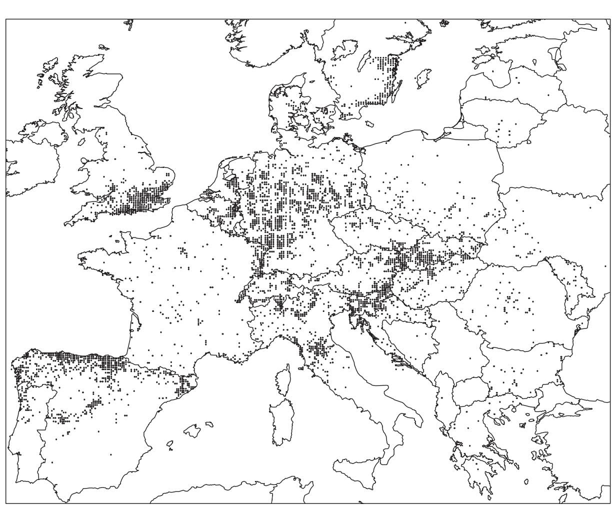

Fig. 9. Distribution of the stag beetle across Europe, where each dot represents at least one record in a 10×10 km^2.

Status and perceived threat

Of the 41 countries contacted, 33 supplied data regarding the status of the beetle, 13 (39%) of which reported it currently absent or extinct (Fig. 8). Of the remaining 20 countries, 12 reported a status from protected to endangered, while only eight (24%) reported that it is common or of no conservation concern. These data suggest that the beetle is in decline, that it is rare on a European wide basis and so highlight the need for a European-wide monitoring programme.

Distribution across Europe

Figure 9 depicts the known distribution of the stag beetle across Europe. Even with such an intensive study as this, it is evident that the map is still influenced by recorder bias; for example, the lack of records in France is probably more indicative of a lack of monitors, rather than a lack of beetles. Nevertheless, these data show that the insect has a wide distribution, from southern Sweden in the north to southern Spain and Greece in the south.

Finer resolution of the status of the insect in different countries can be obtained by examination of the distribution maps in each (Fig. 10). In Spain (Fig. 10a), there appears that there might have been a retraction in the range, with the majority of pre-1970 records occurring in the south and east of the country. A similar situation exists in Portugal, where the majority of older records are in the south of the range. In Spain and Portugal, there is a marked absence in the hotter, more southerly parts of these countries.

Similar contractions in range are perhaps evident in Belgium and the Netherlands (Fig. 10b) and Italy (Fig. 10c), while the situation in the Baltic states (Fig. 10d) may present cause for concern, with the beetle being absent in Estonia, showing a possible decline in range to just one 10 km^2 in Latvia, while in Lithuania it may be distributed in a central corridor of distribution, but here the records (while old) are not dated and so further comment is inappropriate.

In Denmark (Fig. 10e), the beetle appears to have become extinct and in neighbouring Sweden there is evidence of a contraction in the range, with the decline being most noticeable in the south west of the country.

The situation in France (Fig. 10f) undoubtedly represents a lack of recorders, rather than a true distribution. In contrast, the UK probably represents the most intensive study of beetle distribution (Fig. 10g), where the older records are mostly on the periphery of the range. The data suggest that the abundance of the insect, based on the number of squares occupied has not changed, but the range in distribution has declined. The recent northern records are all of single specimens and are likely to represent beetles moved accidentally by human transportation, rather than breeding populations.

