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INSECT BIODEMOGRAPHY

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■ **Abstract** Biodemography is an emerging subdiscipline of classical demography that brings life table techniques, mortality models, experimental systems, and comparative methods to bear on questions concerned with the fundamental determinants of mortality, longevity, aging, and life span. It is important to entomology because it provides a secure and comprehensive actuarial foundation for life table and mortality analysis, it suggests new possibilities for the use of model insect systems in the study of aging and mortality dynamics, and it integrates an interdisciplinary perspective on demographic concepts and actuarial techniques into the entomological literature. This paper describes the major life table formulae and mortality models used to analyze the actuarial properties of insects; summarizes the literature on adult insect life span, including a discussion of basic concepts; identifies the major correlates of extended longevity; and suggests new ideas for using demographic concepts in both basic and applied entomology.

CONTENTS

INTRODUCTION

Biodemography is an emerging subdiscipline of classical (human) demography that brings life table techniques, mortality models, experimental systems, and comparative methods to bear on questions concerned with the fundamental determinants of mortality, longevity, aging, and life span (2, 112, 141, 197, 199). Although the literature on the use of demographic concepts and techniques in biology in general and in entomology, ecology, and evolution in particular is extensive and dates back to early decades of the last century (123, 150, 152), the historical emphasis has been on its use in the context of stable population theory (10, 49), animal life tables (58), and population biology (120). In contrast, the focus of biodemography is on understanding the underlying actuarial mechanisms rather than on applying demographic and actuarial tools to particular biological problems.

Biodemography is important to entomology for at least three reasons. First, because it has deep roots in classical demography (173), biodemography provides a more secure actuarial foundation than currently exists in both basic and applied insect ecology. Second, it opens up new possibilities for the use of insect model systems in studying both life span concepts and the fundamental determinants of aging and mortality (197). Third, it exposes entomology to an entirely new body of literature on actuarial techniques and concepts (15, 117, 129) that is potentially of enormous importance to a field concerned, to greater and lesser degrees and in vastly different contexts, with death, survival, and longevity.

The broad aim of this review is to bring into sharper focus the importance of understanding the mortality and longevity properties of adult insects and, in turn, stimulate interest in new types of life table studies that focus on both insect life span and large-scale research methods. The paper has the following four specific objectives: (*a*) to describe the major formulae and models used to analyze the actuarial properties of insects, including life tables, mortality parameters, and

mortality models; (*b*) to summarize the concepts and data on adult insect life spans, including a discussion of basic concepts and terms, within- and between-order differences, and comparative demography; (*c*) to synthesize the literature concerning the ecological and sociological framework within which insect life spans evolved and to identify the major correlates of extended longevity; and (*d*) to suggest new ideas for using demographic concepts in both basic and applied entomology. Although my emphasis is on insects, the techniques, models, and concepts are general and thus apply to a wide range of plant and animal species (79, 104, 106, 161).

INSECTS AS MODEL SYSTEMS

One of the stumbling blocks to the use of model insect systems for studying the fundamental principles of mortality dynamics and aging is the mistaken belief that, because causes of death in different animal species (including humans) are often completely unrelated to causes of death in insects, little can be learned from detailed knowledge of age-specific mortality in insects. This perspective is based on the "theory of the underlying cause"—if the starting point of a train of events leading to death is known (e.g. pathogen in insects or cancer in humans), death can be averted by preventing the initiating cause from operating (49). The problem with this perspective is that death is seen as a single force—the Grim Reaper with the scythe. A more apt characterization that applies to deaths in all species is given by Kannisto (108) who notes that deaths are better viewed as the outcome of a crowd of "little devils," individual potential or probable causes of death, who sometimes hunt in packs and reinforce each other's efforts and at other times are independent. Inasmuch as underlying causes of death are frequently context specific and difficult to distinguish from immediate causes, and their postmortem identification in many species ranges from arbitrary to impossible, studying the causes of death often provides little insight into the nature of aging. If aging is considered to be a varying pattern of vulnerability to environmental insults, then the most important use of model insect systems for research concerning aging and mortality dynamics is in the interpretation of their age patterns of mortality as proxy indicators of frailty (30).

