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Harmonia axyridis in Great Britain: analysis of the spread and distribution of a non-native coccinellid

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Abstract *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) is native to Asia, and was widely introduced as a biocontrol agent of aphids and coccids in Europe and North America. In Europe *H. axyridis* is considered to be an invasive alien species. Although not known to have been deliberately introduced to Great Britain, it was first recorded there in 2004, in south-east England. *Harmonia axyridis* arrived in Great Britain by various means, primarily from mainland Europe, but also from Canada. Extensive national and local media coverage, and a dedicated website (http://www.harlequin-survey.org), facilitated public involvement in recording *H. axyridis* in Great Britain; in excess of 4,000 verified records of the species were received between 2004 and 2006. Through detailed mapping, the objective of our study was to quantify and analyse the spread of *H. axyridis* in its early stages of invasion in Great Britain. Our data shows that between 2004 and 2006, the species spread north through Great Britain at the rate of 58 km year^{-1} and west at the rate

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of 144.5 km year^{-1}. In England *H. axyridis* spread north to Yorkshire and west to Cornwall by the end of 2006, and also reached Wales. Recorded occurrence (of one or more *H. axyridis* individuals at larval, pupal and/or adult stage) in 10 km squares in Great Britain was: 2004—51; 2005—149; 2006—447. Records of juvenile *H. axyridis* extend through most of the recorded British range of the species, and we present evidence of bi-voltinism in the population in 2006.

Keywords Alien species · Biological control · Coccinellidae · Harlequin ladybird · *Harmonia axyridis* · Invasive species · Non-native species

Introduction

The recording of biological events in Great Britain has a long tradition; detailed recording of many taxa has been carried out since the nineteenth century (Harding 1990). Biological records for Britain and Ireland are integrated and distributed through the National Biodiversity Network (NBN) gateway (http://www.searchnbn.net), an interactive mapping website holding in excess of 27 million records for over 8,500 species. The biological recording infrastructure in Great Britain provides an effective tool for monitoring species undergoing rapid range expansions. Analysis of long-term datasets showed that various taxa (e.g. dragonflies, butterflies, spiders and fish), are moving northwards in Great Britain in response to climate change (Hickling et al. 2006). Invasive species are regarded as one of the most serious threats to biodiversity (Glowka et al. 1994). The monitoring of biological invasions is vital, in order to understand the population dynamics, habitat tolerance and impact on native taxa, of the invading species. In Great Britain, monitoring projects for invasive insects include the horse chestnut leafminer *Cameraria ohridella* Deschka and Dimic (Lepidoptera: Gracillariidae) (http://www.forestresearch.gov.uk/leafminer), and the rosemary beetle *Chrysolina americana* L. (Coleoptera: Chrysomelidae) (http://www.rhs.org.uk/research/projects/rosemary_beetle.asp).

The harlequin ladybird or multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is native to Asia (e.g. Dobzhansky 1933; Kuznetsov 1997) and was introduced to North America and Europe to control pest aphid and coccid species on a range of crops (e.g. Adriaens et al. 2003; Koch 2003). It established in North America in 1988 (Chapin and Brou 1991), spread very rapidly (Koch 2003), and became the dominant coccinellid in many areas (Colunga-Garcia and Gage 1998; Smith et al. 1996; Tedders and Schaefer 1994). In mainland Europe, *H. axyridis* was first marketed as a biocontrol agent in 1995 (Coutanceau 2006), established in the late 1990s and expanded its range rapidly, especially from 2002 (Brown et al. 2007). It is not known to have been deliberately introduced to Great Britain, but arrived by various means, including flight and on produce from mainland Europe and in packing cases from Canada (Majerus et al. 2006a; Roy et al. 2005). There is no doubt that *H. axyridis* is an effective aphid predator, and its presence may be welcomed by some. However, there is concern in Europe about the rapid increase in distribution and abundance of *H. axyridis*, and its impact on non-target species (Adriaens et al. 2003; Majerus et al. 2006b; Roy et al. 2006). Although most biocontrol companies have stopped selling *H. axyridis* in Europe, a non-flying variety is still available from Biotop (http://www.biotop.fr).

