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INVASION NOTE

Invasive host caught up with a native parasitoid: field data reveal high parasitism of *Harmonia axyridis* by *Dinocampus coccinellae* in Central Europe

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Abstract The harlequin ladybird, *Harmonia axyridis*, is considered to be one of the most invasive insect species worldwide. Its invasion success and extreme speed of range expansion has been partially attributed to weak control of its populations by natural enemies. Previously published data on emergence rates of the hymenopteran parasitoid *Dinocampus coccinellae* support the enemy release hypothesis: *H. axyridis* has been consistently less successfully parasitized compared to native ladybird species. In this study, we show that since 2016, i.e., 10 years after its arrival in Central Europe, several populations of *H. axyridis* in the Czech Republic have a very high prevalence of *D. coccinellae* parasitism. *D. coccinellae* emerged from 46% of *H. axyridis* individuals in the most parasitized population. Moreover, *H. axyridis* was more parasitized than the native *Coccinella septempunctata* in seven of nine investigated co-occurring populations. The meta-analytically pooled estimate of *D. coccinellae* emergence rate from *H. axyridis* across the Czech populations (this study) is thirteen times higher than the pooled estimate for invasive populations of this beetle elsewhere (historical data up to 2016). We hypothesize that some Central European populations of *D. coccinellae* have evolved to overcome the immune system of *H. axyridis,* which was previously thought to be responsible for the high larval mortality of *D. coccinellae*. As parasitism rates are highly variable in time and space, we encourage future research investigating the determinants of parasitoid prevalence in *H. axyridis* and other large ladybird species on a continental scale.

Keywords Adaptation · Biological control · Enemy release hypothesis · Evolution · Natural enemies · Host preference

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Introduction

The harlequin ladybird, *Harmonia axyridis* (Pallas, 1773) (Coleoptera, Coccinellidae), originating from

Eastern Asia, is considered one of the most invasive insect species worldwide (Brown et al. 2011; Roy et al. 2016). In the last 25 years, the species has spread across extensive areas in North America, South America and Europe. Invasive populations have also established in Africa, West Asia and even New Zealand (Roy et al. 2016). In areas invaded by *H. axyridis*, abundant populations have become established that can potentially threaten native ladybird species (Roy et al. 2012, 2016). The invasive success of *H. axyridis* has at least partly been attributed to weak control of invasive populations by natural enemies, such as predators, parasitoids, and parasites (Comont et al. 2014; Haelewaters et al. 2017; Ceryngier et al. 2018). Lower predation rates and parasite loads in invasive compared to native species are predicted by the enemy release hypothesis (ERH; Roy et al. 2011; Haelewaters et al. 2017). In general, the existing evidence indicates the validity of the ERH regarding *H. axyridis*: invasive populations of the species suffer lower mortality from natural enemies than native ladybird species (Ceryngier et al. 2018). Nevertheless, invasions are dynamic and adaptations of native natural enemies to novel hosts over time are possible and even predicted by evolutionary theory (Cox 2004; Roy et al. 2011). For example, parasitism rates by *Phalacrotophora* flies (Diptera, Phoridae) have significantly increased in European populations of *H. axyridis* since 2008, indicating an ongoing adaptation of the parasitoid to the novel host (Ceryngier et al. 2018). Analogously, increasing parasitism rates in time have been observed for *Hesperomyces virescens* (Fungi, Ascomycota, Laboulbeniales) infecting *H. axyridis* in invaded areas (Haelewaters et al. 2017). Nowadays, some natural enemies such as *Phalacrotophora* spp. and *Hesperomyces virescens* are known for higher parasitism rates in *H. axyridis* compared to native ladybird species (Haelewaters et al. 2016, 2017; Ceryngier et al. 2018). These findings highlight the need for repeated investigation of the relationships between invasive species in novel environments and native natural enemies.

