



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

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9 **Abstract** *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) is native to Asia, and  
10 was widely introduced as a biocontrol agent of aphids and coccids in Europe and North  
11 America. In Europe *H. axyridis* is considered to be an invasive alien species. Although not  
12 known to have been deliberately introduced to Great Britain, it was first recorded there in  
13 2004, in south-east England. *Harmonia axyridis* arrived in Great Britain by various means,  
14 primarily from mainland Europe, but also from Canada. Extensive national and local media  
15 coverage, and a dedicated website (<http://www.harlequin-survey.org>), facilitated public  
16 involvement in recording *H. axyridis* in Great Britain; in excess of 4,000 verified records of  
17 the species were received between 2004 and 2006. Through detailed mapping, the  
18 objective of our study was to quantify and analyse the spread of *H. axyridis* in its early  
19 stages of invasion in Great Britain. Our data shows that between 2004 and 2006, the

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A2 the ladybird *Harmonia axyridis* as a model species".

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20 species spread north through Great Britain at the rate of 58 km year<sup>-1</sup> and west at the rate  
21 of 144.5 km year<sup>-1</sup>. In England *H. axyridis* spread north to Yorkshire and west to Cornwall  
22 by the end of 2006, and also reached Wales. Recorded occurrence (of one or more  
23 *H. axyridis* individuals at larval, pupal and/or adult stage) in 10 km squares in Great  
24 Britain was: 2004—51; 2005—149; 2006—447. Records of juvenile *H. axyridis* extend  
25 through most of the recorded British range of the species, and we present evidence of  
26 bi-voltinism in the population in 2006.

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

## 29 Introduction

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

45 The harlequin ladybird or multicolored Asian lady beetle, *Harmonia axyridis* (Pallas)  
46 (Coleoptera: Coccinellidae), is native to Asia (e.g. Dobzhansky 1933; Kuznetsov 1997)  
47 and was introduced to North America and Europe to control pest aphid and coccid species  
48 on a range of crops (e.g. Adriaens et al. 2003; Koch 2003). It established in North America  
49 in 1988 (Chapin and Br ou 1991), spread very rapidly (Koch 2003), and became the  
50 dominant coccinellid in many areas (Colunga-Garcia and Gage 1998; Smith et al. 1996;  
51 Tedders and Schaefer 1994). In mainland Europe, *H. axyridis* was first marketed as a  
52 biocontrol agent in 1995 (Coutanceau 2006), established in the late 1990s and expanded its  
53 range rapidly, especially from 2002 (Brown et al. submitted). It is not known to have been  
54 deliberately introduced to Great Britain, but arrived by various means, including flight and  
55 on produce from mainland Europe and in packing cases from Canada (Majerus et al.  
56 2006a; Roy et al. 2005). There is no doubt that *H. axyridis* is an effective aphid predator,  
57 and its presence may be welcomed by some. However, there is concern in Europe about the  
58 rapid increase in distribution and abundance of *H. axyridis*, and its impact on non-target  
59 species (Adriaens et al. 2003; Majerus et al. 2006b; Roy et al. 2006). Although most  
60 biocontrol companies have stopped selling *H. axyridis* in Europe, a non-flying variety is  
61 still available from Biotop (<http://www.biotop.fr>).

62 *Harmonia axyridis* has the potential to contribute to biotic homogenization (McKin-  
63 ney and Lockwood 1999) and to negatively impact on up to 1,000 species in Great  
64 Britain (Majerus in press). These are primarily insects (including non-target Homoptera,



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

74 Uniquely, the early detection of *H. axyridis* in Britain presented the opportunity to study  
75 the spread of an invasive animal from the year of its arrival (Majerus et al. 2006b). There is  
76 no evidence to suggest that *H. axyridis* was established in Great Britain before 2004 and  
77 circumstantial evidence that argues against its presence prior to that year (Majerus and Roy  
78 2005). Through detailed mapping of adult and juvenile stages, the objective of our study  
79 was to quantify and analyse the spread of *H. axyridis* in its early stages of invasion in Great  
80 Britain. A further objective was to investigate the voltinism of *H. axyridis* in Great Britain,  
81 to determine whether there was evidence of multiple generations per year.