Harmonia axyridis has the potential to contribute to biotic homogenization (McKinney and Lockwood 1999) and to negatively impact on up to 1,000 species in Great Britain (Majerus 2007). These are primarily insects (including non-target Homoptera, alternative

prey, members of aphidophagous and coccidophagous guilds) and parasites, parasitoids, pathogens and symbionts of theses species (Majerus 2007). In the USA, *H. axyridis* has been declared a potential pest of fruit production and processing, as the species sometimes feeds on the juices of ripe fruits, such as apples, pears and grapes, in autumn (Koch 2003). *Harmonia axyridis* may become seriously pestilent to the native fauna of Great Britain (Majerus et al. 2006b). This pest status may extend directly to humans, as *H. axyridis* tends to form very large overwintering aggregations of thousands of individuals, often on or in buildings (Adriaens et al. 2003; Kidd et al. 1995). Some such aggregations were observed in England in 2006 (Brown and Roy 2007).

Uniquely, the early detection of *H. axyridis* in Britain presented the opportunity to study the spread of an invasive animal from the year of its arrival (Majerus et al. 2006b). There is no evidence to suggest that *H. axyridis* was established in Great Britain before 2004 and circumstantial evidence that argues against its presence prior to that year (Majerus and Roy 2005). Through detailed mapping of adult and juvenile stages, the objective of our study was to quantify and analyse the spread of *H. axyridis* in its early stages of invasion in Great Britain. A further objective was to investigate the voltinism of *H. axyridis* in Great Britain, to determine whether there was evidence of multiple generations per year.

Material and methods

Data collection

The spread of *H. axyridis* was monitored by utilising the extensive biological recording community in Great Britain, coupled with engagement of the general public. Recent advances in technology, and high levels of public access to the internet and digital photography, enabled a web-based biological survey to be set up. The Harlequin Ladybird Survey (http://www.harlequin-survey.org) was one of the first online surveys of its kind in Great Britain. It was launched in March 2005 in response to the first report of *H. axyridis* in Great Britain, in September 2004 (Majerus 2004). The survey benefited from high levels of media interest, including the front page of The Times on 15 March 2005. Members of the British public showed great willingness to look for *H. axyridis*, and to register their sightings with the survey.

The dataset presented here comprises 4,117 species records of *H. axyridis* in Great Britain between 2004 and 2006. Each record represents a verified sighting of *H. axyridis* on a given date, and comprises one or more individual ladybirds observed from one or more life stages (larva, pupa and adult; records of eggs were not included). 76% of these records were received from members of the British public by post, or entered online at the Harlequin Ladybird Survey website or UK Ladybird Survey website (http://www.ladybird-survey.org); the latter was set up to encourage the recording of native ladybirds. Verification of the records was made by the authors after receipt of either a specimen or photograph. Most photographs were received as digital images attached to emails. The remaining 24% of records were received from coleopterists and other naturalists, and in particular from the London and Essex Ladybird Survey. Such records were not verified by the authors but are regarded as accurate and so have been included in the dataset. A further 4,316 online records were received that remain unverified (i.e. no photograph or specimen was sent), or were verified as another species, and so are not included in the analyses. Verified records were regularly uploaded to the database of the National Biodiversity

Network. There they could be viewed via online maps, which helped to encourage further recording.

Each species record includes the following data: recorder name; location of sighting (the grid reference of the Ordinance Survey British national grid reference system); locality/site name (not included for all records); date of sighting; life stage observed (larva, pupa, adult); number of each life stage observed (assumed to equal 1, if not specified); and determiner name. Additional optional attributes include the number of each colour form of any adults observed (included for 82% of records), and supplementary comments, including habitat and/or behavioural information.

Three main colour forms of adult *H. axyridis* have been found in Great Britain: f. *succinea*, f. *spectabilis* and f. *conspicua*. The *succinea* complex has been divided into many subforms (e.g. *siccoma*—0 spots; *frigida*—6 spots; *novemdecimsignata*—19 spots) (Dobzhansky 1933), but is treated as a single form here. Thus f. *succinea* has elytra with a ground colour of yellow, orange, or red, and 0–21 black spots, which may or may not be fused. *Forma spectabilis* has black elytra with four yellow, orange, or red spots or other shaped markings, which sometimes contain a central black spot. *Forma conspicua* is as f. *spectabilis*, but with only two spots.

