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Comparison of the thermal performance between a population of the olive fruit fly and its co-adapted parasitoids

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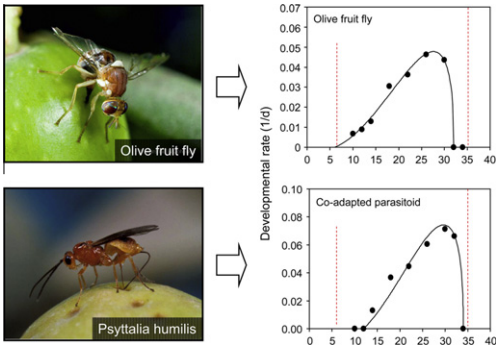
HIGHLIGHTS

- We describe thermal performance profiles for olive fruit fly and two of its parasitoids.
- We compared the tested insect's development, survival, and reproduction.
- Slight thermal profile differences were found between the fruit fly and both parasitoids.
- Changes in the thermal adaptations between parasitoid and host may impact controls.

GRAPHICAL ABSTRACT

Thermal co-adaptation of host and parasitoid effects classical biological control.



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ABSTRACT

Long-term separation of a host from its native parasitoids may result in divergent thermal adaptation between host and parasitoid. The olive fruit fly, *Bactrocera oleae* (Rossi), most likely originated from Sub-Saharan Africa, but has since had a long invasion history in cultivated olives that spans geographical barriers and continents. This study compared three major thermal performance profiles (development, survival, and reproduction) across a wide range of temperatures (10–34 °C) among a Californian population of the olive fruit fly and two African parasitoids, *Psyttalia lounsburyi* (Silvestri) and *Psyttalia humilis* (Silvestri), believed to have co-adapted with the fruit fly in its native range. Temperature ranges for the development and survival were 10–30 °C for the fly, 10–28 °C for *P. lounsburyi*, and 14–32 °C for *P. humilis*. There was no difference in any thermal performance measured between two *P. humilis* populations (Kenya and Namibia) tested. The most suitable temperature ranges for reproduction were 22–30 °C for the fly, 18–32 °C for *P. humilis*, and 18–26 °C for *P. lounsburyi*. The results showed slight differences in the thermal profiles among olive fruit fly and both parasitoids species, with *P. humilis* being more heat tolerant whereas *P. lounsburyi* was less heat tolerant than the fruit fly. The results are discussed with respect to thermal co-adaptation and classical biological control of the olive fruit fly.

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1. Introduction

The co-adaptation of insect parasitoids and their host often results in balanced population densities (Price et al., 1980). Classical biological control is an attempt to restore the host–parasitoid balance after the targeted pest, most often an herbivore, invades a non-native habitat (Hoddle, 2004). However, it is a misconception to assume that the parasitoid will adapt equally-well to a non-native habitat as its host (Roderick and Navajas, 2003). The alignment of co-adapted traits, such as host plant cues, may be lost by long-term separation of parasitoid and host that results from the geographic expansion of the host's range. Therefore, understanding the ecological consequences of long-term separation on those co-evolved traits that govern parasitoid–host interactions is fundamentally important for classical biological control, and yet these issues are rarely addressed (Roderick and Navajas, 2003; Thomas and Blanford, 2003).

The olive and its associated pests and their natural enemies may be an ideal system to study the effects of long-term separation on co-adapted parasitoid–host traits. The extensive history of olive cultivation has obscured details of geographic invasions by the olive fruit fly, *Bactrocera oleae* (Rossi), one of the olive's primary co-evolved herbivores. The olive fruit fly is thought to have originated in Sub-Saharan Africa (Nardi et al., 2005), where wild olives (*Oleae europaea* ssp. *cuspidate*) are endemic and from which domesticated olives (*O. europaea* ssp. *europaea*) were derived and cultivated over 5000 years ago (Zohary, 1994). Cultivated olives were moved along with human expansion and are now grown throughout the world where suitable climates are found, and the olive fruit fly has been associated with olives since biblical times. Molecular analyses suggest the herbivore followed olive cultivation, with an initial northward expansion from Sub-Saharan Africa into North Africa and the Mediterranean basin, and then a westward expansion through Europe and eventually to North America (Augustinos et al., 2005; Nardi et al., 2005,2010).

