REVIEW

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Harmonia axyridis (Coleoptera: Coccinellidae) as a host of the parasitic fungus *Hesperomyces virescens* (Ascomycota: Laboulbeniales, Laboulbeniaceae): A case report and short review

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Abstract. *Hesperomyces virescens* is an ectoparasite of some Coccinellidae, which until the mid-1990s was relatively rarely only reported from warm regions in various parts of the world. Analysis of the host and distribution data of *H. virescens* recorded in the Western Palaearctic and North America reveals several trends in the occurrence and abundance of *H. virescens*: (1) it has recently been much more frequently recorded, (2) most of the recent records are for more northerly (colder) localities than the early records and (3) the recent records are mostly of a novel host, the invasive harlequin ladybird (*Harmonia axyridis*). While in North America *H. virescens* is almost exclusively found on *H. axyridis*, all European records of this association are very recent and still less numerous than records of *Adalia bipunctata* as a host. However, based on a relatively few published cases of the *H. axyridis-H. virescens* association in Europe and the case described in this paper, it is clear that the harlequin ladybird is currently the main host of this parasite. These changes in the abundance and geographical distribution of *H. virescens* are probably linked to some features of *H. axyridis*, such as its abundance, multivoltinism with overlapping generations, high level of promiscuity and overwintering in mass aggregations. The occurrence of these features in one species may make it especially suitable for *H. virescens* and other parasites that require close contact of host individuals for efficient transmission. Indeed, some of the data indicate that parasites other than *H. virescens*, like the podapolipid mite *Coccipolipus hippodamiae* and allantonematid nematodes of the genus *Parasitylenchus* may also heavily parasitize *H. axyridis*. We hypothesize that the acquisition of *H. axyridis* as a host by *H. virescens*, *C. hippodamiae* and *Parasitylenchus* spp. may have further consequences for the abundance and distribution of these parasites, including the expansion of their ranges to other continents colonized by invasive populations of this ladybird and areas in Asia where *H. axyridis* is native.

INTRODUCTION

Fungi of the order Laboulbeniales are obligate ectoparasites of insects and other arthropods, but beetles (Coleoptera) are their most common hosts (Weir & Hammond, 1997; Majewski, 2008). Compact thalli of Laboulbeniales attach to the cuticle of the host by a melanized terminal part of the basal cell called the foot. Thalli may be present over the entire surface of the integument of its host. Some species, however, occur only on specific parts of the body of their host. Laboulbeniales are relatively benign parasites that do not kill their hosts and rarely have an adverse effect on them (Tavares, 1979; Kaur & Mukerji, 2006; Majewski, 2008).

Ladybird beetles (Coccinellidae) are the hosts of four species of the laboulbenialean genus *Hesperomyces*, with *H. virescens* Thaxter the most frequently recorded (Ceryngier et al., 2012). *H. virescens* is recorded infecting a wide array of ladybird hosts in many parts of the world, including North and South America, the Caribbean, Borneo, Melanesia, Japan, Near East, North Africa and Europe (Thaxter, 1931; Santamaria et al., 1991; Ceryngier et al., 2012).

One of the reported hosts of *H. virescens* is the harlequin ladybird, *Harmonia axyridis* (Pallas), an invasive species of Asiatic origin that from the late 1980s onwards rapidly expanded its range, at the beginning in the United States and currently in North and South America, Europe and Africa (Brown et al., 2011). The association between *H. axyridis* and *H. virescens* was first reported in Ohio (USA) in 2002 (Garcés & Williams, 2004) and subsequently at many localities in eastern and central United States, with the percentage parasitization often reaching 70–100% (Riddick & Schaefer, 2005; Harwood et al., 2006a, b; Riddick, 2006, 2010; Nalepa & Weir, 2007; Riddick & Cottrell, 2010).

In the winter of 2006/2007, *H. virescens* was recorded for the first time on *H. axyridis* in Europe at an hibernation site of this beetle at Meise near Brussels (Belgium). At that time one out of 203 individuals of *H. axyridis* (about 0.5%) was found to bear *H. virescens* thalli but four years later (winter 2010/2011), at the same site, 96.5% of the overwintering *H. axyridis* were infected (De Kesel, 2011). There are now other European records of *H. axyridis* infected with *H. virescens* from the Nether-

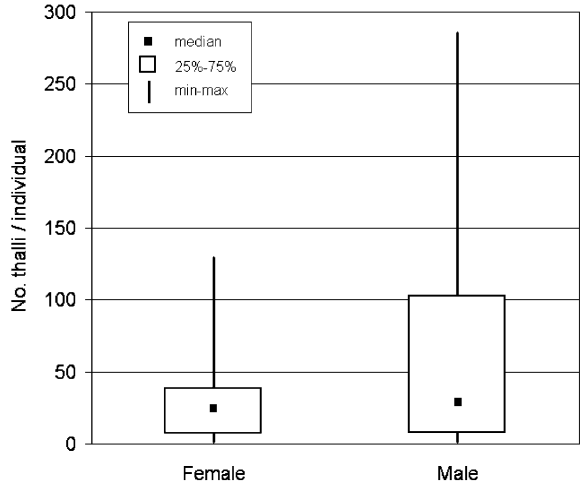

Fig. 1. Number of *Hesperomyces virescens* thalli on male and female *Harmonia axyridis* hosts.