The spatial resolution of the records is variable, and while approximately 20% include a grid reference, enabling resolution to 100 m, the other approximate 80% of records were derived at 1 km resolution from a UK postal code (UK Government Data Standards Catalogue, http://www.govtalk.gov.uk/gdsc/html/frames/PostCode.htm). The option on the online recording form to enter the location via a UK postal code was provided to make the entry of records easier for members of the public unfamiliar with the grid reference system. Whilst the resolution is thus reduced for these records, the reduction in user error (e.g. the problem of grid reference eastings and northings being transposed), is an advantage (Majerus et al. 1990). The postal code method was applicable for sightings of *H. axyridis* made within 200 m of a specified postal code, so could not be used for a minority of records where the ladybird was seen in a semi-natural habitat.

Variability in recording effort (both temporally and spatially) is clearly an issue when analysing a dataset of the kind presented here. Other factors being equal, more records will come from areas with a higher density of recorders. Across Great Britain there were a number of particularly active local groups or individuals, which contributed hotspots of recorder activity, potentially biasing the results for certain areas, e.g. London, because of the high activity of the London and Essex Ladybird Survey. The Harlequin Ladybird Survey benefited from a high profile and enjoyed frequent local and national media attention, thus potentially increasing the volume of records received at certain times. To minimise these effects, the data have mostly been analysed in terms of the presence of *H. axyridis* in 10 km squares (1 km squares for juveniles) by year. Thus, whether the species was recorded just once or many times in any given square in a year, is not reflected in the analyses. To many recorders, juvenile stages were less noticeable and more difficult to identify than the adult stage, thus generally limiting the recording of juveniles.

The possibility of a reporting bias towards sightings early in the season also existed (i.e. some recorders may have reported their first sighting of *H. axyridis*, but not subsequent sightings). In order to minimise this effect, the importance of recording multiple sightings was stressed to recorders. The peaks in record numbers observed late in each year also suggest that any effect of this potential bias was minor.

Rate of spread

The location of the northern range margin of *H. axyridis* in Great Britain was measured by calculating the mean northing of the ten most northerly 10 km squares occupied each year (Hickling et al. 2006). The location of the range margins in the westerly and north-westerly directions were calculated each year using the same method. There is a very strong assumption that *H. axyridis* colonised Great Britain primarily from the coastal regions of northern France, Belgium and the Netherlands (Majerus et al. 2006a), hence the inclusion of the north-westerly direction.

Seasonal pattern

The seasonal pattern of *H. axyridis* sightings in 2005 and 2006 were examined. *Harmonia axyridis* was first recorded in Great Britain in July 2004, so that year was excluded from the analyses because of incomplete data. The data are weekly counts of the occurrence of *H. axyridis* in grid squares. For adult *H. axyridis* 10 km squares were used, but for juveniles (i.e. larvae and pupae), because of a lower number of records, 1 km squares were used.

Seasonal patterns were analysed using a Generalized Additive Model (GAM) in which the counts varied randomly about a smooth trend described by a cubic smoothing spline (Green and Silverman 1994). The degrees of freedom for the fitted GAM were determined using cross-validation (leaving out each data point in turn) and minimising the cross-validation Poisson deviance. A GAM was fitted separately to data from 2005 and 2006 to describe the seasonal pattern of observations in each year. The number of sightings was generally higher throughout 2006 compared to 2005, but the GAM curves allow comparison of the shape of the seasonal pattern each year. The null hypothesis of equality of shape in 2005 and 2006 implies that curves differ by some constant factor, i.e. parallel on a log scale. The alternative hypothesis allows different curves in each year. The test-statistic is $F = \{(D_{null} - D_{alt})/(df_{null} - df_{alt})\}/D_{alt}/df_{alt}$, where D denotes the residual deviance and df is the corresponding degrees of freedom. On the null hypothesis, the statistic follows an F distribution with $(df_{null} - df_{alt})$ and df_{alt} degrees of freedom. The analysis was performed using the statistical package Genstat 6 (Payne et al. 2002).

