

First detailed report of brood parasitoidism in the invasive population of the paper wasp *Polistes dominulus* (Hymenoptera, Vespidae) in North America

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Abstract The European paper wasp *Polistes dominulus* (Christ) is a model system in the fields of behavioral ecology, ecological immunology, and invasion biology. Since its introduction to the US in 1978, its invasion success has been attributed, in part, to a lack of parasites or parasitoids infecting this population. This is despite the number of parasites which infest the native population and the generalist polistine parasites and parasitoids documented in sympatric North American species. Multiple studies have cited low parasite pressure as evidence that the invasive population of *P. dominulus* is benefiting from a post-invasion release from enemies. Here, we present the first well documented case of parasitoidism of the invasive population of *P. dominulus* in North America.

Keywords *Chalcoela iphitalis* · Enemy release hypothesis · Parasitic moths · Invasion biology · Pyralidae

Polistes dominulus (Christ) paper wasps are native to North Africa, Europe, and parts of Asia and were introduced to North America in 1978, in Massachusetts (Cervo et al., 2000; Eickwort, 1978 in Liebert et al., 2006; Hathaway,

1981). These primitively eusocial insects are highly adapted to nesting in building eaves and as such have a historic close association with humans (Gamboa et al., 2004). Both the native and invasive populations are model study systems in the fields of behavioral ecology, ecological immunology, and invasion biology (see Starks and Turillazzi, 2006 for a review; Wilson-Rich and Starks, 2010). Their proficiency at hunting lepidopteran larvae (in addition to other arthropods), coupled with their expected range increase with global climate change, spawned concern over the invasive population's potential ability to cause dramatic ecological community shifts (Nannoni et al., 2001; Liebert et al., 2006).

Paper wasps, such as *P. dominulus*, are named for the nests they construct with paper and saliva. These nests and resident brood are host to parasites and parasitoids, including predacious Lepidoptera larvae, Hymenoptera, Diptera, and Strepsiptera (all of which are recorded in the native populations) (Hughes et al., 2003; Yamane, 1996; Rusina, 2008). However, the invasive population in North America lacks such parasitism (Gamboa et al., 2004; Cervo et al., 2000). Lower parasitism pressure (as predicted by the enemy release hypothesis), along with higher nest productivity than sympatric native species, is posited as contributing to their successful invasion (see Liebert et al., 2006 for a review). Here, we report the collection of two parasitized *P. dominulus* nests of the invasive population in Massachusetts.

Two *P. dominulus* nests were collected from building eaves in late July 2009, from Lincoln, Massachusetts, USA. Nests were active at the time of collection and contained 53 and 86 nest cells, with pupal caps and 4 and 5 wasps on the nests (expected colony sizes for this location at this time of year) (pers. obs.). These nests were maintained in independent glass and screened enclosures. On the nights of

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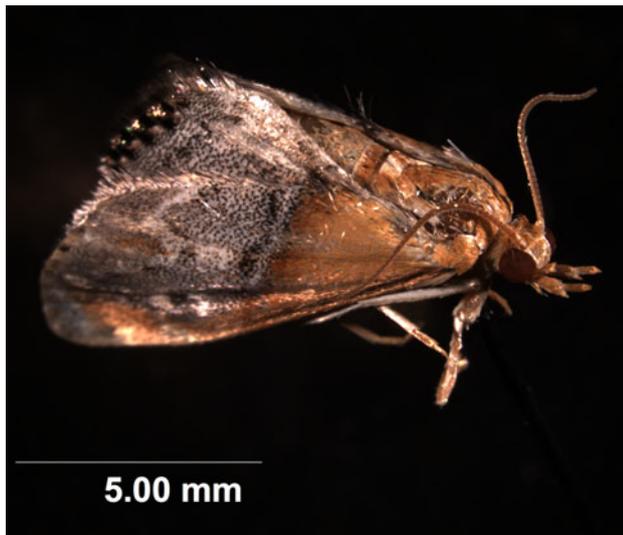