In this study, we focus on the prevalence of the parasitoid *Dinocampus coccinellae* (Schrank, 1802) (Hymenoptera, Braconidae) in Central European populations of two large ladybird species: *H. axyridis* and *Coccinella septempunctata* Linnaeus, 1758, a common native species in the area. *Coccinella septempunctata* represents an optimal host for *D. coccinellae*, with reported field emergence rates of 15–20% (Majerus 1997; Koyama and Majerus 2008). *Dinocampus coccinellae* is a species with a cosmopolitan distribution, known to parasitize more than 50 ladybird species, mainly in the tribe Coccinellini, less frequently in the tribe Chilocorini (Ceryngier et al. 2012, 2018; Maqbool et al. 2018). *Dinocampus coccinellae* is well known for its parthenogenetic mode of reproduction and extensive host manipulation (Balduf 1926). Paralysed ladybird hosts 'guard' *D. coccinellae* cocoons until emergence of the adult parasitoid and this host manipulation is mediated by a symbiotic RNA virus (Dheilly et al. 2015). Existing data on parasitism and emergence rates of *D. coccinellae* from several ladybird species indicates that the species prefers larger ladybird species as hosts as they probably provide more adequate food resources for the parasitoid (Ceryngier et al. 2012). From this perspective, *H. axyridis* would also represent an optimal host species for *D. coccinellae* but in reality this is not the case. The emergence rates of *D. coccinellae* from *H. axyridis* are much lower than reported for many other ladybird species of similar body size (Obrycki 1989; Ceryngier et al. 2012; Castro-Guedes and Almeida 2016; Ceryngier et al. 2018). Nevertheless, laboratory trials, as well as field data, indicate that there are no strict host preferences in *D. coccinellae*, i.e., the frequency of attacks and egg laying behaviour on *H. axyridis* is comparable to other ladybird species of similar size. This apparent contradiction has been explained by the low ability of the parasitoid to overcome the *H. axyridis* immune defences: the larval development of *D. coccinellae* within *H. axyridis* is efficiently hampered by the host immune system (Firlej et al. 2007, 2012). A possible proximate mechanism was revealed by Firlej et al. (2007), who reported abnormal growth patterns of parasitoid-derived teratocytes and lower absolute numbers of teratocytes in *H. axyridis* compared to a native, optimally-sized host species. It is important to note that *H. axyridis* seems to be a suboptimal host also in its native range (Koyama and Majerus 2008).

Methods

Populations of *H. axyridis* and *C. septempunctata* were sampled at 15 sites in the Czech Republic between 2015 and 2018. Some sites were sampled repeatedly, resulting in a total of 21 *H. axyridis* and 11 *C. septempunctata* samples. In nine cases, the individuals of both ladybird species were collected concurrently at the same site (= co-occurring populations, details in Table 1). Collected adult beetles were transported to the laboratory and accommodated in Petri dishes (9 cm in diameter) in groups of 8–10 individuals. The groups consisted of mixtures of males and females, i.e., sexes were not separated, and ladybirds continued mating and reproduction during laboratory observations. Ladybirds were fed ad libitum with frozen eggs of *Ephestia kuehniella* (Zeller, 1879) and provided with water in cotton wool. Petri dishes were cleaned, and food and water were renewed every other day. Beetles were reared under standardized laboratory conditions (23 °C, photoperiod 16L:8D, relative humidity ca. 60%) for 4 weeks which is sufficient for parasitoid emergence as its complete development within an adult host takes ca. 20 days at 23 °C (Berkvens et al. 2010). Emergence rate of *D. coccinellae*, i.e., proportion of ladybird individuals that produced a *D. coccinellae* pupa (never more than one), was recorded for each ladybird population.

For the nine co-occurring populations, we used a paired *t* test to compare parasitoid emergence rates from native (*C. septempunctata*) and invasive (*H. axyridis*) ladybirds, and a Pearson's correlation to evaluate the relationship between emergence rates from the two host species. These analyses were performed in R version 3.0.1 (R Development Core Team 2018).