lands, Germany and several Belgian localities (Steenberg & Harding, 2010; De Kesel, 2011; Haelewaters & De Kesel, 2011; Haelewaters et al., 2012). So far, this fungus is not reported attacking *H. axyridis* within its native (Asiatic) range, although it is reported infecting *Coccinula crotchi* (Lewis) and *C. sinensis* (Weise) in the eastern part of its range (Japan) (Ceryngier et al., 2012).

Herein, we report other European case of the harlequin ladybird heavily infected with *H. virescens*. Then the host-*H. virescens* records for the Western Palaearctic and North America are analyzed chronologically and possible mechanisms responsible for the establishment and rapid expansion of the recently emerged *H. axyridis*-*H. virescens* association determined. Finally, we speculate on potential consequences of this novel association for the further spread of the parasite.

CASE REPORT

On a sunny day in mid-January 2010, an aggregation of *H. axyridis* individuals was spotted on an outside wall of a building on the campus of Justus-Liebig University, Giessen, Germany (50°34′N, 8°40′E). Superficial examination of this aggregation showed that many of the beetles were heavily infected with laboulbenialean parasites. The beetles were therefore collected and subsequently killed by freezing at –80°C. Later on they were sexed and checked under stereoscopic microscope for infection with fungus, which was identified as *H. virescens*. For infected individuals, the numbers of thalli were counted and their location on the host noted.

Altogether, 134 *H. axyridis* individuals were collected, of which 106 (79.1%) were infected with *H. virescens*. The percentage infection of females (59 out of 74 individuals infected = 79.7%) was very similar to that of males (47 out of 60 individuals infected = 78.3%). On average, there were more thalli on males than females (63.4 thalli per male vs. 30.9 thalli per female), but this difference was not significant (Mann-Whitney U-test: Z = –0.91, P = 0.36, Fig. 1).

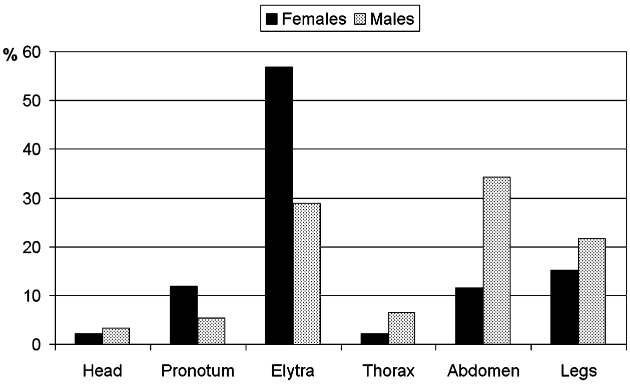

Fig. 2. Distribution of *Hesperomyces virescens* thalli on male and female *Harmonia axyridis* hosts.

H. virescens thalli were found on various parts of the hosts' body and were statistically significantly differently distributed on male and female hosts (chi-square test: $\chi^2 = 581.3$, df = 5, P < 0.001) (Fig. 2). In females, the majority of thalli (57%) were located on the elytra, while in males on the ventral surface of the abdomen (34%), but also frequently on the elytra (29%) and legs (22%). This difference indicates that an important but not the only way in which *H. virescens* is transmitted between hosts is during mating. The importance of mating for the transmission of the parasite is reported by other researchers (Welch et al., 2001; Garcés & Williams, 2004; Harwood et al., 2006a; Riddick, 2006) along with other kinds of direct contact between hosts, especially when they aggregate during winter (Riddick & Schaefer, 2005; Nalepa & Weir, 2007).

NEWLY EMERGENT HOST-PARASITE ASSOCIATION

Non native species invading new areas often experience the loss of parasites through a process called "enemy release", and the opposite process, i.e. the acquisition of parasites native to invaded areas is less frequent (Prenter et al., 2004; Torchin & Mitchell, 2004). The association between *Harmonia axyridis* and *Hesperomyces virescens* is an example of the latter, less frequent, process. The case described above can be included with an increasing body of evidence that the invasive populations of the harlequin ladybird are not only susceptible to some native parasites such as *H. virescens*, the mite *Coccipolipus hippodamiae* (McDaniel & Morrill) (Rhule et al., 2010; Riddick, 2010) and allantonematid nematodes (Harding et al., 2011; Roy et al., 2011b; Poinar & Steenberg, 2012), but also contribute to their dispersal, increase in prevalence and intensity of infection.

