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Ontogenic behavioral consistency, individual variation and fitness consequences among lady beetles

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ABSTRACT

The potential relevance of complete metamorphosis for the individual variation in sets of behavioral traits and their fitness consequences in predatory species led to the present study. A set of nine behavioral traits were assessed for the larvae and adults of a pyrethroid-resistant and a susceptible population of the lady beetle *Eriopis connexa*. The aim was to assess: 1) the average individual behavioral (pheno)types and their within-population variation, 2) their ontogenic behavioral consistency from larva to adult, and 3) whether the observed correlated sets of behavioral traits can impact fitness. The average behavioral type differed between populations. The pyrethroid-resistant population consistently exhibited lower aggressiveness (as larvae) and exploration, but showed higher activity, as well as larva sociality, and sometimes boldness than the susceptible population. Behavioral trait variation was higher among pyrethroid-resistant individuals, particularly during the larval stage, but there was significant behavior correlation between larvae and adults, regardless of the insect population. Reduced aggressiveness, and to a lesser extent intermediate levels of boldness against heterospecific individuals were associated with higher population growth. Besides shedding light on the ontogenic consistency of behavioral traits and their fitness impact, our results also suggest that reduced aggressiveness is associated with predator population increase, but may compromise its effectiveness as a biocontrol agent.

1. Introduction

Animal behavior, as an observable integrated response resulting from the organism's physiology and interaction with its environment, is paramount for the individual's fitness. Curiously, although animal behavior is expressed as a set or suite of responses, it is usually studied as isolated traits with a range of consequences for individual organisms, particularly when insects are considered (Weiss and Adams, 2013). Such a practice neglects to recognize the co-occurrence and potential correlation of sets of behavioral traits and their consequences.

The crucial importance of animal personality and behavioral syndromes to an animal's survival and fitness led to a dramatic increase in the research on these subjects for the last 20 years (e.g., Gosling, 2001; Wolf and Weissing, 2012; Weiss and Adams, 2013; Kralj-Fišer and Schuett, 2014). That is to say, an animal's survival and fitness are critically influenced by both its personality, or its integrated set of behavioral tendencies (Uher, 2010; Morales et al., 2013), and its behavioral syndrome, or how their individual behavioral differences are consistent across developmental stages and/or contexts (Dingemanse and Reále, 2005; Sih et al., 2004a, 2004b, 2012; Sih and Bell, 2008; Webster and Ward, 2011).

Despite the substantial increase in both animal personality and behavioral syndrome studies, personality-related research specifically centering on invertebrates and insects has been wholly lacking, limited to very few species and contexts (Pinter-Wollman, 2012; Jandt et al., 2014; Kralj-Fišer and Schuett, 2014; Modlmeier et al., 2015). The omission of insect personality in behavioral-focused research may be attributable to a couple of non-exclusive reasons. First is the general public's unappealing view of insects, which is often reflected in their rather modest use in zoomorphic metaphors of human personality, unlike other animals. Second is the traditional belief that insects are automata stereotypically responding to stimuli, exhibiting few, if any, integrated and indi-

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vidual differences in behavior (Keller, 1993; Sommer and Sommer, 2011; Brembs, 2013; Jandt et al., 2014; Kralj-Fišer and Schuett, 2014).

The scant research that has investigated insect personality has heavily focused on social insects. The emphasis on social insects in personality-related research is likely due to the readily analogous comparisons to other social animals, particularly primates (Wray and Seeley, 2011; Pinter-Wollman, 2012; Kralj-Fišer and Schuett, 2014). Fruit flies and crickets have also received attention of personality-related studies, but insect pest species and their natural enemies lag far behind, despite their economic importance, diversity, and suitability as experimental models for such studies (Mather and Logue, 2013; Kralj-Fišer and Schuett, 2014). For example, among insect pests of agricultural importance, the pea aphid *Acyrthosiphon pisum* (L.) (Hemiptera: Aphididae), and the stored product beetles confused flour beetle (*Tribolium confusum*) du Val (Coleoptera: Tenebrionidae) and maize weevil (*Sitophilus zeamais* Motsch. (Coleoptera: Curculionidae)) have provided vital eco-evolutionary and applied insights (Schuett et al., 2011, 2015; Nakayama et al., 2012; Morales et al., 2013; Eiseke and Meyhöfer, 2015; Malia et al., 2016). Additionally, while natural enemies were not targeted in such studies, their relevance in insect personality research has been recently recognized (Kralj-Fišer and Schuett, 2014; Eiseke and Meyhöfer, 2015).

The complete metamorphosis of holometabolous insects is one of the peculiar traits that favors the use of insects as models for personality-related research (Wilson and Krause, 2012; Kralj-Fišer and Schuett, 2014). As an animal's genes, environment, and their interaction determine personality development, drastic morphological and physiological changes that occur between larva and adult stages may potentially affect personality development. That is to say, complete metamorphosis has the potential to compromise personality trait consistency and correlation during ontogeny, which in turn may impact the organism's population and associated community (Eiseke and Meyhöfer, 2015; Modlmeier et al., 2015).