LIFE TABLES

Background

Despite the extensive literature on the physiology, behavior, ecology, and evolution of adult insects, information on life table traits of adults for most species, particularly their mortality and longevity, are anecdotal, derived from small numbers, or nonexistent. Virtually all of the classic papers on insect life tables are concerned either with the life budget for all stages of natural populations (92, 193, 194) or with the net maternity schedule (4, 10, 72) but not with adults per se.

There are three general categories of life tables that are used to gather insect actuarial data: (*a*) "Lotka" life tables, which are tables used to order age-specific birth (m_x) and survivorship (l_x) in columns to compute various population statistics associated with the Lotka stable population model (123), such as net reproductive rate and intrinsic rate of increase (4, 10); (*b*) field life tables, which are tables used primarily to determine an insect's "life budget" by attempting to identify different causes of death and to measure stage-specific attrition (92, 125, 137, 176, 193; also see 9, 51, 52, 94, 194); and (*c*) classical life tables, which are tables that refer to the conventional tools borrowed from demography and the actuarial sciences to analyze the mortality experience of cohorts (58, 151, 173). These distinctions among the different categories of life tables in the ecology and entomology literature are important because they help clarify the distinct purpose of tables in each category. The Lotka life table is used in the context of population fitness (42), the field life table is used in both basic and applied insect ecology to understand how natural populations are regulated, and the classical life table is used primarily to understand the age dynamics of adult populations studied under controlled laboratory conditions. My focus in this paper is exclusively on classical life table methods applied to insects.

Classical Life Tables

The basic life table is one of the most important conceptual and analytical tools in entomological research because it serves as a framework for organizing data on age-specific mortality and survival; provides detailed, transparent descriptions of the actuarial properties of a cohort; generates simple summary statistics such as life expectancy and survival rate; and has a basic form that can be expanded, condensed, or modified for analyzing different types of data such as death-by-cause (26). There are two general forms of the life table: (*a*) the cohort life table, which provides a longitudinal perspective in that it includes the mortality experience of a particular cohort from birth (or eclosion) to death of the last individual; and (*b*) the current life table, which is cross-sectional. For this table, it is assumed that throughout its lifetime a hypothetical cohort is subject to the age-specific mortality rates that prevail for the actual population over a specified time period. The cohort and current life tables are often referred to in the entomology and ecology literature as age-dependent and time-dependent tables, respectively (176). Both types of life tables may be either complete or abridged. The life table functions are computed each time unit (day) in the former but over larger periods (days or weeks) in the latter. Both forms may be used in either a single-decrement table, where all causes of death are lumped, or a multiple-decrement table, where deaths are separated by cause (25).

The Single-Decrement Table

The definitions and formulae for the five main functions of a single-decrement, complete life table (both cohort and current versions) are given in Table 1, and an

TABLE 1 Parameters, description, notation, and formulae for a single decrement life table

Parameter or model type	Description	Notation	Formula
Cohort survival	Fraction alive at age x	l_x	$\frac{N_x}{N_0}$
Age-specific (period) survival	Fraction alive at x surviving to $x+1$	p_x	$\frac{l_{x+1}}{l_x}$
Age-specific (period) mortality	Fraction alive at x dying prior to $x+1$	q_x	$1-\frac{l_{x+1}}{l_x}$
Death distribution	Fraction of original cohort dying between x and $x+1$	d_x	$l_x - l_{x+1}$
Expectation of life at age x	Average number of days remaining to individual age x	e_x	$\frac{1}{2}+\frac{l_{x+1}+l_{x+2}+\cdots+l_\omega}{l_x}$
Standard deviation	Standard deviation for death distribution (d_x schedule)	$S_{\hat{q}_x}$	$\hat{q}_x\sqrt{\frac{1}{D_x}(1-\hat{q}_x)}$
95% Confidence intervals	Confidence intervals for age-specific mortality, q_x	$CI_{95\%}$	$\hat{q}_x \pm 1.96\, S_{\hat{q}_x}$