The importance of the harlequin ladybird for the spread of *H. virescens* is illustrated by the analysis of past and present records of the latter in the Western Palaearctic region (Table 1) and, especially, in North America (Table 2). Early records of *H. virescens* in the Western Palaearctic are scanty and limited to the Mediterranean Basin (Israel, Morocco, south-eastern France and Spain). In that period, the most frequently reported host of *H. virescens* was *Chilocorus bipustulatus* (L.). From the

TABLE 1. Details of the records of *Hesperomyces virescens* for the Western Palaearctic region.

Date[1]	Region	Coordinates	Year average temp. (°C)[2]	Host	Reference
1934	Rehovot (Israel)	31°54´N, 34°49´E	19	*Chilocorus bipustulatus*	Hecht (1936)
before 1937	Casablanca (Morocco)	33°32´N, 07°35´E	17	*Chilocorus bipustulatus*	Maire & Werner (1937)
1961–62	southeastern France	~ 44°N, 07°E	15	*Adalia decempunctata*	Iperti (1964)
1960s	southeastern France	~ 44°N, 07°E	15	*Adalia bipunctata*	G. Iperti, unpubl. (in Hodek, 1973)
spring 1964	Kfar Warburg (Israel)	31°43´N, 34°44´E	24.9	*Chilocorus bipustulatus*	Benjamin (1989)
1965	Kfar Warburg (Israel)	31°43´N, 34°44´E	24.9	*Chilocorus bipustulatus*	Applebaum et al. (1971)
1966	Rehovot (Israel)	31°54´N, 34°49´E	19	*Chilocorus bipustulatus*	Kamburov et al. (1967)
1966	Rosh Hanikra (Israel)	33°05´N, 35°06´E	23.4	*Chilocorus bipustulatus*	Kamburov et al. (1967)
1966	Ashqelon (Israel)	31°40´N, 34°33´E	24.9	*Chilocorus bipustulatus*	Kamburov et al. (1967)
1970	Kfar Warburg (Israel)	31°43´N, 34°44´E	24.9	*Chilocorus bipustulatus*	Applebaum et al. (1971)
1970	Givat Brenner (Israel)	31°52´N, 34°48´E	19	*Chilocorus bipustulatus*	Applebaum et al. (1971)
before 1974	Saint-Martin-de-Crau (France)	43°38´N, 04°49´E	15	*Psyllobora vigintiduopunctata*	Balazuc (1974)
1985	Santa Fé del Montseny (Spain)	41°44´N, 02°27´E	14.3	*Propylea quatuordecimpunctata*	Santamaria (1989)
1994	Knokke-Heist (Belgium)	51°20´N, 03°17´E	10	*Psyllobora vigintiduopunctata*	De Kesel (2011)
before 1996	London (England)	51°31´N, 06°55´E	10	*Adalia bipunctata*	Weir & Beakes (1996)
1995–97	Berlin (Germany)	52°30´N, 13°25´E	9	*Adalia bipunctata*	Webberley et al. (2006)
1996	Braunschweig (Germany)	52°16´N, 10°30´E	8	*Adalia bipunctata*	Webberley et al. (2006)
1996	Parma (Italy)	44°48´N, 10°20´E	11	*Adalia bipunctata*	Webberley et al. (2006)
1996	Novara (Italy)	45°27´N, 08°37´E	11.5	*Adalia bipunctata*	Webberley et al. (2006)