Results

Abundance and rate of spread

Harmonia axyridis has spread rapidly in Great Britain (Fig. 1a). Recorded occurrence (of one or more *H. axyridis* individuals at larval, pupal and/or adult stage) in 10 km squares in Great Britain was: 51 in 2004; 149 in 2005; 447 in 2006; representing a 2.9-fold increase from 2004 to 2005 and a 3.0-fold increase from 2005 to 2006. There was a 2.7-fold increase in the number of adult *H. axyridis* records, and a 2.9-fold increase in the number of individual adults recorded, from 2005 to 2006 (Table 1).

The number of 10 km squares with records of juvenile *H. axyridis* increased from 8 in 2004, to 51 in 2005, and 75 in 2006 (Fig. 1b). In 2004, evidence of *H. axyridis* breeding was restricted to London and East Anglia, with juveniles recorded in a wider range of counties in 2005 (notably Kent and Derbyshire). Further evidence of breeding was

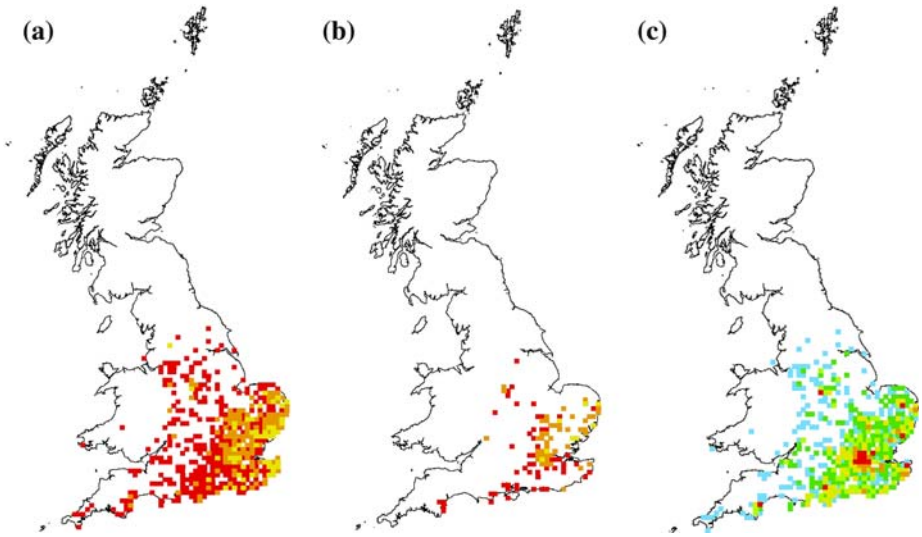

Fig. 1 *Harmonia axyridis* occurrence in 10 km squares in Great Britain from 2004 to 2006. For (**a**) and (**b**), where a square has been recorded in more than one year, occurrence in the earliest year is shown (yellow = 2004; orange = 2005; red = 2006). (**a**) Adults and juveniles; (**b**) Juveniles only; (**c**) Density of records of adults and juveniles; (red = 50+ records per square; orange = 20–49; yellow = 10–19; pale green = 6–9; dark green = 2–5; blue = 1)

recorded across south-east England, and west as far as Devon, and north as far as Yorkshire, in 2006 (Fig. 1b).

Northerly spread (Fig. 2a) distances per year were: 19 km between 2004 and 2005; 97 km between 2005 and 2006; mean—58 km year^{-1}. Westerly spread (Fig. 2b) distances per year were: 107 km between 2004 and 2005; 182 km between 2005 and 2006; mean—144.5 km year^{-1}. North-westerly spread (Fig. 2c) distances per year were: 81.2 km between 2004 and 2005; 107.5 km between 2005 and 2006; mean—94.3 km year^{-1}.

