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Dual resistance to lambda-cyhalothrin and dicrotophos in *Hippodamia convergens* (Coleoptera: Coccinellidae)

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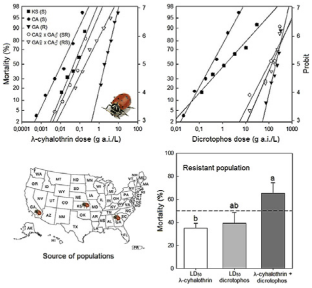
HIGHLIGHTS

- *Hippodamia convergens* from Georgia were resistant to both lambda-cyhalothrin and dicrotophos.
- *H. convergens* from California and Kansas were susceptible to both materials.
- Inheritance of lambda-cyhalothrin resistance was X-linked and recessive.
- Inheritance of dicrotophos resistance was autosomal and dominant.
- Simultaneous exposure to LD_{50}s of both materials increased mortality of resistant beetles.

GRAPHICAL ABSTRACT



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ABSTRACT

Insecticide resistance is usually associated with pests, but may also evolve in natural enemies. In this study, adult beetles of three distinct North American populations of *Hippodamia convergens* Guérin-Méneville, and the progeny of reciprocal crosses between the resistant and most susceptible population, were treated topically with varying concentrations of lambda-cyhalothrin and dicrotophos. In addition, the LD_{50}s of both insecticides were applied in combination to resistant individuals. The developmental and reproductive performance of each population was assessed in the absence of insecticide exposure to compare baseline fitness. California and Kansas populations were susceptible to both materials, whereas Georgia (GA) beetles exhibited a resistance ratio (RR_{50}) of 158 to lambda-cyhalothrin and 530 to dicrotophos. Inheritance of lambda-cyhalothrin resistance was X-linked, whereas inheritance of dicrotophos resistance was autosomal. Mortality of resistant beetles treated with a mixture of LD_{50}s of both materials was twice that of those treated with lambda-cyhalothrin alone, but not significantly different from those receiving dicrotophos alone. Life history parameters were largely similar among populations, except that Georgia beetles had higher egg fertility relative to susceptible populations. We conclude that the high levels of resistance to lambda-cyhalothrin and dicrotophos in Georgia beetles reflect heavy loads of these insecticides in local environments, most likely the large acreage under intensive cotton cultivation.

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1. Introduction

There exists a need to address the impact of pesticides, not only on target pests, but also on non-target arthropods and natural enemies, i.e., parasitoids and predators (Biondi et al., 2012; Cloyd and Dickinson, 2006; Croft and Brown, 1975; Theiling and Croft, 1990). The agronomic value of many insecticides has been diminished due to resistance evolution in numerous pest species (Elzen et al., 1992; Jiang et al., 2011; Whalon et al., 2015). However, it has also become evident that certain natural enemy populations, given repeated exposure to pesticides, can evolve resistance to them in much the same manner as the pests themselves (Croft and Morse, 1979; Pathan et al., 2008; Pree et al., 1989; Rodrigues et al., 2013a). The evolution of pesticide resistance can be influenced by many intrinsic factors, such as genetic makeup of the species, metabolic physiology, and behavior patterns, in addition to extrinsic 'operational factors' that relate to pesticide properties, their application frequency and coverage (Forgash, 1984; Georghiou and Taylor, 1977; Rosenheim and Tabashnik, 1990; WHO, 1957).

Herbivores are products of an evolutionary 'arms race' with plants; the latter have responded to herbivory by evolving a diversity of physical and chemical defenses, while the former have evolved a variety of detoxifying enzymes and other counter-adaptations to overcome them (Bowers, 1992; Levin, 1976). By contrast, arthropod predators have faced lower selective pressures to tolerate or detoxify harmful substances in their food supply. The evolution of resistance by members of the third trophic level is further challenged by the fact that any survivors of pesticide applications typically face a scarcity of prey, which may drive them to migration or local extinction (Croft and Brown, 1975). Furthermore, the rotation of insecticides with differing modes of action, an approach conventionally recommended for delaying the evolution of resistance in pest populations, may also serve to weaken directional selection for pesticide resistance in natural enemy populations (Georghiou, 1972; Pree et al., 1989). Collectively, these factors may explain the low numbers of resistant natural enemies (ca. 50) included in an ever-growing database of arthropod species resistant to one or more pesticides (ca. 600; Whalon et al., 2015).