1997–2005	Bayreuth (Germany)	49°57´N, 11°34´E	7	*Adalia bipunctata*	Webberley et al. (2006)
1998	London and surroundings (England)	~ 51°30´N, 07°30´E	10	*Adalia bipunctata*	Welch et al. (2001)
1999	London and surroundings (England)	~ 51°30´N, 07°30´E	10	*Adalia bipunctata*	Welch et al. (2001)
1999	Vienna (Austria)	48°12´N, 16°22´E	10.2	*Adalia bipunctata*	Christian (2001)
2000	Vienna (Austria)	48°12´N, 16°22´E	10.2	*Adalia bipunctata*	Christian (2001)
2001	Vienna (Austria)	48°12´N, 16°22´E	10.2	*Adalia bipunctata*	Christian (2001)
2001	Sannicandro Garganico (Italy)	41°50´N, 15°34´E	11.4	*Adalia decempunctata*	Castaldo et al. (2004)
2001	Perama (Greece)	39°41´N, 20°51´E	14.3	*Coccinula quatuordecimpustulata*	Castaldo et al. (2004)
2001	Amfithea (Greece)	39°41´N, 20°52´E	14.3	*Tytthaspis sedecimpunctata*	Castaldo et al. (2004)
2002	Stockholm (Sweden)	59°20´N, 18°04´E	6	*Adalia bipunctata*	Webberley et al. (2006)
2003	Lyon (France)	45°46´N, 04°50´E	11	*Adalia bipunctata*	Webberley et al. (2006)
before 2006	Utrecht (the Netherlands)	52°05´N, 05°06´E	8	*Adalia bipunctata*	Webberley et al. (2006)
winter 2006/2007	Meise (Belgium)	50°57´N, 04°18´E	10	*Harmonia axyridis*	De Kesel (2011)
2007	Warsaw (Poland)	52°09´N, 21°03´E	8	*Adalia bipunctata*	M.W. Kozlowski (pers. comm.)
winter 2007/2008	Copenhagen (Denmark)	55°41´N, 12°34´E	8	*Adalia bipunctata*	Steenberg & Harding (2010)
2008	De Kaaistoep (the Netherlands)	51°35´N, 05°03´E	9	*Harmonia axyridis*	Haelewaters et al. (2012)
spring 2009	Hohenstein (Germany)	50°12´N, 08°06´E	10	*Harmonia axyridis*	Steenberg & Harding (2010)
2009	De Kaaistoep (the Netherlands)	51°35´N, 05°03´E	9	*Harmonia axyridis*	Haelewaters et al. (2012)
Jan. 2010	Giessen (Germany)	50°34´N, 08°40´E	8	*Harmonia axyridis*	this paper
2010	De Kaaistoep (the Netherlands)	51°35´N, 05°03´E	9	*Harmonia axyridis*	Haelewaters et al. (2012)
Dec. 2010	Ukkel (Belgium)	50°48´N, 04°20´E	10	*Harmonia axyridis*	De Kesel (2011)
Feb. 2011	Brasschaat (Belgium)	51°18´N, 04°30´E	10	*Harmonia axyridis*	De Kesel (2011)
Feb.–Mar. 2011	Meise (Belgium)	50°57´N, 04°18´E	10	*Harmonia axyridis*	De Kesel (2011)
Mar. 2011	Mechelen (Belgium)	51°01´N, 04°28´E	10	*Harmonia axyridis*	De Kesel (2011)
Sept. 2011	Winchester (England)	51°04´N, 01°18´E	9	*Chilocorus renipustulatus*	Hubble (2011)
May 2013	České Budejovice (Czech Rep.)	48°58’N, 14°28’E	8	*Harmonia axyridis*	P. Ceryngier, unpubl.