Fig. 1 The polistine brood parasitoid *Chalcoela iphitalis* (Walker) (Lepidoptera: Pyralidae), one of 12 which eclosed from two nests of the invasive *Polistes dominulus* (Christ) collected in Lincoln, Massachusetts, USA, in July of 2009

July 28th and 29th, a total of 12 moths eclosed from the two nests and were collected from the sides of the enclosures (Fig. 1). On July 30th, no new moths were found in the enclosures; however, a pair of wings matching the morphology of the other collected moths was found. These were presumably the remains of a moth which had eclosed and been consumed by the *P. dominulus* nest members (see Strassmann, 1981 for similar observations of *P. exclamans*). The moths were identified as the brood parasitoid *Chalcoela iphitalis* (Walker) (Lepidoptera: Pyralidae) by Mark Metz of the Smithsonian National Museum of Natural History (Washington, D.C.).

Chalcoela iphitalis inhabit most of North America and are known to parasitize polistine and vespid paper wasp brood, including *Mischocyttarus basimacula* Cameron, *P. annularis* (L.), *P. exclamans* Viereck, *P. fuscatus* (F.), *P. carnifex* (F.), *P. instabilis* (Saussure), *P. major* (Palisot de Beauvois), and *P. metricus* Say (Scudder and Cannings, 2007; Nelson, 1968). During the summer, when the polistine nest is active, *C. iphitalis* larvae depredate wasp larvae as brood ectoparasitoids (Riley, 1893; Rau, 1941). Following consumption of one or multiple wasp larvae, *C. iphitalis* larvae construct cocoons consisting of layers of silk interspersed with air pockets (Rau, 1941). The characteristic webbing of these moths was noted in both of our parasitized nests (Fig. 2). This webbing appeared to be ignored by the resident wasps of both of our nests. Such observations are in keeping with those of Nelson (1968) who noted that visibly parasitized cells appear to be either tolerated by the wasps due to an inability of the wasp to tear through the webbing or perhaps remain unnoticed by

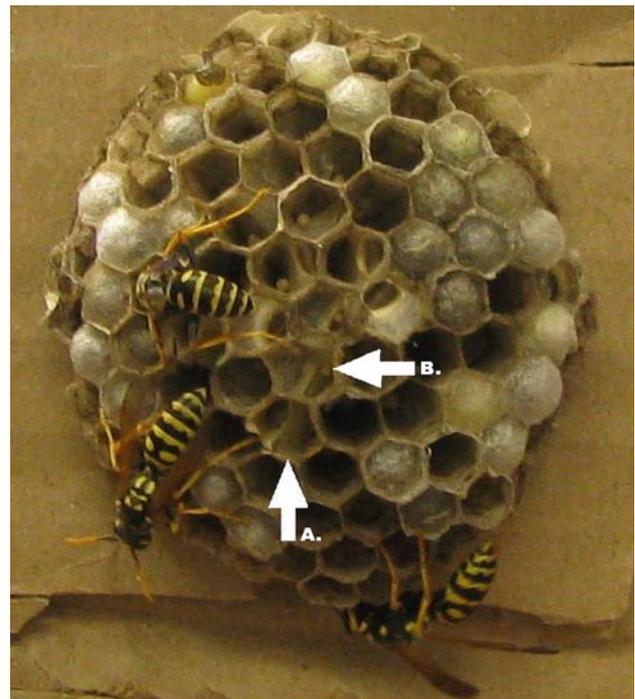


Fig. 2 Nest of *Polistes dominulus* (Christ) infested with the brood parasitoid *Chalcoela iphitalis* (Walker) collected in Lincoln, Massachusetts, USA in July of 2009. Arrow A diagonal webbing of the parasitoid cocoon. Arrow B a *P. dominulus* egg oviposited on a *C. iphitalis* cocoon

the resident wasps, as wasp eggs and first instar larvae are often noted on the top of the moth's cocoon. Such oviposition behavior was observed on both of the parasitized nests noted in our study (Fig. 2).