example application on the medfly (Mediterranean fruit fly, *Ceratitis capitata*) is presented in Table 2. The main functions include cohort survival, l_x; age-specific mortality, q_x; period survival, p_x; expectation of life at age x, e_x; and frequency distribution of deaths, d_x. Two additional life table measures include the standard deviation of the frequency distribution of deaths and the 95% confidence intervals for age-specific mortality, $CI_{95\%}$. Full descriptions of life table methods are contained in references 26, 29, 43, and 139, and the complete medfly life table is in references 26, 27, 38.

MORTALITY

Importance of Age-Specific Mortality

Because each of the life table functions can be derived independently from the original cohort data and all but expectation of life can be used to derive the other functions, it is often inferred that no single function has precedence (176). Although this is true algebraically, it is not true biologically or demographically. The age-specific mortality schedule—the series of probabilities that an individual alive at age x dies before age $x+1$—serves as the foundation for all other functions.

TABLE 2 Complete cohort single-decrement life table for 1.2 million Mediterranean fruit flies, *C. capitata*

Age (days [x])	Number living (N_x)	Fraction surviving (l_x)	Period survival (p_x)	Period mortality (q_x)	Frequency of deaths (d_x)	Expectation of life (days) (e_x)
0	1,203,646	1.00000	1.00000	0.00000	0.0000	20.8
1	1,203,646	1.00000	0.99856	0.00144	0.0014	19.8
2	1,201,913	0.99856	0.99599	0.00401	0.0040	18.9
3	1,197,098	0.99456	0.99492	0.00508	0.0050	17.9
4	1,191,020	0.98951	0.99362	0.00638	0.0063	17.0
5	1,183,419	0.98320	0.99247	0.00753	0.0074	16.1
10	1,105,164	0.91818	0.97018	0.02982	0.0274	12.1
11	1,072,209	0.89080	0.96214	0.03786	0.0337	11.4
20	575,420	0.47806	0.90772	0.09228	0.0441	8.3
21	522,319	0.43395	0.90320	0.09680	0.0420	8.0
50	10,782	0.00896	0.84854	0.15146	0.0014	6.7
51	9,149	0.00760	0.86403	0.13597	0.0010	6.8
80	181	0.00015	0.93370	0.06630	0.0000	20.6
81	169	0.00014	0.92308	0.07692	0.0000	21.0
100	62	0.00005	1.00000	0.00000	0.0000	27.8
101	62	0.00005	1.00000	0.00000	0.0000	26.8
170	2	0.00000	1.00000	0.00000	0.0000	1.5
171	2	0.00000	0.00000	1.00000	0.0000	0.5
172	0	0.00000	0.00000	1.00000	0.0000	0.0

[a]Data from references 27 and 38.

There are at least four reasons why understanding age-specific mortality is important (34). First, death is an event that indicates a change of state from living to dead—a failure of the system; in contrast, survival is a nonevent, inasmuch as it is a continuation of the current state. This orientation toward events rather than nonevents is fundamental to the analysis of risk and hazard rates. Second, an individual can die owing to a number of causes, such as predators, parasites, or disease. Therefore, mortality can be separated by causes of death, thus shedding light on the biology, ecology, and epidemiology of deaths; the frequency distribution of causes; and the likelihood of dying from a particular cause by age and sex. This concept of "cause" obviously does not apply to survival. Third, the value of the mortality rate at a specified age is independent of demographic events at other ages. In contrast, cohort survival to age x(l_x) is conditional on survival through