[1] The notation "before + year of publication" is used when the date of the record is not given in the paper; a range of years is used when the precise date is not given but the period of study is; if records for more than one year are reported in a given paper, each of these years is treated as a separate record. [2] Many years' average annual temperature recorded at the weather station nearest to the reported locality (according to www.weatherbase.com/).

TABLE 2. Details of the records of *Hesperomyces virescens* for North America.

Date[1]	Region	Coordinates	Year average temp. (°C)[2]	Host	Reference
before 1891	Los Angeles, California	34°03´N, 118°14´W	18.3	*Chilocorus stigma*	Thaxter (1891)
before 1931	Auburn, Alabama	32°36´N, 85°00´W	18	*Hippodamia convergens*	Thaxter (1931)
Jul.–Nov. 2002	Wooster, Ohio	40°48´N, 81°56´W	9	*Harmonia axyridis*	Garcés & Williams (2004)
Dec. 2002	Mt. Gretna, Pennsylvania	40°15´N, 76°28´W	10.8	*Harmonia axyridis*	Riddick & Schaefer (2005)
Jul.–Oct. 2003	Oktibbeha Co., Mississippi	33°27´N, 88°48´W	17	*Harmonia axyridis*	Riddick (2006)
Oct. 2003	Weaverville, North Carolina	35°43´N, 82°27´W	13.5	*Harmonia axyridis*	Nalepa & Weir (2007)
Oct. 2003	Cary, North Carolina	35°47´N, 78°44´W	15.8	*Harmonia axyridis*	Nalepa & Weir (2007)
Dec. 2003	Cary, North Carolina	35°47´N, 78°44´W	15.8	*Harmonia axyridis*	Nalepa & Weir (2007)
Mar. 2004	Cary, North Carolina	35°47´N, 78°44´W	15.8	*Harmonia axyridis*	Nalepa & Weir (2007)
May–Aug. 2004	Silver Lake Farm, Kentucky	38°13´N, 84°49´W	12.2	*Harmonia axyridis*	Harwood et al. (2006a)
May–Aug. 2004	Silver Lake Farm, Kentucky	38°13´N, 84°49´W	12.2	*Psyllobora vigintimaculata*	Harwood et al. (2006a)
May–Aug. 2004	Silver Lake Farm, Kentucky	38°13´N, 84°49´W	12.2	*Brachiacantha quadripunctata*	Harwood et al. (2006a)
May–Aug. 2004	Silver Lake Farm, Kentucky	38°13´N, 84°49´W	12.2	*Cycloneda munda*	Harwood et al. (2006a)
Jun.–Oct. 2004	Oktibbeha Co., Mississippi	33°27´N, 88°48´W	17	*Harmonia axyridis*	Riddick (2006)
2004	Lexington, Kentucky	38°02´N, 84°30´W	12	*Coccinella septempunctata*	Harwood et al. (2006b)
2005	Lexington, Kentucky	38°02´N, 84°30´W	12	*Coccinella septempunctata*	Harwood et al. (2006b)
2005	Frankfort, Kentucky	38°12´N, 84°52´W	13.1	*Coccinella septempunctata*	Harwood et al. (2006b)
2005	Brookings, South Dakota	44°19´N, 96°48´W	6	*Harmonia axyridis*	Harwood et al. (2006b)
2005	Fayetteville, Arkansas	36°04´N, 94°09´W	14	*Harmonia axyridis*	Harwood et al. (2006b)
2005	Perkins, Oklahoma	35°58´N, 97°02´W	15.4	*Harmonia axyridis*	Harwood et al. (2006b)
2005	State College, Pennsylvania	40°47´N, 77°52´W	9	*Harmonia axyridis*	Harwood et al. (2006b)
2005	Jefferson Co., West Virginia	39°19´N, 77°53´W	11.7	*Harmonia axyridis*	Harwood et al. (2006b)
2005	Lexington, Kentucky	38°02´N, 84°30´W	12	*Harmonia axyridis*	Harwood et al. (2006b)
2005	Frankfort, Kentucky	38°12´N, 84°52´W	13.1	*Harmonia axyridis*	Harwood et al. (2006b)
Apr.–Oct. 2007	Byron, Georgia	32°39´N, 83°46´W	17.6	*Harmonia axyridis*	Riddick & Cottrell (2010)
Apr.–Oct. 2007	Byron, Georgia	32°39´N, 83°46´W	17.6	*Hippodamia convergens*	Riddick & Cottrell (2010)
Apr.–Oct. 2007	Byron, Georgia	32°39´N, 83°46´W	17.6	*Olla v-nigrum*	Riddick & Cottrell (2010)
Dec. 2007	Leland, Mississippi	33°24´N, 90°59´W	17.5	*Harmonia axyridis*	Riddick (2010)
Dec. 2008	Grenada, Mississippi	33°47´N, 89°46´W	17	*Harmonia axyridis*	Riddick (2010)
Dec. 2008	Stoneville, Mississippi	33°27´N, 90°55´W	17.5	*Harmonia axyridis*	Riddick (2010)
Dec. 2008	Benoit, Mississippi	33°40´N, 91°08´W	17.3	*Harmonia axyridis*	Riddick (2010)
Jan. 2009	Delta National Forest, Mississippi	32°49´N, 90°49´W	17.3	*Harmonia axyridis*	Riddick (2010)

[1,2] as in Table 1.

mid-1990s, this parasite is recorded more frequently and usually from much more northerly localities in Europe, often in towns and cities, which as a rule are warmer than surrounding rural areas and hence termed urban heat islands (Oke, 1973). The effect of such an urban heat island on *H. virescens* was demonstrated by Welch et al. (2001). They found a clear negative correlation between the prevalence of this parasite on the two-spot ladybird, *Adalia bipunctata* (L.), and distance of the sampling site from the centre of London. Up to a 50% prevalence was recorded in the centre while some 25 km from the centre, outside the urban area, no infection was detected. The relatively recent European records of *H. virescens* mostly refer to *A. bipunctata* as the host, but the majority of most recent observations are for a novel host, *H. axyridis*. The European data on the prevalence of *H. virescens* on *H. axyridis* clearly show it has increased over time. In samples of *H. axyridis* from light-traps collected over several years at De Kaaistoep (the Netherlands), there was no evidence of infection in 2007, but 0.4% were infected in 2008, 3.9% in 2009 and 7.2% in 2010 (Haelewaters et al., 2012). Infection of *H. axyridis* with *H. virescens* in winter aggregations increased from 0.5% in winter 2006/2007 (Meise near Brussels, De Kesel, 2011) and 0.9% in spring 2009 (Hohenstein near Frankfurt, Steenberg & Harding, 2010) to 79.1% in January 2010 (Giessen, this study) and 96.5% in February-March 2011 (Meise, De Kesel, 2011).