The olive fruit fly invasion into the Mediterranean basin was, apparently, without the herbivore's suite of co-adapted parasitoids found in Sub-Saharan Africa (Copeland et al., 2004; Tzanakakis, 2003; Wharton, 1989). This created thousands of years during which this parasitoid–host system was likely separated, and during which the herbivore continued to adapt to changes in the olive brought about by cultivation. The California population of the olive fruit fly is of eastern Mediterranean origin (Nardi et al., 2010; Zygouridis et al., 2009) and therefore represents a host population that had been separated from its parasitoids in Sub-Saharan Africa. There are evident effects of this long-term separation. For example, wild olive fruit are small with year-round availability (Copeland et al., 2004), whereas cultivated olive fruit are larger and typically have a fall to winter harvest period. Olive fruit fly parasitoids, which co-adapted with the fly in the wild olive hosts, have relatively short ovipositors, resulting in lower percentage parasitism as olive fruit size increased through domestication (Wang et al., 2009b,c). Other researchers have suggested that cultivation often results in physical changes to the habitat or the host plant that can alter the parasitoid–host relationship (Hawkins et al., 1999; Tylianakis et al., 2007). Long-term geographic separation might also result in the herbivore's adaptation to different environmental changes, such as climate, which can also affect parasitoid–host interactions (Hawkins, 1994; Yang and Rudolf, 2010). Climatic adaptability is, in fact, a key factor determining whether an introduced parasitoid can establish and proliferate in the non-native region occupied by its host (Hoelmer and Kirk, 2005).

Here, we compared the thermal performances of a California population of the olive fruit fly and two Sub-Saharan Africa parasitoids: *Psyttalia lounsburyi* (Silvestri) and *Psyttalia humilis* (Silvestri). Thermal performance curves can be used to explore hypothetical changes in trait performance resulting from adaptation to new environments (Huey and Kingslover, 1989). The parasitoids tested are part of a guild of braconid parasitoids found attacking olive fruit fly in Sub-Saharan Africa, which also includes *Utetes africanus* (Szépligeti) and *Bracon celer* (Szépligeti) (Copeland et al., 2004; Neuenschwander, 1982; Wharton et al., 2000). However, most of the early biological control efforts against the olive fruit fly in Europe used *Psyttalia concolor* (Szépligeti), a parasitoid from northern Africa that is morphologically similar to *P. humilis* but can be distinguished using molecular analysis (Rugman-Jones et al., 2009). Augmentative releases of *P. concolor* have been practiced for over 50 years in Europe (Daane and Johnson, 2010) and while this parasitoid has established in some southern regions (Miranda et al., 2008), it has largely failed to build large numbers and provide adequate control. One researcher suggested this was due, in part, to *P. concolor*'s poor climatic adaptability to some olive regions (Loni, 1997). Our particular interest was to explore possible consequences of the long-term separation of a host, a California population of the olive fruit fly that originated in the eastern Mediterranean basin, from its co-adapted parasitoids from Sub-Saharan Africa. Results are discussed with respect to thermal co-adaptation and biological control of the olive fruit fly.

2. Materials and methods

2.1. Olives and insect culture

Studies were conducted from 2009 to 2010 at the University of California's Kearney Agricultural Center (KAC) in Parlier, California (USA), and the University of California's Insectary and Quarantine Facility (Berkeley I&Q) in Berkeley, California. All insect colonies were maintained using similar methodologies and environmental conditions (24 ± 2 °C, 16 L:8 D photoperiod, 40–60% RH).

The olive fruit fly colony was established in 2003 from flies collected in Davis, California; as noted previously, this population originated from the eastern part of the Mediterranean. The colony was maintained on olives with additions of field-collected flies each year to maintain colony vigor, as described previously (Wang et al., 2009a). In brief, adult flies were held in Bug Dorm2 cages (BioQuip, Rancho Dominguez, California, USA) with water, honey, and hydrolyzed yeast (Fisher Biotech, Fairlawn, New Jersey, USA). Olives were exposed to gravid adult females until each fruit had 3–5 oviposition scars. Infested olives were then distributed over wire mesh that rested 2 cm above a plastic tray (36 × 18 × 10 cm). Larvae matured after approximately 10 days and dropped into the tray where pupae were collected and then placed into Bug Dorm2 holding cages.

The *P. lounsburyi* colony was established from parasitoids reared from olive fruit flies infesting wild olives collected in 2002 in the Burguret Forest on the slope of Mount Kenya (elevation 1960–2062 m). From 2002 to 2005, the colony was maintained on olive fruit fly at the USDA-ARS European Biological Control Laboratory (EBCL) in Montferrier, France, with new collections of wild populations from the Burguret Forest added to the colony in 2002, 2003, and 2005. From 2006 to 2009, the *P. lounsburyi* colony was reared on the Mediterranean fruit fly (hereafter referred to as Medfly), *Ceratitis capitata* (Wiedemann), in an artificial diet at EBCL and the Israel Cohen Institute. The parasitoid was shipped, from EBCL and Israel, to California in 2009.

Two different populations of *P. humilis* were tested, one originated from Kenya (hereafter referred to as *P. humilis* KA) and the other from Namibia (hereafter referred to as *P. humilis* NA). The *P. humilis* KA colony was established with material reared from Medfly infesting coffee berries collected in 2000 in the central