## 82 Material and methods

### 83 Data collection

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

94 The dataset presented here comprises 4,117 species records of *H. axyridis* in Great  
95 Britain between 2004 and 2006. Each record represents a verified sighting of *H. axyridis*  
96 on a given date, and comprises one or more individual ladybirds observed from one or  
97 more life stages (larva, pupa and adult; records of eggs were not included). 76% of these  
98 records were received from members of the British public by post, or entered online at  
99 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.  
100 Verification of the records was made by the authors after receipt of either a specimen or  
101 photograph. Most photographs were received as digital images attached to emails. The  
102 remaining 24% of records were received from coleopterists and other naturalists, and in  
103 particular from the London and Essex Ladybird Survey. Such records were not verified  
104 by the authors but are regarded as accurate and so have been included in the dataset. A  
105 further 4,316 online records were received that remain unverified (i.e. no photograph or  
106 specimen was sent), or were verified as another species, and so are not included in the  
107 analyses. Verified records were regularly uploaded to the database of the National  
108



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

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

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

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

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

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



156 Rate of spread

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

164 Seasonal pattern

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

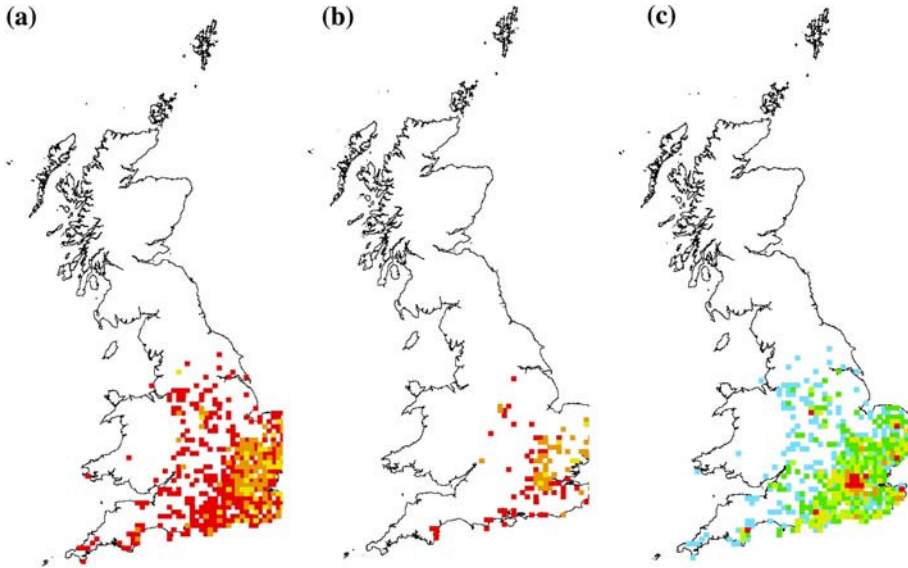
171 Seasonal patterns were analysed using a Generalized Additive Model (GAM) in which  
172 the counts varied randomly about a smooth trend described by a cubic smoothing spline  
173 (Green and Silverman 1994). The degrees of freedom for the fitted GAM were determined  
174 using cross-validation (leaving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

185 **Results**

186 Abundance and rate of spread

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

193 The number of 10 km squares with records of juvenile *H. axyridis* increased from 8 in  
194 2004, to 51 in 2005, and 75 in 2006 (Fig. 1b). In 2004, evidence of *H. axyridis* breeding  
195 was restricted to London and East Anglia, with juveniles recorded in a wider range of  
196 counties in 2005 (notably Kent and Derbyshire). Further evidence of breeding was



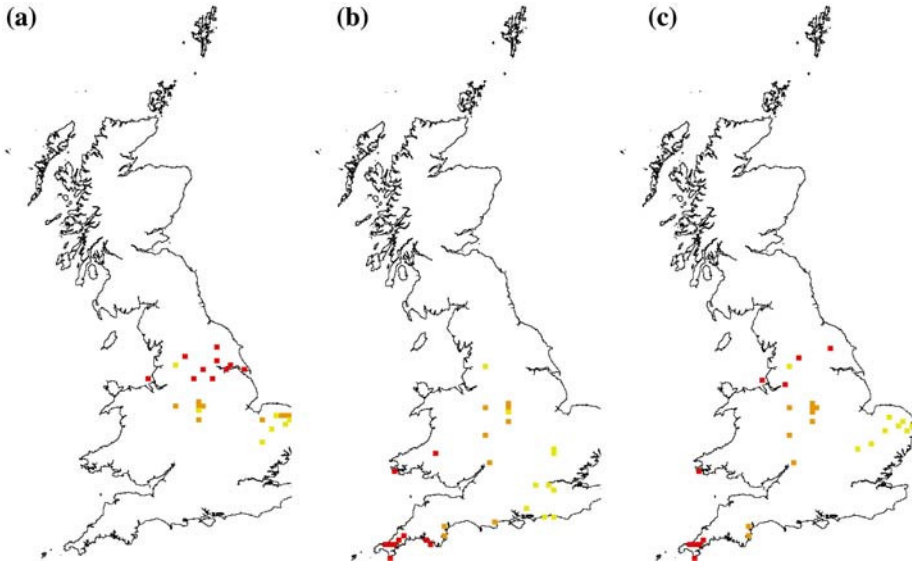
**Fig. 1** *Harmonia axyridis* occurrence in 10 km squares in Great Britain from 2004 to 2006. For (a) and (b), where a square has been recorded in more than one year, occurrence in the earliest year is shown (yellow = 2004; orange = 2005; red = 2006). (a) Adults and juveniles; (b) Juveniles only; (c) 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)