In North America, the connection between spread of the harlequin ladybird and expansion of *H. virescens* is even clearer (Table 2). The only North American records of ladybirds infected with *H. virescens* preceding the invasion by *H. axyridis* are those reported by Thaxter (1891, 1931) from California and Alabama of *Chilocorus stigma* (Say) and *Hippodamia convergens* (Guérin-

Méneville), respectively. More than 70 years after the latter of Thaxter's reports, *H. virescens* is a common parasite of *H. axyridis* in a considerable area of the United States with the reported localities ranging between about 33°N (Mississippi and Georgia) and 44°N (Brookings in South Dakota). Apart from the numerous records of *H. axyridis* as a host of *H. virescens*, there are several recent reports of other species of ladybird being infected, but the prevalence of this parasite on these species is much lower than on *H. axyridis* (Harwood et al., 2006a, b; Riddick & Cottrell, 2010).

To conclude, both in Europe and North America, there has been a considerable northward range shift of the fungus over the last few years. In addition, *H. axyridis*, a ladybird that has recently become established on both continents, is a highly suitable and susceptible host of *H. virescens* and currently its major host.

HOW DID *H. AXYRIDIS* ACQUIRE *H. VIRESCENS* IN INVADED AREAS?

A relatively long period of time elapsed between the harlequin ladybird becoming established in North America and the first records of *H. virescens* infections of *H. axyridis*. The first feral North American population of *H. axyridis* was recorded in 1988 (Chapin & Brou, 1991) and the first *H. virescens* infection of this ladybird in 2002 (Garcés & Williams, 2004), that is, a period of 14-years elapsed between these two events. In Europe, however, the time delay was half that recorded in North America: from 1999, when the first feral *H. axyridis* population was reported by Tolasch (2002) to 2006, when the first infection of *H. axyridis* by *H. virescens* was reported by De Kesel (2011).

That there was a delay may indicate that the fungus required some time to adapt to the novel host and/or transfer of the fungus from one host species to another generally occurs infrequently. The latter possibility seems quite probable, taking into account the unique life cycles of the laboulbenialean fungi, which is likely to hamper their transmission between hosts belonging to different species. Laboulbeniales do not produce conidial spores, sclerotia or other structures enabling to survive in unfavourable conditions. They can only propagate by means of short-lived viscous ascospores (De Kesel, 1995a), which after release from the perithecium, must promptly adhere to the cuticle of a host, germinate and produce new thalli (Tavares, 1979; Weir & Hammond, 1997; Majewski, 2008). Due to this, most laboulbenialean parasites can only be transmitted between hosts during direct body contact, usually during copulation (De Kesel, 1995b; Weir & Hammond, 1997; Majewski, 2008). Sexual transmission is probably the most important way in which *H. virescens* is transmitted, and this is often indicated by the different distribution of the parasite thalli on male and female hosts. Males tend to bear most thalli on their ventroposterior surface and females on their dorsoposterior surface (Welch et al., 2001; Garcés & Williams, 2004; Harwood et al., 2006a; Riddick, 2006; this study). Of the non-sexual direct contacts among hosts that may result in parasite transmission probably the most important is that which occurs in overwintering aggregations (Riddick & Schaefer, 2005; Nalepa & Weir, 2007). In the initial transfer of *H. virescens* to *H. axyridis* both sexual and non-sexual bodily contacts among hosts could have played a part. Interspecific matings or mating attempts occasionally occur in ladybirds (Majerus, 1997; Nedved & Honek, 2012) and such incidents may be associated with parasite transmissions (Majerus, 1997). On the other hand, ladybirds sometimes overwinter in mixed (heterospecific) aggregations (Hodek, 2012), which may also facilitate interspecific transmissions. However, although there is some data (De Kesel, 1996) that indicate that interspecific transmission may easily occur in some Laboulbeniales, as recently shown by Cottrell & Riddick (2012), transmission of *H. virescens* between hosts belonging to different species is rare, even if infected and healthy ladybirds are confined in the limited space of a Petri dish, whereas, when infected and uninfected individuals of the same species of ladybird (*H. axyridis* or *Olla v-nigrum* (Mulsant)) are similarly confined parasite transmission frequently occurs. The obstacles to interspecific transmission of *H. virescens* would have delayed the initial transfer of the fungus to *H. axyridis*. In Europe this initial transfer probably happened sooner than in the United States, possibly because many of the areas of Europe invaded by *H. axyridis* were already colonized by relatively abundant populations of *H. virescens*, mainly infecting a very common host species, *A. bipunctata* (Table 1). As *A. bipunctata* and *H. axyridis* have very similar ecological niches (Harmon et al., 2007; Adriaens et al., 2008; Roy et al., 2012), various interactions between them, including body contacts, are probably frequent. The two species are known to form mixed winter aggregations, and in such aggregations individuals heavily infected with *H. virescens* occur (Steenberg & Harding, 2010).

WHAT MAKES *H. AXYRIDIS* AN EXCEPTIONALLY SUITABLE HOST?