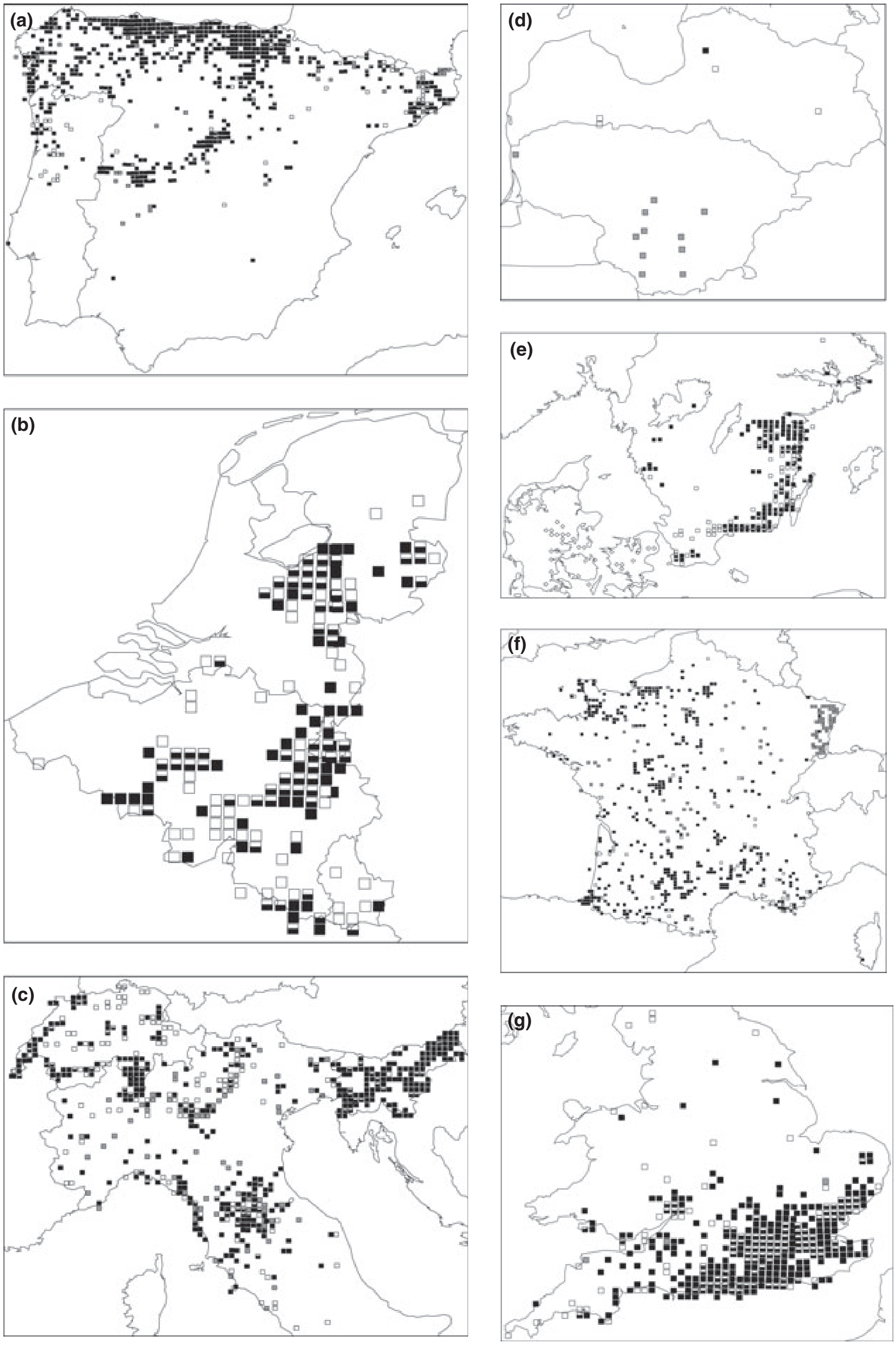

Fig. 10. Distribution maps of the stag beetle in different European countries. (a) Spain and Portugal; (b) Belgium, the Netherlands, and Luxembourg; (c) Italy; (d), Estonia, Latvia, and Lithuania; (e) Denmark and Sweden; (f) France; (g) United Kingdom; (h) Czech Republic; (i) Ukraine; (j) Bulgaria, Greece, and Romania; (k) Germany; (l) Poland and (m) Albania, Bosnia-Herzegovina, Croatia, and Serbia. Filled circles represent records post-1st January 1970, open circles, pre-1st January 1970. Half-filled circles represent records before and after 1 January 1970. Grey circles represent records with no date.