Table 1 Summary of Harlequin Ladybird Survey data from Great Britain (Note—records of large aggregations without a specific number of ladybirds recorded have been excluded)

Life stage	Year	No. verified records	Total no. *H. axyridis* recorded	Mean no. *H. axyridis* per record	Maximum no. *H. axyridis* recorded
Larva	2004	13	54	4.2	10
	2005	182	1,817	10.0	266
	2006	145	1,410	9.7	200
Pupa	2004	5	27	5.4	10
	2005	81	1,194	14.7	227
	2006	23	231	10.0	53
Adult	2004	119	344	2.9	25
	2005	1,045	6,180	5.9	399
	2006	2,825	17,641	6.2	689

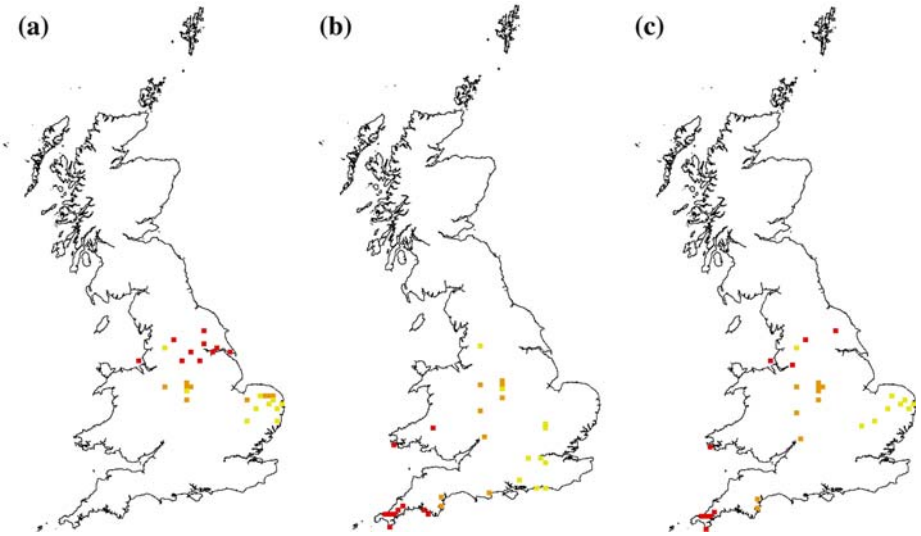

Fig. 2 Range margin of *H. axyridis* in 10 km squares in Great Britain from 2004 to 2006. Where a square has been recorded in more than one year, occurrence in the earliest year is shown (yellow = 2004; orange = 2005; red = 2006). (**a**) Ten most northerly squares per year; (**b**) Ten most westerly squares per year; (**c**) Ten most north-westerly squares per year

The density of records received was highest in and around London, and was also high in parts of East Anglia and along the south coast of England, particularly in Kent, Sussex, Hampshire and Devon (Fig. 1c). There is also a notable hotspot in Derby, the only location in central-north England with a large number of verified records (Fig. 1c).

The mean number of adults per record increased year on year, from 2.9 in 2004, to 5.9 in 2005, and 6.2 in 2006 (Table 1). The trend was different for the juvenile stages, which appear to peak in 2005 (however, see discussion). A similar pattern was observed for the maximum counts observed in each year (Table 1).

Seasonal pattern

Adults

The seasonal patterns of spread of adult *H. axyridis* in 2005 and 2006 were significantly different ($F_{12,78} = 2.52$, $P = 0.007$). The main difference in the smoothed curves was during the period 23–34 weeks, where there was a seasonal peak observed in 2006, which was not observed in 2005 (Fig. 3a and b).

Juveniles

The seasonal patterns of spread of juvenile *H. axyridis* in 2005 and 2006 were significantly different ($F_{6,89} = 3.57$, $P = <0.001$). The main difference is the extra peak around week

