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Biodemography of a long-lived tephritid: Reproduction and longevity in a large cohort of female Mexican fruit flies, *Anastrepha ludens*

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Abstract

Age of sexual maturity, daily and lifetime reproductive rates, and life span were recorded in a laboratory cohort of Mexican fruit flies consisting of over 1100 females maintained individually. The results revealed that, relative to the medfly, the Mexfly is slower maturing (14 vs 17 days), more fecund (1400 vs 650–1100 eggs/female), and longer lived (50 vs 35 days). The results reinforced the generality of several earlier findings on the medfly including the deceleration of mortality at older ages and the weakness of the correlation between the rate of egg laying at early ages and both subsequent reproduction and remaining longevity. Discussion includes perspectives on the role of artificial selection in shaping the demographic traits of the mass-reared strain of Mexfly used in this study, as well as the overall significance of large scale biodemographic studies in understanding aging and longevity.

Keywords: Biodemographic studies; Mexfly; Medfly

1. Introduction

Although the literature in biogerontology, biodemography and ecology contains life history information on a wide variety of invertebrate and vertebrate species, there appears to be published data on only three species (all invertebrates) in which life span and age-specific birth rates were derived from large numbers of individuals maintained in solitary confinement under controlled conditions. These include the nematode, *Caenorhabditis elegans* (Chen et al., 2005; Johnson et al., 2001), the fruit fly, *Drosophila melanogaster* (Clark and Guadalupe, 1995; Curtsinger et al., 1992; Promislow et al., 1996; Tatar et al., 1996), and the Mediterranean fruit fly, *Ceratitis capitata* (Carey, 2003). Remarkably, *Homo sapiens* is the only other species for which data on reproductive histories are available for large numbers of individuals (Wood, 1994).

There are several reasons why large-scale biodemographic studies of individuals are important. First, a large database on individual-level reproduction provides stronger statistical power for assessing the relationship between early reproduction and old-age mortality as well as for correlating lifetime reproduction and total longevity (Bell and Koufopanou, 1986; Chippindale et al., 1997; Partridge, 1987). The use of extraordinarily large initial numbers of individuals is particularly important for mortality estimates at advanced ages. Second, comparative biodemographic studies of closely-related species are possible when detailed birth and death data exists on large numbers of individuals of multiple species. For example, the results of large-scale biodemographic study on a new fruit fly species will shed light

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on whether many of the observations on the medfly concerning age patterns of reproduction and reproductive costs (Carey, 2003) are unique to the medfly or more general. Third, subtle age patterns of reproduction at the level of the individual shed important light on inter- and intra-individual aging. For example, a patterns of sporadic or intermittent egg laying at older ages are difficult to characterize when observed in a small number of older individuals but much easier and more definitive when these patterns are observed in larger numbers.

Because of the paucity of species upon which large-scale biodemographic studies have been conducted and thus the limited perspective on the relationship between birth and death rates at the level of the individual, we initiated a study to monitor age-specific reproduction and life span in over 1100 individual Mexican fruit flies (*Anastrepha ludens*), commonly known as Mexflies. Our broad objectives were to add a new species to the limited literature involving large-scale biodemographic studies and, because the Mexfly is closely related to the medfly, to create a database for use in making biodemographic comparisons of the two species, particularly comparisons between the species-specific relationship of longevity and reproduction. Our specific goals were to determine the age-specific patterns of reproduction in Mexfly subcohorts, to examine the cost of reproduction (i.e. relationship between reproduction at young ages and longevity), and to document individual life span and lifetime reproduction in a large cohort of flies.

2. Methods and materials

2.1. Background

The Mexican fruit fly, *A. ludens*, belongs to the dipteran family Tephritidae—a group of about 4000 species referred to as the 'true' fruit flies that is distributed throughout most of the world (Christenson and Foote, 1960). Members of this group (which includes the Mediterranean fruit fly, *C. capitata*, commonly known as the medfly) lay eggs in intact fruit using their sharp ovipositor rather than on decaying fruit as do their distant relatives the gnat-sized vinegar flies in the family Drosophilidae (also referred to as pomace flies).

The genus of the Mexfly *Anastrepha* is a large Neotropical group with over 190 known species (Norrbom and Foote, 1989) that are endemic to the American tropics and subtropics and distributed from Central American and the West Indies to Argentina and Chile. The distribution of *A. ludens* is restricted to Mexico and northern countries of Central America (Aluja, 1994). The life cycle of the Mexfly is typical of most tephritids (Bateman, 1972; Christenson and Foote, 1960; Fletcher, 1989) where adult mated females deposit their eggs within host fruit, the eggs hatch into larvae within 2–4 days and begin feeding on the fruit pulp. Within 1–2 weeks, the larvae complete their development and exit the fruit to pupate in the ground. After about 2 weeks, the adults emerge from the pupae and begin laying eggs in one to two weeks, depending on mating, host, dietary and climatic conditions. The literature on this species indicates that it lays between 800 and 1200 eggs/female over its lifetime and lives an average of 20–40 days (Baker, 1944; Berrigan, 1988; Berrigan et al., 1988; Liedo et al., 1992; Mangan, 2003).

2.2. Source of flies

The Mexflies used in the current study were reared from pupae taken from the fruit fly mass-production facility (Vargas, 1989) in Metapa, Mexico (Liedo et al., 1993; Vargas, 1989). The general history of the Mexfly strain currently used for mass rearing is similar to that for many tephritid species used in factory production (Leppla, 1989) (P. Liedo, personal communication) involving (i) colonization of flies several decades earlier (i.e. originally collected in the 1960s from infested fruit near Monterrey, Mexico); (ii) small-scale rearing for use in pilot studies for several decades; (from 1960 to 1980); (iii) periodical addition of wild-caught flies to increase vitality and enhance genetic diversity including introduction of wild-caught flies in 2003; and (iv) constant improvement in both rearing technology and increase in scale. The Mexfly used in the current study fits the criteria of a 'domestic phenotype'—that combination of phenotypic traits that enables an animal to adapt to man and the captive environment man provides for that species (Price, 1984). This strain can thus be considered a 'periodically refreshed' laboratory biotype several hundred generations removed from the wild adapted to adult crowding and for ovipositing into either an artificial medium (moist chamois-like material) or nylon mesh.

2.3. Experimental framework

The biodemographic study of Mexfly females was conducted at the fruit fly mass rearing facility near Metapa, Chiapas, Mexico. Rearing conditions throughout this period were 26 ± 2 °C, $80 \pm 10\%$ relative humidity and 12:12 light: dark cycle. The Mexfly adults used in this study were obtained from the regular rearing process and maintained in $4 \times 4 \times 10$ cm plastic cages. The eggs were laid on a 1.5 cm wide black silicon stripe applied over mesh covering the front of each cage. Water and ad libitum food (3:1 sugar-yeast dry mixture dissolved in water) were provided as droplets on slides each day. At eclosion a single adult of each sex was placed in each individual cage. Males were replaced with same-aged, virgin males if the male died before the female. A total of 34 successive cohorts of 10, 25, 50 or 100 pairs were set up at irregular intervals (number varied according to time available to technicians) and daily