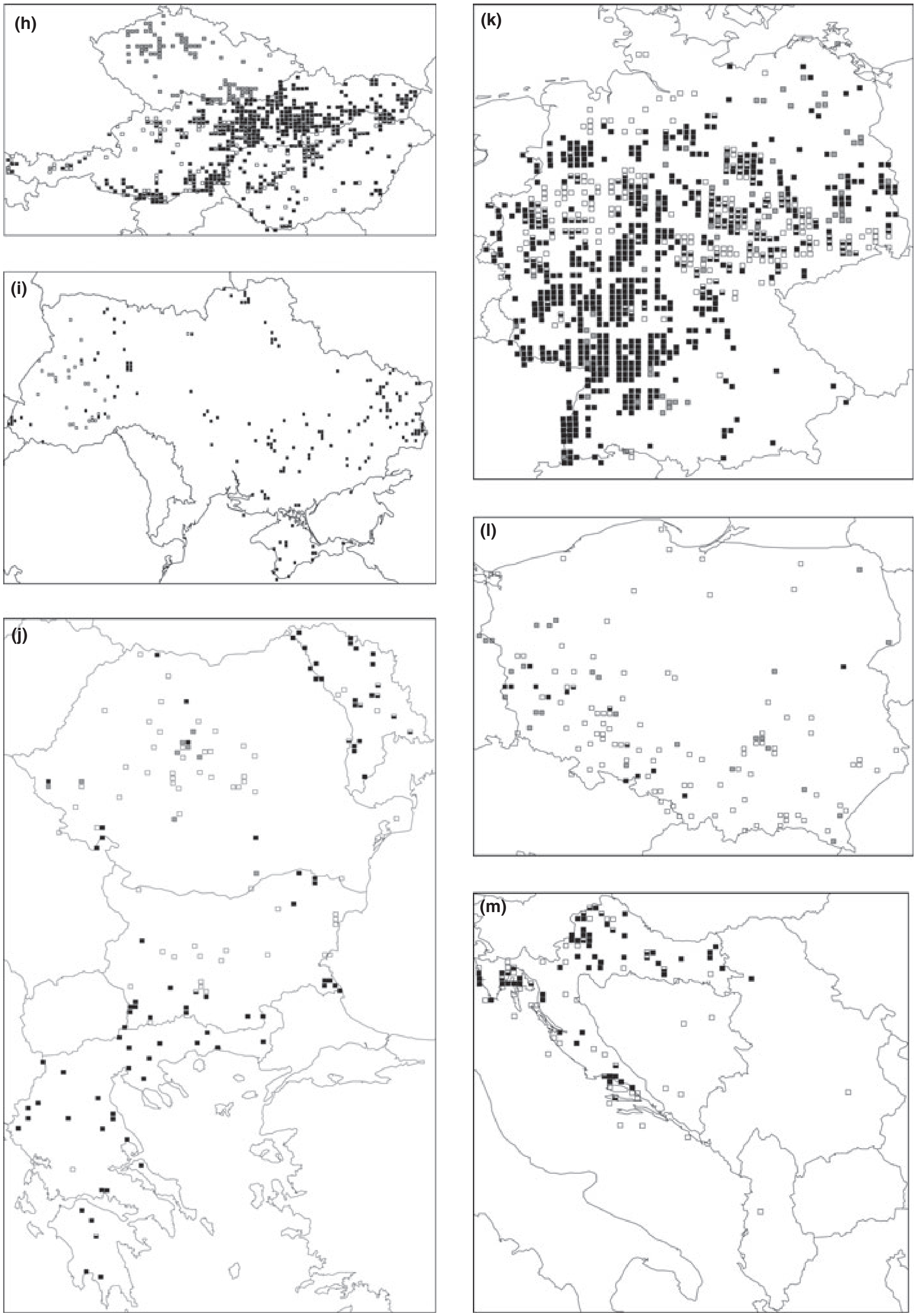

Fig. 10. *(Continued).*

The Czech Republic (Fig. 10h) shows a patchy distribution, although there are no dates confirmed in the data which makes it impossible to reflect the actual post-1970 distribution. Slovakia shows little cause for concern, with the beetle enjoying a wide post-1970 distribution while Hungary shows a good distribution in the northern and north-central parts of the country, but there is suggested evidence of a decline in western and south-eastern parts. In Ukraine (Fig. 10i), the beetle appeared to have been largely restricted to the west of the country prior to 1970, but after this time, it has only been recorded from just one 10 km^2 in the south of the country. Potential dramatic declines in range are also apparent in Romania and Bulgaria (Fig. 10j). Having once been widely spread in these countries, there are now just scattered records, similar to the distribution in neighbouring Greece. However, in Bulgaria at least, this may be due to lack of monitoring effort rather than an actual decline (B. Gueorguiev, unpubl.).