The enemy release hypothesis assumes that an invasive species can gain a numerical advantage over native species because it is less limited by natural enemies than the native species. In addition, according to the so called evolution of increased competitive ability hypothesis, invaders can respond to a lack of natural enemies by reallocating resources from defense to growth and/or reproduction (Blossey & Nötzold, 1995). It is supposed that both these mechanisms may contribute to *H. axyridis* invasiveness (Roy et al., 2011a, b; Sloggett, 2012). However, as pointed out by Sloggett (2012), the initial benefit for the invader from the evolution of increased competitive ability may in a later phase of the invasion change into a disadvantage when the invader becomes more susceptible to native enemies. This may partly explain the recent success of *H. virescens* in utilizing *H. axyridis* as a host. However, for the establishment of a stable host-parasite association, the host has to be both susceptible to infection and suitable for the parasite. It seems that certain features of *H. axyridis* make it more suitable for certain parasites, including *H. virescens*, than most other ladybirds.

The harlequin ladybird is a highly ubiquitous, polyphagous (Hodek & Evans, 2012), multivoltine (Koch, 2003; Hodek, 2012) and promiscuous species (Osawa, 1994) that forms large aggregations during winter (Koch, 2003; Wang et al., 2011). Each of these features alone is not unique among ladybirds, but taken together make *H. axyridis* unique in respect of its potential suitability for some parasites, especially those that require close contact between hosts for efficient transmission. As a common and widespread generalist, *H. axyridis* can produce very large populations capable of hosting abundant populations of parasites, which due to the promiscuity of *H. axyridis*, may be effectively transmitted during mating. Transmission between different generations of the host can be achieved by inter-generational host matings that are likely to occur in populations of multivoltine hosts with overlapping generations (Welch et al., 2001; Knell & Webberley, 2004). In *H. axyridis*, its multivoltine life cycle and long adult life may result in a considerable overlap between generations. According to Savoiskaya (1970, ref. in Nedved & Honek, 2012), *H. axyridis* adults may live and reproduce for periods as long as three years. Overwintering of *H. axyridis* in mass aggregations may further facilitate the spread of parasites.

Because of the attributes mentioned above, *H. axyridis* has contributed considerably to the rapid expansion in the distribution of *H. virescens*. However, other parasites may also experience similar novel host driven expansions. Recently, *H. axyridis* was recorded as a host of the ectoparasitic mite *C. hippodamiae* in North America (Mississippi, USA) (Riddick, 2010) and Europe (north-central Poland) (Rhule et al., 2010). Our unpublished data indicate that this host-parasite association is also quite common in other regions in Poland. *C. hippodamiae* has a similar mode of transmission to *H. virescens*. Both are mainly sexually transmitted (Ceryngier et al., 2012) and, therefore, for the spread of both these species *H. axyridis* should be similarly suitable. However, the effects of these two parasites on their hosts are quite different. While *H. virescens* is thought to be relatively harmless (Weir & Beakes, 1996; Nalepa & Weir, 2007, but see also Kamburov et al., 1967), *C. hippodamiae* causes sterility of female hosts (Hurst et al., 1995; Webberley et al., 2004) and increases winter mortality, especially of male hosts (Webberley & Hurst, 2002). Thus, the latter is likely to be an important factor limiting the abundance of ladybirds, which may be desirable in terms of the biological control of the invasive *H. axyridis*.

Other parasites that have recently been discovered infecting *H. axyridis*, both in Europe and North America, are nematodes belonging to the family Allantonematidae. A recently described species, *Parasitylenchus bifurcatus* Poinar & Steenberg is recorded infecting a Danish population of *H. axyridis* since 2009 (Harding et al., 2011; Poinar & Steenberg, 2012) and in 2009 allantonematid nematodes were found infecting *H. axyridis* in Minnesota (USA) (Roy et al., 2011b). In contrast to ectoparasitic *Hesperomyces* and *Coccipolipus*, Allantonematidae are endoparasites. The effect of these nematodes on hosts is not directly lethal, although they are recorded as reducing the survival of *H. axyridis* (Poinar & Steenberg, 2012). It is also suggested (Poinar & Steenberg, 2012) that allantonematid parasites may severely affect other fitness parameters of their hosts, such as male and female fertility or mating success. With the exception of *Howardula* sp., which infects *A. bipunctata* larvae in England (Hariri, 1965), all other reports of Allantonematidae from ladybirds, including those quoted above and older ones of *Parasitylenchus coccinellinae* Iperti & van Waerebeke from France (Iperti & van Waerebeke, 1968) and India (Narsi Reddy & Narayan Rao, 1984), are of the parasitization of adult beetles, usually those with multivoltine life cycles. This may suggest that, as in *H. virescens* and *C. hippodamiae*, sexual contacts between hosts play a part in the transmission of the allantonematids and, hence, the harlequin ladybird is potentially a very suitable host for these nematodes. The mode of transmission of *Parasitylenchus* spp. is currently unknown. It is supposed that infective females may penetrate into a new host through its tracheae, soft cuticle between sclerites or reproductive organs (Ceryngier et al., 2012). For this close contact during mating it may facilitate transmission.