It is therefore of interest why certain groups of predators appear less susceptible to pesticides than most parasitoids (Theiling and Croft, 1988; Tillman and Mulrooney, 2000; Williams et al., 2003), their prey (Croft and Brown, 1975; Gesraha, 2007), or even key pest species (Spíndola et al., 2013). For example, species of predatory Coccinellidae appear reasonably tolerant to, or compatible with, a variety of pesticides when these are used responsibly in integrated pest management programs (Michaud, 2012). There are also notable examples of resistance, such as populations of *Coleomegilla maculata* (DeGeer) that exhibit resistance to both DDT and organophosphates (Atallah and Nettles, 1966; Head et al., 1977). Similarly, pyrethroid resistance has been reported in populations of *Stethorus gilvifrons* Mulsant (Kumral et al., 2011), *Eriopis connexa* (Germar) and *Hippodamia convergens* Guérin-Méneville (Rodrigues et al., 2013a, 2013b).

Hippodamia convergens is a cosmopolitan species that exploits a wide range of aphid prey on graminaceous and herbaceous plants. It is widely recognized as an important biological control agent of aphids in many agroecosystems including various cereal crops (Michaud and Qureshi, 2006; Rice and Wilde, 1988), cotton (Whitcomb and Bell, 1964) and cruciferous vegetables (Rodrigues et al., 2013b). Pesticide use regimes vary considerably among these crops, partly as a function of their relative value. For example, low value cereal crops such as wheat and sorghum may be grown for many crop cycles on the High Plains of the USA without receiving a single insecticide application, not because pests are completely absent, but because background biological control is generally sufficient and economic thresholds for treatment are high. On the other hand, the broad diversity of agricultural crops grown in the central valleys of California renders it difficult to infer insecticide exposure history for those *H. convergens* populations that are routinely harvested in large numbers from their overwintering aggregations in the Sierra Nevada Mountains, and subsequently sold across the rest of North America. Although these beetles migrate from summer feeding sites to overwintering sites within California, the Rocky Mountains effectively isolate these populations from gene flow from central and eastern North America, even though their own genetics are being regularly introduced to disparate geographic locations (Obrycki et al., 2001), along with the parasitoids and diseases that infect them (Bjornson, 2008). In contrast, cotton and other crops (tobacco, soybean, etc) in southeastern USA have historically received frequent insecticide applications. For instance, cotton fields have experienced an average reduction in annual insecticide applications from 14.4 to about three following the successful boll weevil eradication program and the widespread adoption of *Bt*-cotton (Haney et al., 2009; Roberts, 2015). It follows that populations of *H. convergens* inhabiting these different cropping systems have radically different histories of pesticide exposure, both quantitatively and qualitatively.

Despite the efficacy of plant-incorporated *Bt* traits against many lepidopteran species, *Bt*-crops are not immune to damage by other herbivores and provide no protection against sucking pests (Torres et al., 2009). For example, various stink bug species have emerged as important pests of cotton, soybean and other crops (Pannizi, 2015) and their control often requires applications of broad-spectrum insecticides, or combinations thereof (Greene et al., 2001; Roberts, 2015; Roberts and Toews, 2015; Snodgrass et al., 2005). Despite the emergence of pyrethroid and OP resistance in many arthropod species (Bass et al., 2014; Jiang et al., 2011; Karatolos et al., 2012; Plapp et al., 1990; Whalon et al., 2015), these compounds retain efficacy against many pests and can be preferred because of their low cost.

Using collections from cotton fields in Mississippi, Tillman and Mulrooney (2000) reported 77–95.0% survival of *H. convergens* when adults were exposed to the recommended field rate of lambda-cyhalothrin in residual and topical bioassays. Likewise, Torres and Ruberson (2005a, 2005b) observed good survival of *H. convergens* in Georgia cotton fields following lambda-cyhalothrin applications and high levels of resistance were confirmed in subsequent laboratory assays (Ruberson et al., 2007; Rodrigues et al., 2013a). In addition, Georgia *H. convergens* survived high rates of dicrotophos (ARSR, personal communication). This and other organophosphate materials have a history of use in cotton going back to the 1950s, when boll weevil resistance to DDT forced a shift to materials with other modes of action (Anonymous, 1958).

The present study was conducted to compare levels of pyrethroid and OP resistance among three disparate *H. convergens* populations with presumably different histories of insecticide exposure: a population from central Kansas assumed to have a history of minimal exposure, a commercially-sourced population from central California with unknown exposure history, and a population from a cotton-growing region in Georgia assumed to have a history of long-term exposure to both pyrethroids and OPs. We hypothesized that heavy insecticide exposure would be a regionally-specific selective force driving the evolution of resistance in local populations of *H. convergens*. We also performed reciprocal crosses between two of these populations to assess their genetic compatibility, and the mode of resistance inheritance. Insecticide formulations combining both pyrethroids and OPs have been used to manage resistance in pest populations (Martin et al.,