In contrast, a country with reliable records is Germany (Fig 10k), where the species is widespread, although the distribution appears to have declined across the central and eastern parts of the country. Other countries that have produced few or no records post-1970 include Poland (Fig. 10l) and Albania, Bosnia-Herzegovina, and Serbia (Fig. 10m). It might be hypothesised that the political unrest in some of these countries has resulted in a lack of recorders, but one country that bucks this trend is Croatia, which has a healthy number of records in recent years (Fig. 10m).

An assessment of the knowledge of the status of *Lucanus cervus* in Europe

Lucanus cervus exhibits similar life history characteristics across Europe, but the most variation is seen in the duration of the larval stage. It is interesting that the size of the adult beetle does not seem to correlate with the extent of the larval stage or the number of instars recorded. In the UK, the larval stage is commonly up to 6 years in captivity and the larvae pass through up to five instars, determined by head capsule width of individuals raised in separate cohorts (Harvey, 2007). This is two instars more than in Germany, the Netherlands, and Spain. Such intraspecific variation in instar number, also described as developmental polymorphism by Schmidt and Lauer (1977) is widespread in insect taxa, occurring in more than 100 species. It is often not apparent which factors might produce such variability, or the physiological mechanisms involved (Esperk *et al.*, 2007), but possible environmental factors are temperature, food quality, and humidity (Zhou & Topp, 2000). Esperk *et al.* (2007) noted that those insects showing variability in instar number demonstrate this even in controlled rearing conditions, postulating that it has become an evolved trait. Therefore, it might be possible that a restricted habitat in the UK has contributed to the evolution of increased larval instar number.

More likely is the fact that the habitat preference of the insect and thus larval host association varies between countries. Across Europe, we found that 52% of stag beetle larval records are associated with rotting oak (*Quercus* spp., mainly *Q. robur*), but in the UK, this figure is only between 9% and 19%, depending on the survey (Percy *et al.*, 2000; Hawes, 2009) and perhaps is a reflection of the lack of such habitat in the UK. This cannot of course be stated unequivocally here, since it is possible that any surveys may do more to survey monitor presence than actual habitat and there will be more urban records in countries such as the UK where survey effort is high. Where the larvae are associated with oak, the state of decay rather than the diameter of the tree/roots seems to be the most important factor, emphasised by the fact that larvae can be found in fence posts and railway sleepers and not just decaying stumps. However, the continued success of any population may be dependent on the quality and quantity of the rotting wood in an area since the quality of the larval diet is instrumental in affecting the size of adult insects (Schoonhoven *et al.*, 2005) and it is possible that larvae in countries such as Spain, the Netherlands, and Germany develop on pabula richer in nitrogen, or some other limiting resource, than those in the UK. Indeed, Tochtermann (1992) suggested that the presence of myoinositol, a ring like six carbon compound found in oak wood, was the reason for larvae reared on this diet to be larger, and this is the most prevalent food source in mainland Europe, but not in the UK.

Larger larvae clearly produce larger adults and the comparisons of adult size revealed that Spanish, Dutch, and German beetles are larger than those in other countries, particularly the UK. Furthermore, the analyses of size variability revealed differences in the constitutions of the different populations. In the UK, variability in adult size was low, with the majority of adult males being relatively small, while in the Spanish, Dutch, and German populations, variability was much higher and most of the individuals in the populations were large. These data come from randomly collected samples and are unlikely to be biased, like those in museums, where the extremes of size tend to be exhibited (Harvey & Gange, 2006). It is likely that the differences in habitat preference and hence quality of larval hosts cause these differences in the populations. Palmer (2002) suggested that size variation within a species is predominantly due to differences in food availability in the larval stage, and such differences in size have been demonstrated in adults of *Brachinus lateralis* (Coleoptera: Carabidae) (Juliano, 1985) and *Onthophagus taurus* (Coleoptera: Scarabaeidae) (Moczek & Nijhout, 2002). However, it is also possible that the distribution of habitats causes variability in size also. On a local scale, Magura *et al.* (2006) investigated body size inequality along an urbanisation gradient in carabids. As the gradient passed from rural to urban, mean size of beetles decreased and so did the Gini and Lorenz asymmetry coefficients, indicating that urban populations showed less variability and consisted mostly of small individuals. They attributed these changes to habitat alteration caused by urbanisation. Meanwhile, on a regional scale, Foster (1964) proposed that animals inhabiting islands were smaller on smaller islands, since there are fewer habitats and greater intensity of competition. Palmer (2002) found just such an effect with *Asida planipennis* (Coleoptera, Tenebrionidae) and this phenomenon may occur in the stag beetle, since in areas such as the UK, where the habitat is largely urban, fewer available habitats may result in greater levels of competition for food and space in larvae and oviposition sites leading to reduced size and size variability.