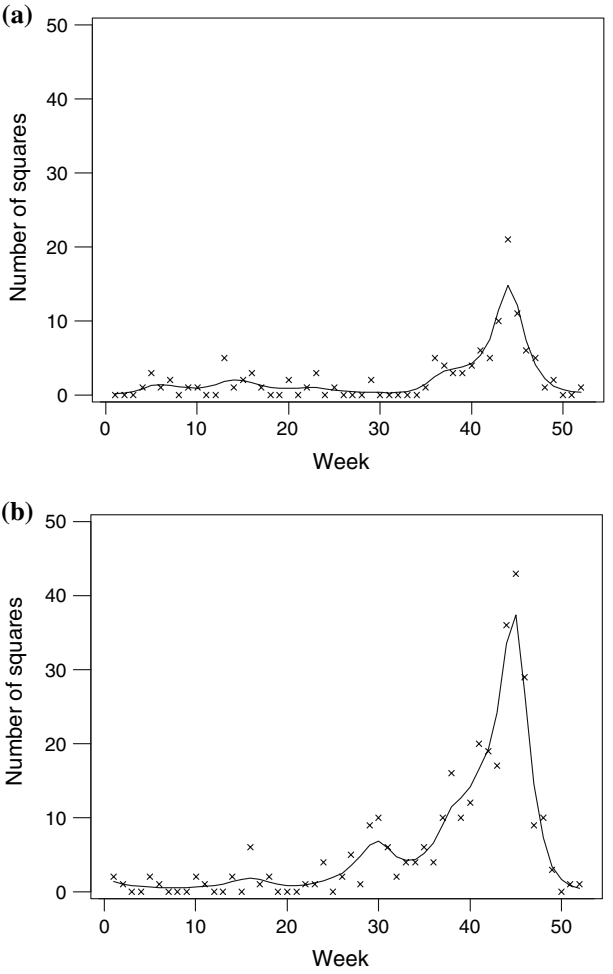

Fig. 3 Adult *H. axyridis* occurrence in 10 km squares in Great Britain with fitted GAMs and degrees of freedom (*df*). (**a**) 2005 ($df = 12$); (**b**) 2006 ($df = 13$)

25 in 2006, and the earlier date of the autumn peak in 2006. For the fitted GAMs, the main peaks occur at week 44 (2005) and week 40 (2006) (Fig. 4a and b).

Discussion

Rate of spread

The rate of spread and increase in abundance of *H. axyridis* in Great Britain has been dramatic. Westerly spread was faster than northerly spread by a factor of approximately 2.5, and this may partly be explained by the likelihood of repeated recruitment of *H. axyridis* from mainland Europe. Indeed, in 2006, eight of the ten most westerly 10 km squares occupied were in the extreme south-west of England and close to the coast, possibly representing new recruits from abroad, rather than spread from the existing British range. This factor is presumed not to apply to the most northerly squares occupied, because

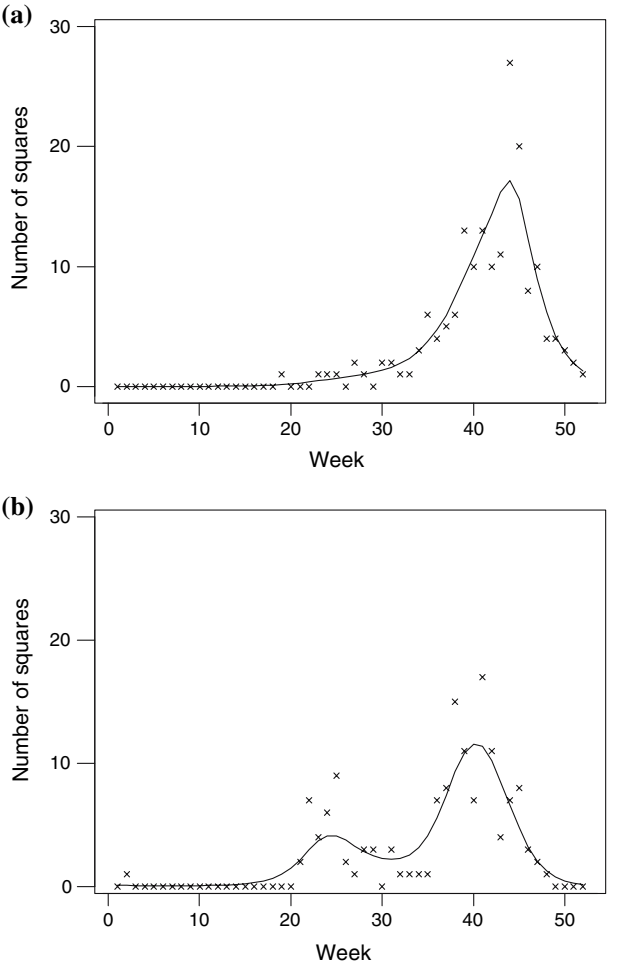

Fig. 4 Juvenile *H. axyridis* occurrence in 1 km squares in Great Britain with fitted GAMs and degrees of freedom (*df*). (**a**) 2005 ($df = 6$); (**b**) 2006 ($df = 6$)