We attempted to address the knowledge gap represented by the lack of personality-related studies on holometabolous insects by exploring the ontogenic consistency of a suit of behavioral traits and its impact upon the reproductive output of individuals from two populations of the lady beetle *Eriopis connexa* (Germar) (Coleoptera: Coccinelidae). This lady beetle species is an important aphid predator in many agroecosystems and pyrethroid-resistant lady beetles can persist longer in pyrethroid-sprayed crops potentially enhancing the biological control of aphids in these crops (Rodrigues et al., 2013a,b; Spíndola et al., 2013; Torres et al., 2015). Pyrethroid resistance is autosomally inherited and incompletely dominant in this species (Rodrigues et al., 2014). The resistance is determined by a major gene likely influenced by secondary genes exhibiting cytochrome P450-dependent detoxification aided by enhanced carboxylesterase activity as the underlying resistance mechanisms (Rodrigues et al., 2013b, 2014).

A set of nine behavioral traits encompassing five personality dimensions or axes (i.e., activity, aggressiveness, boldness/shyness, exploration/avoidance, and sociality; Reále et al., 2007) were sequentially assessed in the (same) larva and adult individuals of two populations of lady beetle, one susceptible and the other (physiologically) resistant to pyrethroid insecticides. Our objective was to characterize the average behavioral type of individuals (i.e., average individuals' phenotypes along five personality dimensions/axes) from each population, the behavioral variability within each population, the ontogenic consistency of personality traits from larva to adult, and the likely consequence of these personality traits for fitness.

We expected behavioral differences to emerge between the two populations of the lady beetle *E. connexa*. Since the susceptible population was not subjected to intensive insecticide selection pressure for resistance, we expected greater behavioral variation within this population (Rodrigues et al., 2013a,b; Spíndola et al., 2013). The complex life cycle of holometabolous insects suggests lack of ontogenic consistency (Wilson and Krauser, 2012; Kralj-Fišer and Schuett, 2014; Modlmeier et al., 2015). However, although the morphological changes in this species are dramatic with metamorphosis, there are no drastic changes in the environmental conditions experienced by larvae and adults of the lady beetle *E. connexa*. This condition favors the detection of ontogenic consistency among behavioral traits between developmental stages (behavioral syndrome) and the potential fitness consequences of these traits.

2. Materials and methods

2.1. Insect populations

Two populations of the predatory lady beetle *E. connexa* were used in the experiments and were derived from previously collected populations maintained at the Entomology Unit of the Federal Rural University of Pernambuco in Recife (State of Pernambuco, Brazil). The insecticide susceptible population originally field-collected from cotton plants in Frei Miguelino county (07°55′90.1″S and 35°51′45.6″W; state of Pernambuco, Brazil) has since been maintained in laboratory with periodical insertions of insects from the field and test for insecticide resistance (Rodrigues et al., 2013a; Torres et al., 2015).

The pyrethroid resistant population originally field-collected from *Brassica* plants in Viçosa county (20°75′73″S and 42°86′96″W; State of Minas Gerais, Brazil) has also been maintained in laboratory with regular insertions of field insects and selection for pyrethroid resistance (Rodrigues et al., 2013a; Torres et al., 2015). The resistance status was periodically checked and maintained via periodic selection using the pyrethroid insecticide lambda-cyhalothrin (Spíndola et al., 2013; Rodrigues et al., 2014; Torres et al., 2015).

Both populations were reared separately under laboratory conditions (27 ± 2 °C temperature, 70 ± 10% relative humidity, and 12 h photoperiod). Following earlier methods (Rodrigues et al., 2013a; Torres et al., 2015), larvae of both populations were provided with eggs *ad libitum* from the Mediterranean flour moth (*Anagasta* (=*Ephestia*) *kuehniella* (Zeller) (Lepidoptera: Pyralidae), and were given (every other day) collard green leaves containing cabbage aphids (*Brevicoryne brassicae* (L.) (Hemiptera: Sternorrhyncha: Aphididae)). Sugar water was also provided during the adult stage to enhance reproduction (Rodrigues et al., 2013a; Torres et al., 2015).

2.2. Behavioral bioassays

The same individuals from the lady beetle populations were used as larvae and adults for both the behavioral and age-structured matrix bioassays in sequential assessments. The behavioral bioassays were sequentially performed during a week for each developmental stage always using the same individuals. Between 29 and 42 individuals of each sex from each population were used in the bioassays; the larva sex was recognized after reaching adulthood. The behavioral bioassays were performed under controlled laboratory conditions, as previously described, between 9:00 am and 6:00 pm. The larvae were tested seven days after hatching (i.e., at their 3rd instar), whereas each corresponding adult was tested two days after emergence.

Seven behavioral bioassays were performed, which focused on the lady beetles' measurable behavioral (or performance) traits. In other words, an individual's ability to perform a task