In the female, size may contribute to fecundity, with larger females producing more eggs, and hence more larvae. Indeed, we found that the large German females tended to produce the largest clutches. Given that we found very little evidence that feeding takes place in the adult stage, all the resources need to be acquired in the larval stage, thus further emphasising the importance of the quality of the larval diet (e.g. Crowe, 1995; Awmack & Leather, 2002). Despite variation in size between populations, the ratio of male:female size was always within the critical range of 0.9–1.6, outside of which mating cannot occur (Harvey & Gange, 2006).

Perhaps of more interest was the fact that allometric relationships between mandible size and total body length varied within the species. One would generally expect these to be constant within a species, but we found that both the slope and intercept of the regression for German beetles was different to that for French, Spanish, and British specimens. Most allometric relationships between armature size and total body size in insects are linear (Knell, 2009) but some holometabolous insects show non linear patterns, demonstrating the presence of different morphs within a species. Such polymorphism has been attributed to genetic or environmental differences (Eberhard & Gutiérrez, 1991) whilst others have suggested that such differences result from the differential allocation of resources with a metamorphosing pupa (Knell *et al*., 2004). Given the differences in size and size variability of German beetles, this may be tentative evidence of genetical differences within the European population of *L. cervus*. Clark (1977) suggested that there may be two subspecies, with *L. c.* facies *cervus* being larger than *L. c.* facies *capreolus*. Even if it is obvious that two subspecies of the same species can not be sympatric we checked and found no evidence of bimodality within populations to support Clark's assertion. However, it is possible that populations in widely separated parts of Europe (e.g. Germany and the UK) differ genetically and this may even cause the differences in larval characteristics, described above. At present, genetical differences must remain speculative, but this problem can be addressed with molecular methods and would be a rewarding area in the study of the population genetics of this insect. Moreover, this research has raised many questions about size variation in the beetle which fall outside the scope of this paper and will require further work.

The survey and distribution analysis revealed that the overall status of the insect across Europe may present cause for concern. Its status was reported as endangered or threatened in 12 of the countries and absent in 13 countries of the 41 providing information. Bartolozzi and Sprecher-Uebersax (2006) reported that the beetle has never been recorded in Iceland, Ireland, Norway, Finland, Cyprus, and Malta. However, accurate records of its abundance (past and present) have been impossible to obtain, due in no small part to the lack of suitable monitoring methods for the species. Harvey *et al*. (2011) describe various methods by which adult beetles can be trapped and counted, thus it is hoped that future surveys may be able to determine changes in the abundance of the insect. Additionally, the use of sex pheromones/semiochemicals might be an important tool to assess conservation status of endangered species, as illustrated by Larsson and Svensson (2009) in their recent work on two other endangered saproxylic beetles, *O. eremita* and *Elater ferrugineus*. Nevertheless, the analysis of the distribution of records across Europe suggests a reduction in the range of the insect. Given that range size and abundance are often strongly correlated (Gaston, 1994), our data suggest that the insect is potentially in serious decline over a large part of its range.

Gaston (1994) stated that inefficient sampling may lead to absences being recorded and even species recorded as extinct which are later proven present. He also stated that estimates of abundance across large spatial scales are often conservative giving a bleaker picture than is accurate. We took in consideration these criticisms for the data set presented here. First, we have tried to present data on a country-by-country basis, but of course political boundaries are irrelevant to an insect. Nevertheless, in some countries, such as France and probably the Baltic States, the lack of beetle records is a likely reflection of a lack of recorders. Although data suggest that the species may be extinct, or nearly so, in some countries (e.g. Denmark, (van Helsdingen *et al*., 1995), Ukraine, Poland, Bosnia-Herzegovina, this study), it is quite possible that organised surveys would lead to the generation of new records. This is exactly what has happened in the UK, where successive national surveys have given a good overview of the species' status (Percy *et al*., 2000; Smith, 2003).