CONSEQUENCES OF THE NOVEL HOST-PARASITE ASSOCIATION

As it is shown above, there has been a considerable increase in the abundance and expansion of the geographical range of *H. virescens* in North America as a result of it acquiring a new host, *H. axyridis* (Table 2). In Europe, an analogous process with another host, i.e. *A. bipunctata,* might have started before the establishment of *H. axyridis*. Before these two waves of *H. virescens* expansion, the majority of records were of parasitization of *Chilocorus bipustulatus* in North Africa and the Near East (Table 1). It seems that in terms of the suitability for *H. virescens*, the most important common feature of the three main hosts (*C. bipustulatus*, *A. bipunctata* and *H. axyridis*) is a multivoltine life cycle. In the Near East, *C. bipustulatus* can produce up to 4–5 generations per year with considerable overlap between generations (Hecht, 1936), which facilitates the efficient between-generation transmission of the fungus. In northern Italy, both *A. bipunctata* and *H. axyridis* completed four generations per year in semi-field experiment (Bazzocchi et al., 2004). Similarly, *H. axyridis* completed four overlapping generations in outdoor experiments in Greece (Katsoyannos et al., 1997). Number of generations per year decreases with increase in climate severity, but even in colder areas *H. axyridis* is regularly at least bivoltine, with the last generation developing much later in the season than in other ladybirds (juvenile stages occur in the field in October or even November) (LaMana & Miller, 1996; Koch, 2003; Adriaens et al., 2008; Brown et al., 2008). The autumnal abundance of *H. axyridis* recorded year by year throughout its whole invasive range has possibly enabled its newly acquired parasite to substantially expand its range toward areas where other potential hosts are univoltine or the second generation develops irregularly and is rarely abundant. Recent climate change may also have affected the range shift of *H. virescens* by modifying the voltinism and overlap in the generations of its hosts. The great increase in the number of European records of *A. bipunctata*-*H. virescens* association in the late 1990s and early 2000s (Table 1) may be a consequence of such climate-induced life cycle changes. Other phenomenon supporting the climate change hypothesis is the present spread in Europe of another species of *Hesperomyces*, *H. coccinelloides* (Thaxter) Thaxter, which infects minute ladybirds in the subfamily Scymninae (Ceryngier, 2013).

One possible outcome of the commonness of the *H. axyridis*-*H. virescens* association may be an extension in the host range of the latter. Although transmission of *H. virescens* between different host species is not frequent (Cottrell & Riddick, 2012), mass infections of *H. axyridis* are likely to result in some inter-specific transmissions. In the United States, several new hosts of *H. virescens* were recorded after *H. axyridis* became its main host (Table 2).

We may also expect that *H. virescens* will establish and become abundant in populations of *H. axyridis* in other parts of its range, such as South America, Africa or Asia. This may happen through transmissions from the host-parasite associations naturally occurring in these areas or from human-mediated intercontinental dispersal of infected ladybirds. The presence of *H. virescens* in South America (Argentina, Brazil) is documented by Thaxter (1931) and Spegazzini (1917, ref. in Thaxter, 1931), but no records are known from sub-Saharan Africa and continental Asia (except the peripheral Near East). However, as the reported distribution of this fungus is nearly cosmopolitan (Thaxter, 1931; Santamaria et al., 1991; Ceryngier et al., 2012), its natural occurrence in these regions cannot be excluded. On the other hand, the potential of *H. axyridis* for spreading between continents is rather high bearing in mind that the only or main source of all the invasive populations of this species on four continents was the same local population, the first North American feral population from Louisiana (USA) (Lombaert et al., 2010).

An interesting issue is the possible transfer of *H. virescens* and other parasites from invasive *H. axyridis* to its native, Asiatic populations. This may take place when this species in Europe spreads to the east and reaches the natural geographic range of their conspecifics. The western border of its native range is not exactly known, but is thought to be somewhere in the central part of Asia (Iablokoff-Khnzorian, 1982; Koch, 2003; Brown et al., 2011). Some Russian authors, however, report *H. axyridis* much further west, in the Ural Mountains (Tyumaseva, 1997; Pekin, 2007; Khabibullin et al., 2009) or even in the Belgorod region of Russia near its border with Ukraine (Bin'kovskaya, 2004; Orlova-Bienkowskaja, 2013). On the other hand, *H. axyridis* spreading from the west was detected in the Kiev region in Ukraine in 2007 (Verizhnikova, 2011). Thus, it is likely that individuals invading from the west will shortly start to mix with native, non-invasive populations of *H. axyridis*. Apart from the threat of being outcompeted by the invasive strain, the polymorphic natives may suffer from parasites vectored by the former. Among these parasites, it is likely that *H. virescens* will be one of the most important.

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