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

199 Northerly spread (Fig. 2a) distances per year were: 19 km between 2004 and 2005;  
 200 97 km between 2005 and 2006; mean—58 km year<sup>-1</sup>. Westerly spread (Fig. 2b) distances  
 201 per year were: 107 km between 2004 and 2005; 182 km between 2005 and 2006; mean—  
 202 144.5 km year<sup>-1</sup>. North-westerly spread (Fig. 2c) distances per year were: 81.2 km  
 203 between 2004 and 2005; 107.5 km between 2005 and 2006; mean—94.3 km year<sup>-1</sup>.

**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. <i>H. axyridis</i> recorded	Mean no. <i>H. axyridis</i> per record	Maximum no. <i>H. axyridis</i> 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; (b) Ten most westerly squares; (c) Ten most north-westerly squares

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

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

212 Seasonal pattern

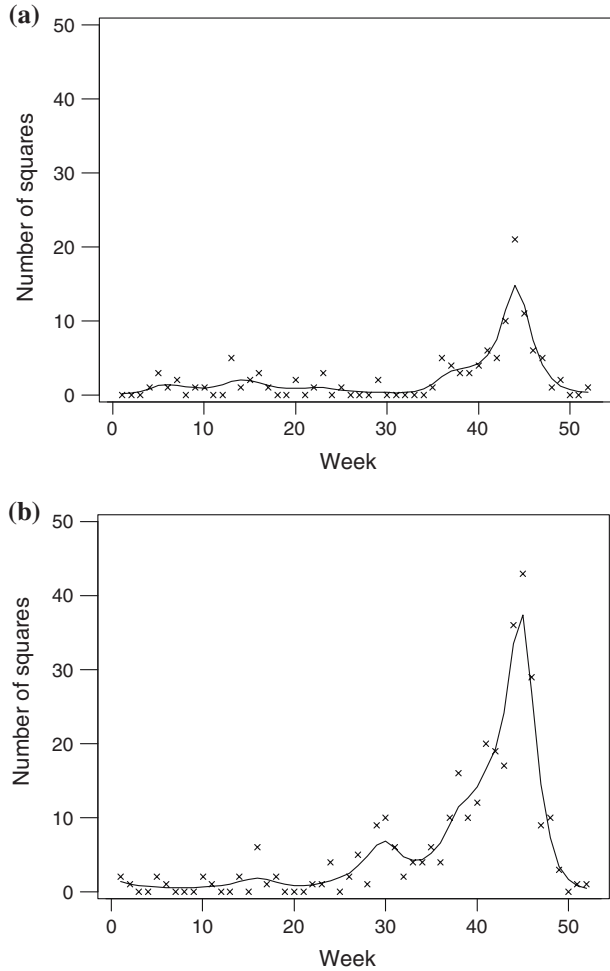
213 Adults

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

218 Juveniles

219 The seasonal patterns of spread of juvenile *H. axyridis* in 2005 and 2006 were significantly  
220 different ( $F_{6,89} = 3.57, P = <0.001$ ). The main difference is the extra peak around week 25