These deficiencies notwithstanding, the distribution maps suggest that the insect may display an aggregated distribution of occurrence at all spatial scales. Across Europe, the distribution seems to occur in distinct 'hotspots', a phenomenon which was noted before within a country (Percy *et al*., 2000) or within a very local area within a country (Pratt, 2000). Aggregated distributions of insects are extremely common in nature (Holt *et al*., 2002) and are again a likely reflection of habitat availability. However, for an insect such as *L. cervus*, such distributions may be critical to the survival of the species. It is known that dispersal distances of both sexes are limited, and may be as low as a few hundred metres (Rink & Sinsch, 2006). Thus, if distances between hotspots exceed dispersal distances, the insect may not exist in a metapopulation context, meaning that the risk of local extinction is high (Kunin & Gaston, 1993). Conservation plans for the insect thus need to take into account the distances between populations and the dispersal ability of the species.

The data used in plotting the maps were taken pre-1970 and post-1970, this makes it very difficult to make definite conclusions based upon the apparent plotted distributions. Coupled with the difference in survey effort between countries any conclusions based upon these data must be viewed with extreme caution. If we accept that the insect is in decline, then we need to understand the reasons, so that successful conservation strategies can be implemented. Our analysis of predation suggests that birds are the main natural predators. Although some of these predatory species have seen recent increases in population size (e.g. magpies, *Pica pica*, according to Gregory & Marchant, 1996), in many instances the main cause of mortality is human activity. Road traffic kills many adults each year (Harvey *et al*., 2011; J. T. Smit & R.F.M. Krekels, unpubl.), while habitat destruction is probably the major cause of larval mortality. Harvey *et al.* (2011) present novel non-destructive methods by which larval presence can be detected and it is hoped that these will lead to a significant reduction in the destruction of larval habitats. Perhaps the best solution is education; the insect is charismatic and popular with the media and is an ideal subject for the engagement of the public in survey work, as demonstrated by the successful UK national surveys of 1998 and 2002 (Percy *et al.*, 2000; Smith, 2003). Given the differences in habitat preferences and possible genetic differences, but similarities in life history characteristics, we suggest that conservation plans for the insect need to be produced that address both regional and local aspects of the insect's autecology.

In summary, we have shown that *L. cervus* is widely distributed across Europe, and, despite wide variations in climate, it shows relatively little variation in its life history characteristics, with a prolonged larval phase and a short adult mating phase. Larval duration varies significantly, as does adult size and size variability. We believe the latter parameters are mainly due to differences in the quality of larval diet, determined by the differences in habitat preference between mainland Europe and the UK. In the former, the insect is associated with oak woodlands, i.e. areas of oak trees where the canopies meet (Rackham, 2006) while in the latter, it is an urban insect, favouring garden habitats. The importance of the urban garden as a habitat for globally declining taxa has also been noted by Goddard *et al.* (in press) as important for bumblebees (*Bombus* sp.) the common frog (*Rana temporaria*). Additionally, there is increasing recognition of the potential value of gardens to biological diversity (Gaston *et al.*, 2004; with private gardens now included in many UK conservation initiatives (Local Biodiversity Action Plans). Thomaes (2009), reports that in Belgium the main habitat of the beetle is urban, with the beetle being least prevalent in agricultural areas. However, the exception to this is in the Continental aspect of Belgium, an area with higher forest cover and less urbanisation where forest edge became the predominant habitat. Furthermore, there may be genetical differences between populations, as shown by the differences in the allometric relationships and size inequality between Germany and the rest of Europe. In many areas, the species appears to be declining in range. However, as stated above, this conclusion needs to be supported by further, more accurate and up to date surveying with consistent effort across the European range, since only then will the true status of the beetle and the requisite conservation measures be determined. Currently, the plotted data are a reflection of records collated over 40 years in countries where surveying effort varies with finance, priority and entomological interest. It is hoped this paper will provide a benchmark for future more focussed collaborative work. This will necessitate different conservation strategies to be implemented across Europe, to take into account the biological and ecological differences identified in this paper.

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