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Biodemography of the Mediterranean fruit fly: Aging, longevity and adaptation in the wild

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ABSTRACT

The purpose of this paper is to summarize recent research on longevity, aging and adaptation in wild medfly populations and in a close relative of the medfly. The key findings include a new life table identity that relates age structure and the distribution of deaths in stationary populations, seasonal variation in the post-capture longevity of trapped medflies of unknown age, greater longevity of once-wild (wild-caught) adult medflies relative to never-wild (laboratory-emerged) individuals, differences in age specificity of different medfly field capture methods, large variation in the sex-specific longevity of six medfly global biotypes (e.g. Kenya; Brazil; Greece), and the extraordinary longevity of the natal fruit fly — a sister species of the medfly. The discussion contains a listing of discoveries derived from this recent research that appear to be unique to the investigations on medfly aging in the wild. It is suggested that studies of aging in wild populations of *Drosophila melanogaster* have the potential to exploit this model organism in an entirely new aging research domain and thus complement the already deep literature on aging in this species.

1. Introduction

Tephritid fruit flies as models for aging research were originally introduced to the gerontology and biodemography literature nearly two decades ago with publication of the large-scale Mediterranean fruit fly (*Ceratitis capitata*) life table study showing that mortality slowed at advanced ages (e.g. Carey et al., 1992). This was the first of a number of papers that exploited one of the strengths of this model system — the availability of large numbers of individuals at low cost. Many of the biodemographic papers published after this early phase involving large-scale experiments focused on questions that required gathering individual-level data on age-specific egg production, disability and mating. Overviews of the results of these studies along with those of earlier large-scale life table experiments are contained in Carey (2003).

Although tephritid fruit flies continue to serve as laboratory models for aging research (Fanson et al., 2009; Papadopoulos et al., 2010; Zou et al., 2009), recent research efforts on medfly biodemography have expanded to include aging in the wild. This is an area of aging science that, with a few important exceptions (e.g. Begon, 1976; Bonduriansky and Brassil, 2002; Sherratt et al., 2010), has been largely neglected for *Drosophila* and other model organisms. Therefore the purpose of this paper is to provide an overview of recent findings concerned with medfly aging in the wild and discuss their implications and importance for aging research in general and *Drosophila* aging research in particular. The research results that I review in this paper are contained in seven different studies, six of which are grouped in two separate sections according to a general theme and one of which is summarized in a separate section. At the end I recap the original discoveries and developments that appear not to have precedents in the literature on the biology and demography of aging.

2. Background

2.1. Importance of research on aging in the wild

All biologists are well aware that life in a captive laboratory environment for model organisms is vastly different from their lives if they were free-ranging animals living in the wild. Whereas laboratory animals are maintained under optimal physical conditions in cages, usually have ready access to food, water, and mates, and are protected from disease, parasites, and predators, these same animals living in the wild may be subject to disease, starvation, desiccation, parasitisation, predation, hypothermia and hyperthermia. Because aging and longevity in the wild may differ so drastically from aging in the laboratory, it is impossible to characterize all of the actuarial

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properties of a species including its lifespan independent of its environment — a fly that is capable of living 6 months in the laboratory might live only a few days or weeks in the wild. Information on aging in both environments is thus complementary and mutually informing in at least two respects. *First*, knowledge of all aspects of aging and longevity in both environments including lifespan extremes, sex longevity differentials, actuarial aging rates, seasonality of frailty, and life table properties of biotypes will reveal which aspects are truly robust (i.e. aging traits that are present in both environments such as the sign of gender longevity differences) and those which are idiosyncratic to or an artefact of a particular environment. *Second*, inasmuch as the evolutionary theories of aging serve as the foundation for much of aging research, particularly for interpreting actuarial patterns at the advanced ages, the results of studies on aging and longevity in evolutionarily-relevant environments can be used to validate certain theories and reject others. Indeed, there is virtually no other way to test evolutionary theories of aging other than the use of data gathered on aging in the wild. This point is underscored by Williams and his co-workers (Williams et al., 2006) who noted that, because of the paucity of field data, the present weight of evidence has failed to establish George Williams' classic hypothesis (Williams, 1957) that low adult death rates are associated with low rates of senescence as a general prediction of the way that environmental hazards shape aging schedules in the wild. It is remarkable that after over half a century there is still no clear consensus on this classic theory because of lack of relevant field data.