of their greater distance from mainland Europe and, in most cases, their lack of proximity to the British coast. Ecological factors such as climate and habitat type may also have influenced the faster westerly spread. In late October and early November 2006 there was an influx of reports of large aggregations of *H. axyridis* adults, mainly at locations close to the south coast of England. Aggregations of hundreds and in a few cases, thousands, of *H. axyridis* were observed (Brown and Roy 2007). Whether these large aggregations represented new recruits from mainland Europe has yet to be determined.

The most closely related species to *H. axyridis* in Great Britain is *Harmonia quadripunctata* (Pontoppidan) (Coleoptera: Coccinellidae). This species is also a relatively recent arrival to Britain, but is now regarded as a native species, having expanded its native range northwards within Europe, and is assumed to have reached Britain by natural means (Majerus and Kearns 1989; Majerus 1994). It is not considered invasive. Although *H. quadripunctata* is far more habitat-specific than *H. axyridis*, and the mechanisms of spread may not be the same, a comparison of the rate of spread of the two species is enlightening. Majerus and Kearns (1989) outline the spread of *H. quadripunctata*. It was

first recorded in Great Britain in West Suffolk (East Anglia) in 1937, and based on earliest records for each vice county, took fifty years to spread west as far as Devon, in south-west England. Our data show that *H. axyridis* took just two years to spread to Devon from a similar starting point in East Anglia.

In Great Britain, the northerly range expansion of some insect groups was calculated by Hickling et al. (2006), giving figures of up to 4.2 km year^{-1} (over a 25 year period) for the most dispersive taxa (dragonflies); but these range expansions were for native species responding to climate change, rather than for invasive species. There is limited quantitative data on the spread of invasive insects in Europe. The spread of the horse chestnut leafminer *C. ohridella* in Germany in the late 1990s was modelled, and the rate of spread calculated to vary between 54 km year^{-1} and 330 km year^{-1} (Gilbert et al. 2004), figures of the same order of magnitude as our calculations for *H. axyridis* in Britain. In eastern North America the rate of range expansion of *H. axyridis* was estimated at 442 km year^{-1} (McCorquodale 1998). As it was probably confounded by many intentional releases at various locations (McCorquodale 1998), this very fast expansion is not a fair comparison with that observed in Great Britain. Expansion was thought to be slower in other parts of North America (Koch et al. 2006).

Abundance and mechanism of spread

Abundance of *H. axyridis* in Great Britain increased rapidly from 2004 to 2006, and this trend is predicted to continue. There is very strong demographic evidence that the spread of *H. axyridis* in Great Britain did not originate from a single immigration event, and that the species arrived at different locations at various times, and by various means. Apart from the spread (by flight) from continental Europe, some specimens of *H. axyridis* are known to have arrived in England on imported flowers from the Netherlands, and in packing cases from Canada (Majerus et al. 2006a). By 2004, *H. axyridis* had sufficient time to adapt to conditions in mainland Europe and was building-up in number and spreading fast. Crossing the English Channel to reach Great Britain was not a major step. It is a coincidence that specimens from Canada were found in Great Britain for the first time in the same year, and it is possible that it had arrived by similar mechanisms in earlier years, but failed to be noticed and failed to establish.