each of the previous ages, life expectancy at age x (e_x) is a summary measure of the consequences of death rates over all ages greater than x, and the fraction of all deaths (d_x) that occurs at young ages will determine how many individuals remain to die at older ages. This independence of mortality rate relative to events at other ages is important because age-specific rates can be compared directly between ages or between populations, which in turn may shed light on differences in relative age-specific frailty or robustness. Fourth, several different mathematical models of mortality have been developed that provide simple and concise means of expressing the life table properties of cohorts with a few parameters. Therefore, the mortality and longevity of different populations can be compared more readily. In short, age-specific mortality is a useful parameter in insect actuarial research because it is conceptually simple, easily measured, readily modeled, and applicable to all species.

Principles of Mortality

Mortality profiles of a wide variety of organisms have similar characteristics due to similarity in evolutionary selection pressures. For example, the characteristic of higher mortality in males than in females during prime reproductive ages is typical in sexually reproducing animals of a large number of vertebrate and invertebrate species (57). The pattern is an evolutionary result of sexual selective pressure on males and, as such, is a general characteristic of a large number of species. Other observed general characteristics include the variable rate of change in mortality with age (rates that decline after the earliest stage and then increase with age) and a slowing of mortality at the most advanced ages (197). Given such generalities, there are also characteristics of mortality profiles that pertain more specifically to a particular species (or other taxonomic group). Such species-level characteristics are imposed in some general pattern.

The mortality experience of all animals, including insects, can be considered at two levels. The general level exhibits a decline after the youngest stage(s), followed by a trough created by the increase through the reproductive life span (the overall U-shaped trajectory), and a sex differential. The specific level pertains to details of the mortality experience unique to a particular taxonomic group, including the actual probabilities of death by age, inflection points of age-specific mortality, the cause-specific probabilities of death, and the age-specific pattern of the sex differential. The observed mortality pattern is a combination of the evolutionary components of the trajectory (which will be common to a large number of species with overlapping life history characteristics) and the proximate age- and sex-specific factors contributing to mortality under certain conditions. For example, in many species, male reproductive competition selects for riskier behavior and results in deaths due to accidents during early adulthood. The general and specific components of any population's mortality schedule can be determined only through comparative and experimental studies using model systems.

Mortality Functions

Basic Functions

The major mortality parameters and formulae are presented in Table 3. Age-specific mortality, q_x, is a discrete quantity, inasmuch as it expresses mortality as the probability of dying over a specific interval (e.g. from day 10 to day 11 or from week 2 to week 3). The continuous (exponential) analog of this measure referred to as the force of mortality, $\mu(x)$, is defined as the mortality rate representing the limiting value of the age-specific mortality rate when the age interval to which the rate refers becomes infinitesimally short (34). The force of mortality is preferred by demographers and actuaries over age-specific mortality, q_x, because it is not bounded by unity (i.e. 1.0), it is independent of the size of the census (age) intervals, and it forms the argument of numerous mortality models, such as the Gompertz model described below. The analytical relationship between the discrete form of mortality, q_x, and its continuous expression is and $\mu(x) = -\ln p_x$ and $p_x = e^{-\mu(x)}$.

Additional and Related Parameters

Central Death Rate The parameter of central death rate, also known as the age-specific death rate, denoted m_x, is defined as the number of deaths occurring in a specified period in a specific age category divided by the population at risk. The central death rate is not a probability but rather an observed rate—the number of individuals that die relative to the number at risk. It is essentially a weighted average of the force of mortality between ages x and $x + 1$. For example, the central death rate at age 10 for the medfly in Table 2 is $m_{10} = 0.03027$, whereas the probability of dying in the age interval 10 to 11 is $q_{10} = 0.02982$. The parameter central death rate is used in computing the life table aging rate.