**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)



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

## 223 Discussion

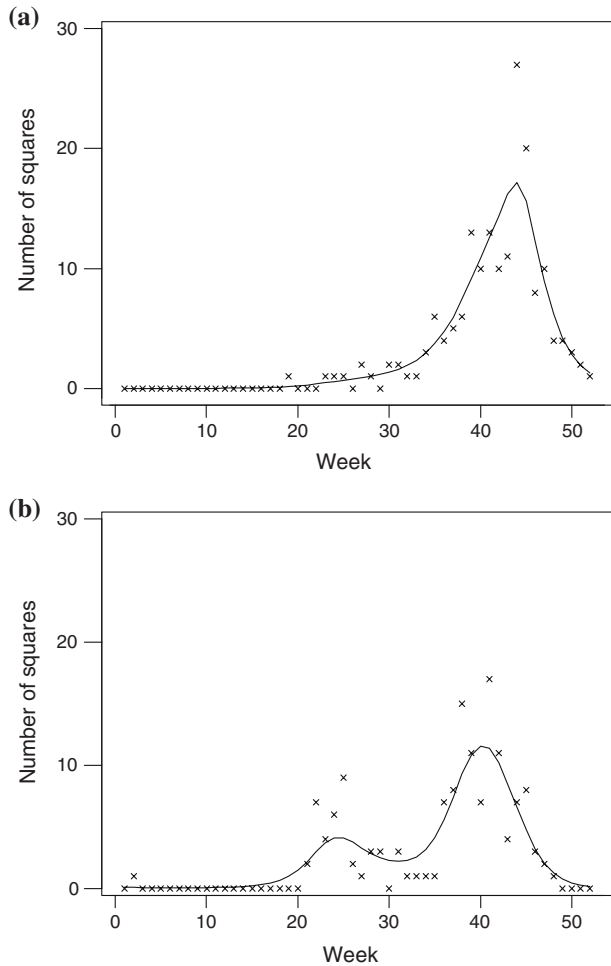
### 224 Rate of spread

225 The rate of spread and increase in abundance of *H. axyridis* in Great Britain has been  
226 dramatic. Westerly spread was faster than northerly spread by a factor of approximately  
227 2.5, and this may partly be explained by the likelihood of repeated recruitment of  
228 *H. axyridis* from mainland Europe. Indeed, in 2006, eight of the ten most westerly 10 km  
229 squares occupied were in the extreme south-west of England and close to the coast,  
230 possibly representing new recruits from abroad, rather than spread from the existing British  
231 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)



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

239 The most closely related species to *H. axyridis* in Great Britain is *Harmonia quadri-*  
240 *punctata* (Pontoppidan). This species is also a relatively recent arrival to Britain, but is now  
241 regarded as a native species, having expanded its native range northwards within Europe,  
242 and is assumed to have reached Britain by natural means (Majerus and Kearns 1989;  
243 Majerus 1994). It is not considered invasive. Although *H. quadripunctata* is far more  
244 habitat-specific than *H. axyridis*, and the mechanisms of spread may not be the same, a  
245 comparison of the rate of spread of the two species is enlightening. Majerus and Kearns  
246 (1989) outline the spread of *H. quadripunctata*. It was first recorded in Great Britain in



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

251 In Great Britain, the northerly range expansion of some insect groups was calculated by  
252 Hickling et al. (2006), giving figures of up to 4.2 km year<sup>-1</sup> (over a 25 year period) for the  
253 most dispersive taxa (dragonflies); but these range expansions were for native species  
254 responding to climate change, rather than for invasive species. There is limited quantitative  
255 data on the spread of invasive insects in Europe. The spread of the horse chestnut leafminer  
256 *C. ohridella* in Germany in the late 1990s was modelled, and the rate of spread calculated  
257 to vary between 54 km year<sup>-1</sup> and 330 km year<sup>-1</sup> (Gilbert et al. 2004), figures of the same  
258 order of magnitude as our calculations for *H. axyridis* in Britain. In eastern North America  
259 the rate of range expansion of *H. axyridis* was estimated at 442 km year<sup>-1</sup> (McCorquodale  
260 1998). As it was probably confounded by many intentional releases at various locations  
261 (McCorquodale 1998), this very fast expansion is not a fair comparison with that observed  
262 in Great Britain. Expansion was thought to be slower in other parts of North America  
263 (Koch et al. 2006).

#### 264 Abundance and mechanism of spread

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

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

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



293 particular, recorders with the London and Essex Ladybird Survey worked diligently in  
294 2005 to gather juvenile records, and provided 46% of all such records; this effort was  
295 reduced to 9% of the total in 2006. A 47% increase in the number of 10 km squares with  
296 juvenile records from 2005 to 2006 suggests that there was in fact an increase in breeding  
297 activity.

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

### 303 Evidence of bi-voltinism

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

### 314 Habitat use

315 The dataset reflects a somewhat urban distribution. Although some of this effect may be  
316 biased by higher recorder effort in urban areas, it is assumed to be the result of genuine  
317 habitat preference by *H. axyridis*. Lime trees, *Tilia* sp. and sycamore trees, *Acer* sp. were  
318 recorded as favoured habitats, and these trees are generally found in Britain in urban  
319 locations, such as parks, gardens, lining roads and churchyards. Whether *H. axyridis* will  
320 thrive in semi-natural habitats is a question that remains to be answered, and an important  
321 one in terms of the potential impact of the species on native coccinellids and other insects.  
322 *Harmonia axyridis* has been recorded in various semi-natural habitats in Great Britain,  
323 including reedbeds, and on planted and self-seeded *Pinus sylvestris* (L.) in East Anglia.  
324 Mature *P. sylvestris* is an important habitat for several native coccinellids, including *Anatis*  
325 *ocellata* (L.), *Myzia oblongoguttata* (L.) and *Myrrha octodecimguttata* (L.) (Majerus  
326 1994). Evidence of the strength of intraguild predation by *H. axyridis* (Pell et al. submitted;  
327 Roy et al. in press; Ware and Majerus submitted; Ware et al. in press) deepens concern that  
328 the species will have a serious negative impact on native coccinellids.

### 329 Conclusion

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



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

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