2.2. Overview of medfly natural history

The medfly belongs to the dipteran family Tephritidae referred to as "true" fruit flies — a group of about 4000 species distributed throughout most of the world (from Christenson and Foote, 1960). Tephritids lay eggs in intact fruit using their sharp ovipositor rather than on decaying fruit as do their distant relatives in the family Drosophilidae. Both genetic and phylogenetic evidence point toward tropical Africa as the medfly's aboriginal home. However, the species is currently distributed throughout a wide range of climatic regions of the world including the Mediterranean, western regions of the Middle East, Central and South America, and the Pacific (Hawaii; Western Australia). Generally speaking, the reproductive biology and life course of medflies are typical of other dipterans including Drosophilids — after emerging from a 3 week preadult phase (egg, larvae, pupae), adults of both sexes begin searching for mates and foraging for food. Following a 5 to 10 day maturation period females lay an average of 700 to 1000 eggs (in laboratory) and survive for 4 to 6 weeks. Unlike *Drosophila melanogaster* most aspects of medfly ecology and behavior in the field are well understood (e.g. Papadopoulos et al., 2001; Vargas et al., 1983). However, one aspect that is poorly understood is its demography in the wild, some insights of which are presented in the next three sections.

3. Aging, longevity and adaptation in the wild

3.1. Medfly population aging: Analytical concepts and empirical studies

3.1.1. Life table equality: Death distribution reveals age distribution

A concept that appears not to have been considered in the development of techniques that can be used to study population aging and age structure in the wild concerns the information contained, not in dead individuals as in many of the historical approaches (e.g. egg load; cuticular hydrocarbons), but in live ones. The concept is this: if groups of individuals are collected from two populations separated in space or time, one for which the average age of individuals in it is greater than the other, the average of the remaining time-to-death of these captured individuals will be less in the older population. Further, the difference between the average ages to death will approximate the difference in the average ages between their populations.

For the idealized case of a stationary (replacement-only) population, the age distribution (and thus average age) of the population can be computed directly from the distribution of the remaining times to death of the individuals across all age classes in the current population. Thus if all individuals in a stationary population were marked at a given moment and their deaths monitored until the last individual died, the exact percentage that dies x-days after the moment of marking will equal the exact percentage of individuals age x in the stationary population. This is despite the mathematical fact that the percentage of all deaths that occur x-days after marking consists of individuals from all age classes.

This non-intuitive but mathematically true relationship is given in papers by Müller and his colleagues (Müller et al., 2004; Müller et al., 2007) and formally derived by Vaupel (2009). The key relations forming the life table identity are outlined in Table 1. The identity is revealed by the equality of the bold type columns c_x and d_{x^*} in the leftmost and rightmost sub-tables. From these data on death distributions of randomly-marked individuals of unknown age in stationary populations it is possible to compute: (1) the age-specific survival schedule, l_x; (2) population age structure; and (3) the probability that an individual chosen at random is one who has lived x years equals the probability the individuals is one who has that number of years left to live (Vaupel, 2009).

One of the most surprising aspects of this discovery is that, despite the extraordinary long history and extensive analytical studies on life tables (e.g. Preston et al., 2001), this identity was unknown prior to its publication in the paper by Müller and his colleagues. The life table equivalence is important because it sheds light on the relationship of age structure and death distributions in a population (albeit stationary and thus idealized) and, in turn, provides an initial analytical framework for constructing more realistic models such as the one used in the next section.

3.1.2. Population aging in wild medflies

Although ecologists have attempted to develop methods for estimating the age of individual insects (e.g. cuticular hydrocarbons; eye capsule pteridines; gene expression) and ultimately the age structure of their populations, the methods are often expensive and the results are always mixed. Indeed none of the technologies provide accurate estimates of individuals at more advanced ages.

An alternative approach to estimating population age structure was developed by Carey, Müller and their colleagues based on a method involving i) data on the remaining lifespans of live-captured individuals and from reference cohorts; and ii) a deconvolution model that is used to estimate population age structure (Carey et al., 2008; Müller et al., 2004; Müller et al., 2007).

This approach used to estimate the age structure of wild medfly populations in Greece, referred to as the captive cohort method, was based on the death distribution of over 4000 medflies captured and monitored in the laboratory over three field seasons (Carey et al., 2008). The method assumed: (1) that relative changes in the patterns of death between cohorts of medflies captured during two or more sampling periods reflects relative changes in their respective population age distributions; (2) that changes in these post-capture death patterns can be used to estimate the actual age structure in the field if both laboratory-reared and wild-caught adult medflies experience the same mortality risk in the laboratory (i.e. memoryless assumption); and (3) the estimated age distribution of wild-caught flies can also be used to infer the actual age structure in the field (assuming flies are captured in proportion to their abundance).

The results revealed that large seasonal differences (i.e. >30 days) existed in the post-capture lifespans of medflies (Fig. 1). The empirical data and the modeling results suggested that: i) major shifts in population age structure (>30 days) occur in wild medfly populations;