To calculate and compare mean emergence rates of *D. coccinellae* from *H. axyridis* in this study and in invasive populations of this beetle elsewhere thus far (1993–2016), we employed the statistical procedures of the meta-analysis of proportions. The proportion of beetles from which a parasitoid emerged was considered a primary outcome for each population. Data from earlier studies were derived from a recent synthesis by Ceryngier et al. (2018). However, data originating from the Czech Republic (collected by O. Nedvěd in 2015–2016) and included in Ceryngier et al. (2018) were combined with the Czech samples collected in the framework of this study. The Freeman-Tukey double arcsine method was applied to transform proportions for the meta-analytic procedures (see Miller 1978, for rationale). An inverse-variance weighted random-effects model with restricted maximum likelihood estimation method was used to combine primary outcomes. The meta-analytically pooled (transformed) estimates were then back-transformed to raw emergence rates. The meta-analytic procedures were performed with R version 3.5.1 (R Development Core Team 2018) using *metafor* package (Viechtbauer 2010).

Results

In total, we investigated parasitism by *D. coccinellae* in 2295 *H. axyridis* individuals and 605 *C. septempunctata* individuals (Table 1). The total parasitoid emergence rate, i.e., pooled across all investigated populations and years, was slightly higher in *H. axyridis* (12.6%) than in *C. septempunctata* (12.2%). In co-occurring populations, i.e., samples collected from the same sites and at the same time, *H. axyridis* was more parasitized than *C. septempunctata* in seven out of nine cases (overall difference was marginally non-significant; paired *t* test: $t = 2.29$, $df = 8$, $P = 0.051$). Emergence rates varied substantially over space and time, ranging from 0 to 46.3% in *H. axyridis* and from 0 to 41.9% in *C. septempunctata*. In co-occurring populations of *H. axyridis* and *C. septempunctata*, *D. coccinellae* emergence rates were strongly correlated (Pearson's correlation: $t = 5.33$, $df = 7$, $P = 0.001$, $r = 0.90$).

The meta-analytically derived mean estimate of recent emergence rates of *D. coccinellae* in Czech populations of *H. axyridis* (data for 2015–2018) significantly differed from the mean emergence rate of this parasitoid in invasive populations of the beetle sampled elsewhere earlier (before 2016). The mean weighted emergence rate in Czech populations was thirteen times higher than in invasive populations elsewhere (Fig. 1).

Discussion

To our knowledge, this is the first report of high *D. coccinellae* emergence rates from the invasive ladybird *H. axyridis*. Higher emergence rates from *H. axyridis* than *C. septempunctata*, as recorded in several co-occurring populations of the two ladybird beetles, indicates that the *D. coccinellae* phenotype for which *H. axyridis* is not a suboptimal host is not limited to a small area. We also show that *D.*

Table 1 Prevalence of *Dinocampus coccinellae* in Central European populations (Czech Republic) of *Harmonia axyridis* and *Coccinella septempunctata*

Site name	Date	*Harmonia axyridis*			*Coccinella septempunctata*			Habitat	GPS coordinates
		Ladybirds sampled	Parasitoids emerged	Emergence rate	Ladybirds sampled	Parasitoids emerged	Emergence rate		
České Budějovice	20.10.2015	280	1	0.004				Buildings (autumn migration)	48.9775000N, 14.4516667E
České Budějovice	26.10.2016	46	12	0.261				Buildings (autumn migration)	48.9775000N, 14.4516667E
Praha—Slatina	12.6.2017	102	37	0.363	57	17	0.298	Corn field	50.0653047N, 14.5768683E
Praha—Farkáň	20.6.2017	136	34	0.25				Lime trees	50.0607439N, 14.3834506E
Praha—Řeporyje	9.8.2017	146	44	0.301	55	8	0.145	Old field (fallow)	50.0361253N, 14.2927625E
Úboč	20.8.2017	120	9	0.075				Reed (pond bank)	49.4377458N, 13.0888817E
Mělník	2.9.2017	87	13	0.149				Vineyard	50.3506800N, 14.4727936E
Praha—Řeporyje	14.9.2017	41	19	0.463	31	13	0.419	Old field (fallow)	50.0361253N, 14.2927625E
České Budějovice	28.9.2017	80	0	0				Buildings (autumn migration)	48.9775000N, 14.4516667E
Praha—Strahov	March 2018	139	7	0.05				Building—windows (overwintering)	50.0762100N, 14.3870450E
Malá Amerika	March 2018	132	3	0.023				Artificial cave (overwintering)	49.9539486N, 14.1764192E
Břízsko	22.4.2018				68	2	0.029	Grassy field margin	49.9048408N, 13.5141419E
Praha—Farkáň	15.5.2018	66	6	0.091	33	5	0.152	Broad-leaved trees + nettles	50.0616803N, 14.3759333E
Praha—Řeporyje	3.6.2018	75	22	0.293	58	14	0.241	Old field (fallow)	50.0361253N, 14.2927625E
České Budějovice	15.6.2018	134	0	0				Shrubs	48.9844444N, 14.4447222E
Mladá Boleslav	24.6.2018				88	0	0	Alfalfa	50.4400000N, 14.9058333E
Třebutičky	24.6.2018	116	4	0.034	117	2	0.017	Weedy patch within arable field	50.5484983N, 14.2566536E