A separate population of *H. axyridis* was evident in Derby (central England) in 2004, which is thought to have originated from specimens arriving with produce to a supermarket in the city (W. Grange, personal communication). Derby was not the most northerly verified location of *H. axyridis* in 2004 (a single specimen was recorded in Lancashire, but with no evidence of subsequent establishment), but is the only place outside of the southeast with multiple verified records of *H. axyridis* in each of 2004, 2005 and 2006. Large numbers of *H. axyridis* (three records each of 50+ individuals) were recorded in Derby in 2005. The colour form profile of the Derby population almost totally lacked melanics in 2004 and 2005 (99.6% f. *succinea*; n = 495), in contrast to other parts of the country, where melanic specimens formed a significant proportion of the population (a mean of 20% melanic specimens were recorded in 2005). The clear difference in colour form profile strongly suggests a genetically distinct population, and further work is in progress to examine this.

The observed reduction in both the number of juvenile records, and mean number of juveniles per record, from 2005 to 2006, is not believed to reflect a true reduction in breeding activity. Rather, this is likely to be the effect of reduced recorder effort. In

particular, recorders with the London and Essex Ladybird Survey worked diligently in 2005 to gather juvenile records, and provided 46% of all such records; this effort was reduced to 9% of the total in 2006. A 47% increase in the number of 10 km squares with juvenile records from 2005 to 2006 suggests that there was in fact an increase in breeding activity.

Examples of invasive species in Great Britain exhibiting a 'boom-and-bust' population cycle are unusual, although this scenario did apply to the rhododendron lacebug *Stephanitis rhododendri* Horvath (Hemiptera: Tingidae) (Williamson 1996). The evidence from almost 20 years as an established introduced species in North America suggests that this will not apply to *H. axyridis* on either side of the Atlantic.

Evidence of bi-voltinism

Some of the common and widespread coccinellid species in Britain, e.g. *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), are limited by the requirement of a winter dormancy period before they can reproduce (Majerus 1994). *Harmonia axyridis* does not have this limit to population growth and may have several generations per year, five having been recorded in Asia (Wang 1986) and four in southern Europe (Katsoyannos et al. 1997). In the cool and damp maritime climate of Great Britain, we predict *H. axyridis* will achieve two, or possibly three, generations per year. There is evidence of a second generation in 2006 in the data presented here, with a summer peak (week 24) and an autumn peak (week 40), in juvenile records. Production of two generations would help to explain the very rapid spread of *H. axyridis* observed.

Habitat use

The dataset reflects a somewhat urban distribution. Although some of this effect may be biased by higher recorder effort in urban areas, it is assumed to be the result of genuine habitat preference by *H. axyridis*. Lime trees, *Tilia* sp. (Tiliaceae) and sycamore trees, *Acer* sp. (Aceraceae) were recorded as favoured habitats, and these trees are generally found in Britain in urban locations, such as parks, gardens, lining roads and churchyards. Whether *H. axyridis* will thrive in semi-natural habitats is a question that remains to be answered, and an important one in terms of the potential impact of the species on native coccinellids and other insects. *Harmonia axyridis* has been recorded in various semi-natural habitats in Great Britain, including reedbeds, and on planted and self-seeded *Pinus sylvestris* L. (Pinaceae) in East Anglia. Mature *P. sylvestris* is an important habitat for several native coccinellids, including *Anatis ocellata* L. (Coleoptera: Coccinellidae), *Myzia oblongoguttata* L. (Coleoptera: Coccinellidae) and *Myrrha octodecimguttata* L. (Coleoptera: Coccinellidae) (Majerus 1994). Evidence of the strength of intraguild predation by *H. axyridis* (Pell et al. 2007; Roy et al. 2007; Ware and Majerus 2007; Ware et al. 2007) deepens concern that the species will have a serious negative impact on native coccinellids.

Conclusion

We predict that the spread of *H. axyridis* in Great Britain will continue at a rapid pace, and that the species will become established in Scotland by the end of 2008. To determine the impact of *H. axyridis* on native species, monitoring of ladybird populations is required in

semi-natural habitats and urban habitats, both of which can support high abundance and species richness. Quantitative research at appropriate spatial and temporal scales is essential, if we are to objectively assess the ecological impact of *H. axyridis*. Field studies need to focus on habitat use by this species and its interactions within the large guild of associated aphidophagous species. *Harmonia axyridis* has many traits that have ensured its status as a successful invasive alien species. The continued population expansion within and beyond its invaded range seems inevitable.

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