Life Table Aging Rate The parameter life table aging rate, denoted k_x, is defined as the rate of change in age-specific mortality with age (101). The measure is based on a relative rather than an absolute rate of change in mortality with age. Life table aging rate is an age-specific analog of the Gompertz parameter, b, since it is a measure of the slope of mortality with respect to age. However, unlike the Gompertz parameter, which assumes constancy of the mortality slope typically over a large age interval, the life table aging rate examines the change over short intervals. Example computations of k_x from the medfly data in Table 1 for ages 4 and 50 are $k_4 = 0.166304$ and $k_{50} = -0.08817$, which indicate that mortality is increasing at >16% per day at day 4 but decreasing at ~8.8% per day at day 50. Additional perspectives for the life table aging rate applied to the medfly and to the cowpea weevil, *Callosobruchus maculatus*, are presented in references 32 and 180.

Life Table Entropy The parameter entropy, denoted H, is a measure of heterogeneity of the distribution of deaths in a cohort. If all individuals die at exactly the same age, the shape of the survival schedule, l_x, is rectangular and $H = 0$. If all

TABLE 3 Selected mortality parameters and formulae, change indicators, and scaling models

Parameter or model type	Description	Notation	Formula or model
General mortality parameters			
Force of mortality	Instantaneous mortality rate	$\mu(x)$	$-\frac{dl(x)}{l(x)dx}$
	Estimation formula 1	μ_x	$-\ln\ p_x$
	Estimation formula 2	μ_x	$-\frac{1}{2}(\ln\ p_{x-1} + \ln\ p_x)$
	Estimation formula 3	μ_x	$\frac{1}{2n}\ln_e\left(\frac{l(x-n)}{l(x+n)}\right)$
Central death rate	Number dying at age x relative to number at risk	$\mathrm{m_x}$	$\frac{q_x}{1-\frac{1}{2}q_x}$
Life table aging rate	Rate of change in age-specific mortality with age	$\mathrm{k_x}$	$\ln(m_{x+1}) - \ln(m_x)$
Mortality smoothing	Smoothing for discrete form	$\hat{q}_x$	$1 - \left[\prod_{y=x-n}^{x+n} p_x\right]^{-(n+1)}$
	Smoothing for continuous form	$\hat{\mu}_x$	$\frac{1}{n+1}\sum_{y=x-n}^{x+n}\mu_y$
Average daily mortality	Daily mortality given expectation of life, e_0	$\overline{\mu}$	$\frac{1}{e_0}$
Entropy	Days gained per averted death	H	$\frac{\sum_{x=0}^{\omega} e_x d_x}{e_0}$
Mortality change indicators (cohort A vs cohort B)			
1a	Mortality increase/decrease (relative)	—	$\frac{\mu_x^A}{\mu_x^B}$
1b	Mortality increase/decrease (absolute)	—	$\mu_x^A - \mu_x^B$
2a	Survival increase/decrease (relative)	—	$\frac{l_x^A}{l_x^B}$
2b	Survival increase/decrease (absolute)	—	$l_x^A - l_x^B$
3a	Life-days gained/lost at age x (relative)	—	$\frac{e_x^A}{e_x^B}$
3b	Life-days gained/lost at age x (absolute)	—	$e_x^A - e_x^B$
Mortality scaling			
Proportional	Age-independent scaling (δ = scaling factor)	$\hat{\mu}_x$	$(1+\delta)\mu_x$
Age-specific	Age-dependent scaling (δ_x = scaling factor)	$\hat{\mu}_x$	$(1+\delta_x)\mu_x$

individuals have exactly the same probability of dying at each age, the shape of the survival schedule exponentially decreases, and $H = 1.0$. Values of $H < 0.5$ suggest that the survival schedule is convex, and values of $H > 0.5$ suggest that the survival schedule is concave. There are three different interpretations of H (195): (*a*) the proportional increase in life expectancy at birth if every individual's death were averted at the first instance; (*b*) the percentage change in life expectancy produced by a reduction of 1% in the force of mortality at all ages; and (*c*) the number of days lost owing to death per number of days lived. The H value for the medfly life table presented in Table 2 is 0.439, indicating a slightly convex survival schedule. The sex-specific medfly H values (37) are 0.477 and 0.393 for females and males, respectively. Thus, the entropy values indicate that the shape of the survival schedule for male medflies is more convex (rectangular) than the survival schedule for female medflies. In short, the entropy parameter provides a useful summary measure for characterizing differences in shapes of survival curves among cohorts.