Table 1 continued

Site name	Date	*Harmonia axyridis*			*Coccinella septempunctata*			Habitat	GPS coordinates
		Ladybirds sampled	Parasitoids emerged	Emergence rate	Ladybirds sampled	Parasitoids emerged	Emergence rate		
Jičín	9.7.2018	54	3	0.056				Old field (fallow)	50.4578878N, 15.3730661E
Unhošt'	12.7.2018	69	14	0.203	18	2	0.111	Lime trees + nettles	50.0656975N, 14.1148708E
Kryry	15.7.2018	178	25	0.14	54	8	0.148	Field margin (nettles)	50.1665375N, 13.4389939E
Kladno	20.7.2018	96	17	0.177	26	3	0.115	Ruderal grassland	50.1521856N, 14.1083161E
Kryry	4.8.2018	86	9	0.105				Field margin (nettles)	50.1691214N, 13.4351744E
Úboč	28.8.2018	112	10	0.089				Reed (pond bank)	49.4377458N, 13.0888817E

Parasitoid emergence rate, i.e., proportion of ladybirds producing a parasitoid pupa, is shown for each ladybird population. In all cases only one parasitoid emerged per host, despite cases of superparasitism at the larval stage are reported for *D. coccinellae* in the literature

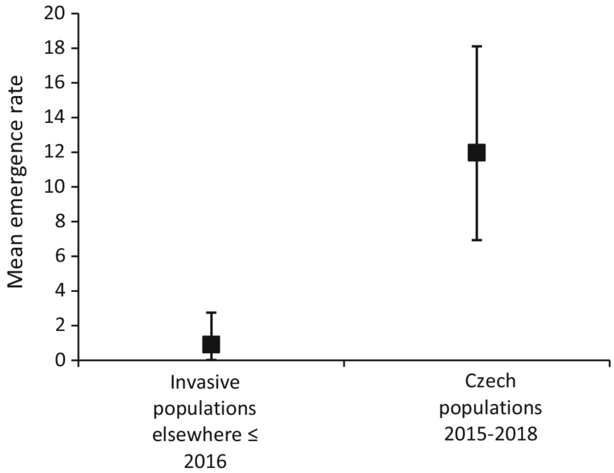

Fig. 1 Meta-analytically estimated mean emergence rates (and 95% confidence intervals) of *Dinocampus coccinellae* in Czech populations of *Harmonia axyridis* (collected 2016–2018 in the framework of this study, plus two recent (2015–2016) Czech samples reported in Ceryngier et al. (2018) and in invasive populations of this beetle sampled elsewhere earlier (1993–2016; data obtained from Ceryngier et al. 2018)

coccinellae emergence rates can considerably vary even between populations separated by a few tens of kilometres from each other.

