Effect of larval growth conditions on adult body mass and long-distance flight endurance in a wood-boring beetle: Do smaller beetles fly better?

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ARTICLE INFO

ABSTRACT

The tropical fig borer, *Batocera rufomaculata* De Geer, is a large beetle that is a pest on a number of fruit trees, including fig and mango. Adults feed on the leaves and twigs and females lay their eggs under the bark of the tree. The larvae bore into the tree trunk, causing substantial damage that may lead to the collapse and death of the host tree. We studied how larval development under inferior feeding conditions (experienced during development in dying trees) affects flight endurance in the adult insect. We grew larvae either in their natural host or on sawdust enriched with stale fig tree twigs. Flight endurance of the adults was measured using a custom-built flight-mill. Beetles emerging from the natural host were significantly larger but flew shorter distances than beetles reared on less favourable substrates. There was no difference in the allometric slope of wing area with body mass between the beetles groups; however flight muscle mass scaled with total body mass with an exponent significantly lower than 1.0. Hence, smaller beetles had proportionally larger flight muscles. These findings suggest that beetles that developed smaller as a result from poor nutritional conditions in deteriorating hosts, are better equipped to fly longer distances in search of a new host tree.

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1. Introduction

The ability of insects to colonize new areas and disperse rapidly has been largely attributed to their flight capability (Johnson, 1966; Roff, 1990). Flight, however, is an energetically costly activity that pushes the physiological design of flying insects to extremes that surpass those of flying vertebrates (Dudley, 2000). The flight muscles of insects exhibit the highest known mass-specific rates of oxygen consumption, as well as the highest mass-specific mechanical power output (Dudley, 2000; Marden, 2000). Their development, maintenance and use require significant amounts of energy, to the point of imposing constraints on other activities of the insect. For example: several migrating insects temporally partition the development of gonads and the flight apparatus in the so-called "oogenesis-flight syndrome" (Johnson, 1963, 1969). In those insects, the flight apparatus develops first, allowing migration or dispersal flight. The gonads develop after migration, often with egg production coinciding with lability of the flight muscles (Johnson, 1969).

A high energetic demand for flight and the associated cost in terms of reduced reproduction, require efficient dispersal strategies, particularly when the distance between suitable patches is large. This is because the benefit of moving to a new patch, in terms of fitness, should exceed the cost of movement (Bowler and Benton, 2005). Variable dispersal strategies within the same species may exist through phenotypic plasticity. In some migrating insects the population includes morphologically distinct individuals adapted for migratory flight, while other, non-migrating, morphs may develop gonads at the expense of flight altogether (Dixon, 1993; Harrison, 1980; Roff, 1990; Roff and Fairbairn, 1991; Tanaka and Suzuki, 1998; Zera and Denno, 1997). The signals for appearance of the migrating morph may be seasonal, density-dependent, diet-related or other (Simpson et al., 2011). Dietary signals are particularly interesting in holometabolous insects because food availability during the larval phase can affect metamorphosis to the adult. First, larval nutrition is a primary factor in determining adult body mass (Chown and Gaston, 2010; Shingleton, 2011). Second, the larva must enter the pupal phase with sufficient energy stores for successful metamorphosis (Arrese and Soulages, 2010). The energy reserve remaining after metamorphosis can then be passed on to the adult. While this may be the only energy source for non-feeding adults, these reserves may be of secondary importance, however, in insects that can feed and replenish their reserves (Arrese and Soulages, 2010). Third and most importantly, food deprivation can affect allometry.

Holometabolous insects are unique in the sense that morphological adult structures, such as the flight apparatus, do not grow in parallel with the increase in body mass of the larva. Rather they develop during the pre-pupal and pupal stages, after the period of food intake and body mass growth (Nijhout and Wheeler, 1996). This can result in a trade-off in resource allocation between various adult body parts during their development (Nijhout and Emlen, 1998; Nijhout and Wheeler, 1996). Morphological traits that grow disproportionally large during development may do so at the expense of other traits, which develop to be smaller (Emlen, 2001; Emlen and Nijhout, 2000; Kawano, 1995; Nijhout and Emlen, 1998). Such disproportional growth in some morphological traits compared to others leads to a change in form, providing a mechanism for phenotypic plasticity (Nijhout and Emlen, 1998).

There are numerous examples showing that starvation during the larval phase leads to morphological changes, including of the flight apparatus. For instance, starved lepidopteran larvae can pupate and metamorphose to adults, with reduced body mass albeit disproportionally large wing area (Angelo and Slansky, 1984; Boggs and Freeman, 2005; Boggs and Niitepold, 2016), and thorax and head mass (Boggs and Niitepold, 2016), presumably making them more efficient flyers. However, only a few studies have directly confirmed the relationship between the nutritional conditions of the larvae and the flight performance of the adults: the quality of diet may be inversely correlated with the tendency to take-off in *Prostephanus truncatus* (Fadamiro et al., 1996); male butterflies, *Pararge aegeria,* growing as larvae on a host plant under drought conditions, showed less territorial perching behaviour and instead tend more to fly from spot to spot within large enclosure (Velde et al., 2013); Male *Malacosoma disstria* moths had a lower flight capacity (shorter flight distances) when, as eggs, they were collected from low density populations and the larvae were fed *ad libitum* in the lab. In contrast, the male moths collected as eggs from high density populations flew on average ∼4-fold larger distances (Evenden et al., 2015); females of the African armyworm moth, *Spodoptera exempta* demonstrated longer tethered flights when they had developed from larvae that came from dense populations (Woodrow et al., 1987); and the beet armyworm (*S. exigua*) performed longer tethered flights after the larvae had been fed sub-lethal doses of the protoxin Cry1Ac (Jiang et al., 2013).

