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Dynamics of in vivo power output and efficiency of *Nasonia* asynchronous flight muscle

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Abstract

By simultaneously measuring aerodynamic performance, wing kinematics, and metabolic activity, we have estimated the in vivo limits of mechanical power production and efficiency of the asynchronous flight muscle (IFM) in three species of ectoparasitoid wasps genus *Nasonia* (*N. giraulti*, *N. longicornis*, and *N. vitripennis*). The 0.6 mg animals were flown under tethered flight conditions in a flight simulator that allowed modulation of power production by employing an *open-loop* visual stimulation technique. At maximum locomotor capacity, flight muscles of *Nasonia* are capable to sustain $72.2 \pm 18.3\,\mathrm{W\,kg^{-1}}$ muscle mechanical power at a chemo-mechanical conversion efficiency of approximately $9.8 \pm 0.9\%$. Within the working range of the locomotor system, profile power requirement for flight dominates induced power requirement suggesting that the cost to overcome wing drag places the primary limit on overall flight performance. Since inertial power is only approximately 25% of the sum of induced and profile power requirements, *Nasonia* spp. may not benefit from elastic energy storage during wing deceleration phases. A comparison between wing size-polymorphic males revealed that wing size reduction is accompanied by a decrease in total flight muscle volume, muscle mass-specific mechanical power production, and total flight efficiency. In animals with small wings maximum total flight efficiency is below 0.5%. The aerodynamic and power estimates reported here for *Nasonia* are comparable to values reported previously for the fruit fly *Drosophila* flying under similar experimental conditions, while muscle efficiency of the tiny wasp is more at the lower end of values published for various other insects.

Keywords: Flight; Power requirements; Muscle mechanical power; Metabolic conversion; Muscle efficiency; Aerodynamic efficiency; *Nasonia*; Wasp

1. Introduction

Throughout the last several years there has been much progress in understanding the underlying mechanisms of insect aerobatic capacity (Fry et al., 2003; Hateren and Schilstra, 1999; Kern and Egelhaaf, 2000; Srygley and Thomas, 2002; Tammero and Dickinson,

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2002). In many species, the extraordinary aerial maneuvers are supported by elaborate sensory feedback that allows these animals changing many aspects of their wing kinematics and thus changes in forces and moments on a stroke-by-stroke base (Lehmann, 2004a,b; Nalbach, 1994; Pringle, 1948; Sane, 2003; Sherman and Dickinson, 2003, 2004; Wigglesworth, 1946). The production and control of aerodynamic forces depend on a variety of different factors including sophisticated unsteady aerodynamic mechanisms, structural mechanics of the skeleton, the interplay in neural activation between flight muscles, and the maximum power output sustained by the flight musculature. Compared to other types of locomotion, the high power demands for flight requires that metabolic activity increases 10–15 times over resting metabolism and it has often been assumed that maximum mechanical power output of the insect flight muscle places the primary limit on the production of aerodynamic forces and aerial maneuverability in an animal (Casey, 1989; Lehmann, 2001; Marden, 1987, 1994). The total metabolic costs of flight, however, also depend on the efficiency with which the locomotor apparatus converts metabolic energy into flight forces that depend on two factors: the chemo-mechanical conversion efficiency of the muscle's mitochondria and contractile apparatus and the efficiency of fluid dynamic processes that underlie aerodynamic lift production (Ellington, 1984b; Josephson, 1985; Stevenson and Josephson, 1990). As a consequence, a systems-level perspective on power production is a necessary bridge in any attempt to link function and performance of the flight musculature with its specific role for wing motion and force control.

Although the maximum mechanical power output and efficiency of the insect flight muscle can be estimated from in vitro biophysical experiments, previous studies have shown that the values estimated from such experiments may be substantially lower than the maxima that must occur in the flying animal. However, it is difficult to determine maximum mechanical power output and thus maximum locomotor capacity in a freely flying insect because it is necessary to elicit peak locomotory performance under experimental conditions during which wing kinematics and metabolic rate are simultaneously measured. Previous studies on vertebrates have tried to circumvent these difficulties in estimation of power output by flying the animals in a gas mixture between oxygen and helium (Chai and Dudley, 1995; Dudley and Chai, 1996). These studies used a strategy in which air density and thus the ability of the flapping wings to produce aerodynamic forces was systematically altered until the animals were incapable of sustained hovering flight. In insects, measurements of both the flight power requirements and the muscle mechanical efficiency can be achieved by flying the animals under tethered flight conditions in a respirometric chamber. Visual stimulation of the flying animal allows then modulations of power output and estimations of locomotor capacity at peak performance (Dickinson and Lighton, 1995; Lehmann and Dickinson, 1997).

In this study we have estimated the dynamics of in vivo muscle mechanical power output and flight efficiency of the insect asynchronous flight muscle (IFM) in three strains of the tiny wasp *Nasonia* (*N. giraulti*, *N. longicornis*, and *N. vitripennis*) flying in a flight simulator. The females of these strains have similar wing- and body size and are capable of long-distance flight, whereas flight capability in males is thought to vary due to wing size-polymorphisms (King, 1993; Whiting, 1967). Peak-performance and working range of the IFM we obtain by changing horizontal and vertical motion of the visual world displayed in the simulator that surrounds the animals. In response to these visual stimuli, the tethered wasps systematically alter wing motion, aerodynamic force production and metabolic activity. By incorporating the measurements into an analytical framework for quasi-steady aerodynamics and energetics of oscillating wing motion, we show how the various components of mechanical muscle power and muscle efficiency vary during flight of the animals.

2. Materials and methods

2.1. Animals

The data within this paper were collected from 3–7-day-old ectoparasitoid bronze wasps *Nasonia* spp. (Collatz and Wilps, 1986; Whiting, 1967). In general, parasitic wasps are model organisms for evolutionary biologists and commonly used to investigate sex allocation, mating behavior, and the influence of cytoplasmically inherited bacteria on hybrid breeding incompatibilities (Bordenstein et al., 2001; King and