Adaptation of natural enemies to novel invasive hosts is proposed by the ERH (Roy et al. 2011), but the speed of this process is variable and highly species-specific. In fact, *D. coccinellae* is not a novel parasitoid for *H. axyridis*, as both species co-occur in the native range of *H. axyridis*, but *H. axyridis* has been widely considered to be a suboptimal host for *D. coccinellae* (Firlej et al. 2007; Koyama and Majerus 2008; Ceryngier et al. 2012). To our knowledge, for *H. axyridis*, emergence rates exceeding 30% have not previously been reported. It is interesting to note that, in laboratory trials, emergence rates are higher from 3rd or 4th larval instars than from adults in *H. axyridis* (Firlej et al. 2007; Berkvens et al. 2010). This pattern contrasts from host stage use in many other ladybird species (Ceryngier et al. 2012) and could be explained by a comparatively weaker immune system in larvae of *H. axyridis,* relative to adults (Řeřicha et al. 2018). Based on the age structure of beetles parasitized in our study (similar proportions of parasitoids emerged from older [= reddish] and younger [= yellowish] individuals), we suppose that investigated *H. axyridis* were mainly infected as adults and parasitism at the larval stage is not a likely explanation for the extremely high emergence rates observed. The strong correlation of emergence rates for co-occurring populations of *H. axyridis* and *C. septempunctata* indicates that *D. coccinellae* does not discriminate between these two species. Slightly higher emergence rates in *H. axyridis* could be linked to behavioural differences between ladybird species (e.g., higher movement activity in *H. axyridis*; Roy et al. 2016).

The recent emergence rates of *D. coccinellae* in Czech populations of *H. axyridis* are much higher compared to invasive populations sampled elsewhere across the globe thus far. The most straightforward explanation to this difference is the ongoing adaptation of Central European *D. coccinellae* populations to *H. axyridis*. However, to validate the hypothesis that Central European *D. coccinellae* populations have evolved a phenotype able to employ *H. axyridis* as a suitable host, experimental data are required. Laboratory data on larval and teratocyte growth patterns are needed to evaluate developmental success of Central European *D. coccinellae* in *H. axyridis*, and various native species (*C. septempunctata* and other large Coccinellini) for comparison. Previous studies indicate that the immune system of *H. axyridis* is able to eliminate a large proportion of *D. coccinellae* eggs (Firlej et al. 2012) and that teratocytes produced by *D. coccinellae* undergo abnormal growth within *H. axyridis* (Firlej et al. 2007). As *D. coccinellae* is not able to discriminate between hosts based on their suitability, i.e., females lay similar numbers of eggs in both suitable and unsuitable hosts (Hoogendoorn and Heimpel 2002; Firlej et al. 2012), egg, and particularly larval mortality have been proposed to be responsible for the low emergence rates observed in *H. axyridis* (Firlej et al. 2007; Ceryngier et al. 2012).

Species invasions are inherently dynamic, and often involve gradual changes in the interactions of invasive species with native species (Cox 2004). Nevertheless, such changes occur over time periods longer than those typically covered by individual studies. The consequences of species invasions thus require repeated reappraisals. Emerging associations with native natural enemies, as predicted by the ERH, are of particular interest in this context as they may also provide an effective way to combat the spread and impact of invasive species (Roy et al. 2011). In the case of *H. axyridis*, the high levels of parasitism allow us to believe that *D. coccinellae* may become a potential candidate for suppressing the abundance of this invasive beetle. However, future research focused on potential population level effects of parasitism by Central European *D. coccinellae* is needed. Recent data suggests that, besides the Czech Republic, a *D. coccinellae* phenotype adapted to *H. axyridis* potentially exists in Italy as well (or has evolved after a few generations of laboratory rearing; Fracanti 2018). Further mapping of the geographical distribution of this phenotype(s) is thus an essential task that might be achieved by a combined investigation of *D. coccinellae* population genetics across Europe and subjecting various *D. coccinellae* populations to laboratory trials testing their ability to develop successfully within *H. axyridis*. Given the parthenogenetic mode of *D. coccinellae* reproduction (Balduf 1926) and dominance of *H. axyridis* in many habitats across Europe (Roy et al. 2016), a fast spread of *D. coccinellae* phenotype that is able to utilize *H. axyridis* as a common host is likely.

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