Here, we examined whether nutrient deprivation during larval growth in the tropical fig-borer, *Batocera rufomaculata* (Coleoptera: Cerambycidae), results in improved long-distance flight performance in smaller adults due to morphological or physiological changes. *B. rufomaculata* is a large beetle with body mass of some specimens exceeding 7.0 g. Data on the biology of this species are sparse. It is a severe pest of fruit trees (mainly fig and mango) in Israel, where the host trees provide food and shelter for the phytophagous adults as well as the site for mating and oviposition. The females lay their eggs beneath the bark of the tree and the hatched larvae develop by boring into the trunk of the host and feeding on its tissues and sap. The larvae pupate inside the tree and the emerging adults chew their way out of the trunk and feed on the leaves and shoots. The developing larvae cause substantial damage to the trunk, often leading to the collapse or death of the host tree (Avidov and Harpaz, 1969; Husain and Khan, 1940). Larvae that develop in dead tree sections pupate and eclose to adults that are much smaller (<30% in body mass) than adults resulting from larvae developing in live trees (Fig. 1 and Results). *B. rufomaculata* were accidently introduced into Israel (likely with timber imported from Sri Lanka) during the late 1940s and have since spread to become significant pests (Avidov and Harpaz, 1969; Halperin and Holzschuh, 1993). Since spreading from infested to new host trees is done only by flying adults, there is interest in evaluating the factors contributing to their long-distance flight. We are unaware of any work to date that has examined the
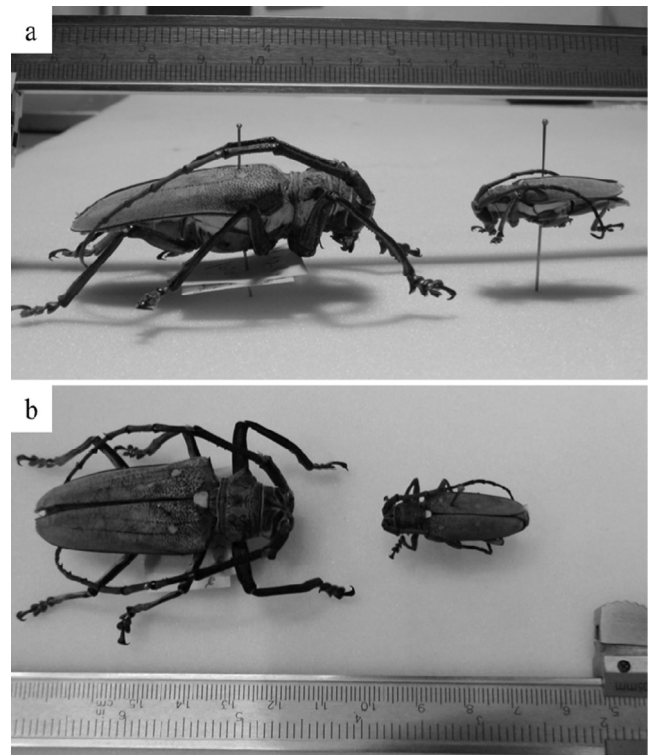
Fig. 1. Side (a) and dorsal (b) views of two male *B. rufomaculata* demonstrating extreme intra-specific variation in adult body size. Photographed specimens are from the Steinhardt Museum of Natural History and National Research Center.

developmental trade-offs of the flight apparatus or the flight capabilities in this species.

Since fig trees provide the food, shelter, oviposition and mate-finding sites of the adults, as well as the substrate for the developing larvae, we examined whether larval growth conditions affect the long-distance flight capabilities of the adults. We hypothesized that larvae developing in healthy host trees would allocate fewer resources towards adult flight, whereas larval growth under deteriorating conditions would lead to allocating more resources to flight. To test this hypothesis we monitored the growth and morphology of beetles as a function of larval diet, and used a custom-built flight-mill to compare the long-distance flight capacity of beetles developing in fig trees with beetles growing on stale branches in the lab.

2. Methods

2.1. Collection of beetles and larvae

Twenty-nine adult beetles were collected from infested fig trees (*Ficus carica*) in several locations in northern Israel during the summer of 2015. The beetles were transported to Tel Aviv University the following day and housed together in two cylindrical cages (diameter = 20 cm, length 1.0 m) with a live fig tree and freshly cut twigs from adjacent fig trees from the I. Meir Segals Garden for Zoological Research. The laid eggs were collected every other day by carefully peeling the bark from the trees and removing the eggs. Each egg was individually placed in a sealed 1.5 ml Eppendorf tube with moist paper and kept at room temperature (25 °C) until it hatched (∼1 week later). The hatched larvae were assigned to the growth-rate experiment as described below.

Adult beetles typically start emerging from fig trees in Israel during May (Avidov and Harpaz, 1969). Four infested fig trees from