As suggested by Rau (1941), like the closely related *C. pegasalis* (Walker), *C. iphitalis* is at least bivoltine. *C. iphitalis* larvae enter diapause while overwintering within wasp nest cells in their cocoons (Nelson, 1968; Rau, 1941). Following this pupal stage, they emerge in the spring, when mating and oviposition occur within 24 h of emergence (Nelson, 1968; Rau, 1941). The second generation of the moths eclose in late July through September when the females of *C. iphitalis* disperse preferentially to uninfested nests (Nelson, 1968; Rau, 1941; Strassmann, 1981). The number of moth eclosions we noted per nest (six) is in keeping with those reported by Whiteman and Landwer (2000) in nests of *P. metricus*.

We did not witness either any interactions between the resident *P. dominulus* nest members and the eclosed moths or among the eclosed moths; however, we did note moth wing remains which suggest an interaction occurred. Behavior of the wasps prior and post moth eclosion was not quantified and thus it is impossible to state whether *P. dominulus* responded to the moths' presence by performing the agitated 'parasite dance' observed in other

species such as *P. exclamans* (denoted by all of the wasps of the nest moving jerkily and walking about the substrate for up to 10 h) (West-Eberhard, 1969 cited in Strassmann, 1981). All moths found to have eclosed from the nests were removed on the day of eclosion and were found on the opposite side of the enclosure from the nest.

Due to *P. dominulus*' affinity for nesting on anthropogenic structures which are both associated with larger colony aggregates [which has been shown by Gillaspay (1973), and Nelson (1968) to increase the likelihood of brood parasitism], and more light pollution [which has been noted to attract Pyralidae moths (Sambaraju and Phillips, 2008; Young, 1997)], it is perhaps not surprising that *C. iphitalis* has increased its host range to include this population of invasive wasps. *C. iphitalis* pupae overwinter in polistine nests and this has been suggested as a selective pressure leading to the general rarity of annual nest reuse by polistine wasps (Strassmann, 1981; Starr, 1976). However, frequency of nest reutilization is both species-specific and population dependent, with certain populations of *P. dominulus* reutilizing old nests with a higher frequency than other polistine wasps (Queller and Strassmann, 1988; see pers. obs. in Liebert et al., 2006; Giovanetti et al., 1996). These observations suggest *P. dominulus* nests, when compared to native, sympatric species' nests, may be particularly susceptible to brood parasitoids such as *C. iphitalis*.

Despite observations regarding a webbing on invasive *P. dominulus* nests possibly arising from pyralidae moth infestations in as early as 2006 (see pers. obs. of Starks and Turillazzi in Liebert et al., 2006), this report is the first detailed documentation of a parasitoid of *P. dominulus* infesting the invasive population of North America, suggesting an increase in host range of the parasitoid to the invasive population. The first record of *C. iphitalis* reared from a *P. dominulus* nest was collected in Columbus, Ohio, July 16th, 1997, by S. Passoa, subsequently deposited in the alcohol collection of the National Museum of Natural History, and noted as a new record by M.M.D. in January, 2008. J.D. Wenzel of Ohio State University and K.M. Pickett of the University of Vermont, authorities on the genus, confirmed the identity of *P. dominulus* as the host (pers. comm.). While our report is the first to publish a detailed description of the confirmed interaction between this native moth parasitoid and invasive wasp species, the previous observations and specimens mentioned above support the conclusion that this interaction may date back 12 years or more.

While *P. dominulus* continues to expand its range throughout the US, much of this territory is also inhabited by the parasitoid moth, *C. iphitalis* (Scudder and Cannings, 2007). While other moths parasitize the broods of North American paper wasps, such as the polistine generalist

C. pegasalis, *C. iphitalis* is considered one of the most frequent brood parasitoids and a common cause of colony mortality (Nelson, 1968; Makino, 1985; Schmid-Hempel, 1998). Our report suggests the ramifications of the *P. dominulus* invasion may be eventually muted by the increased host range of native polistine predators and parasites. Future work on the immunology of this wasp in relation to native populations should take into consideration this host inclusion by this parasitoid. Parasitoidism may also influence the epidemiological spread of this invasion and may be particularly relevant to those interested in using this or other polistine species for the biocontrol of lepidopteran crop pests (Nannoni et al., 2001; Gould and Jeanne, 1984).

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