Average Lifetime Mortality The inverse of life expectancy at birth, e_0, is the average mortality experienced by the cohort, denoted $\overline{\mu}$. More generally, the inverse of life expectancy at age x, e_x, is the average mortality experienced by the cohort beyond age x, denoted $\overline{\mu}_x$. Example values of $\overline{\mu}_x$ from the medfly data presented in Table 2 for ages 50 and 100 days reveal the peak and decrease in overall pattern of age-specific mortality: $\overline{\mu}_{50} = 0.150$ and $\overline{\mu}_{100} = 0.036$.

Mortality Change Indicators Kannisto (109) described several different mortality change indicators, some of which are included in Table 3. These indicators reflect both the relative (proportional) and absolute (arithmetic) differences in three parameters—mortality, survival, and expectation of life. Expressing differences in mortality between two cohorts (mortality change indicator 1a [Table 3]) as a proportion reflects relative changes with age and is particularly useful when mortality is low and thus absolute differences are small. However, proportional differences at low mortality rates may be substantial (i.e. an order of magnitude difference between $q_x = 0.0001$ and $q_x = 0.001$) and therefore better highlight significant differences in the underlying biology. In contrast, absolute differences in mortality terms (indicator 1b [Table 3]) are useful when absolute risks are high (i.e. small proportional differences between $q_x = 0.4$ and $q_x = 0.5$ but a substantial absolute difference). Similar reasoning applies to both relative and absolute differences between two cohorts in survival and expectations of life. For example, relative differences are especially useful when comparing these properties at old ages, when the probabilities of survival and the remaining life expectancies are both quite small. However, absolute differences may be more useful at the younger ages, when survival and life expectancies are greater.

An important use of both relative and absolute differences in age-specific mortality is in identifying mortality crossovers (129)—an attribute of the relative rate of change and level of age-specific mortality rates in two populations. One

group is "advantaged" (i.e. lower relative mortality) and the other "disadvantaged" (i.e. higher relative mortality). The disadvantaged population must manifest age-specific mortality rates markedly higher than the advantaged population through middle age, at which time the rates change. An example of a male-female mortality crossover in the medfly is presented in references 32 and 37.

Mortality Scaling Observed mortality (μ_x) can be scaled in one of two ways to create a modified mortality schedule ($\hat{\mu}_x$): proportional scaling and age-specific scaling (Table 3). Proportional scaling changes the level of observed mortality by a constant amount at all ages, whereas age-specific scaling changes mortality at each age by a specified proportion (26).

Threshold Mortality

A major concern of any study designed to estimate the actuarial rate of aging in a cohort (i.e. the Gompertz parameter, b) is the decrease in sample size at older ages due to attrition. However, this problem of insufficient sample size may also apply to the measurement of mortality at young ages even when the number of individuals at risk is at or near the initial number, n. This has been referred to as the "left-hand boundary problem" (157) that occurs whenever the "actual" mortality rate is $<1/n$. For example, a mortality rate of $\mu = 0.001$ cannot be detected with a sample size of $n = 100$ because when a single individual dies the estimate will be $\mu = 1/100 = 0.01$. The main point is that, even though the number of individuals at risk is highest at the youngest ages, a sample size constraint still exists inasmuch as mortality is often quite low at young ages and thus lower than $1/n$. In general, in studies with small samples sizes (number at risk), the observed death rates do not provide reliable estimates of the underlying distribution of the probability of death.

Mortality Models

There are three principal justifications for postulating an analytic form for mortality and survival functions (15). First, many phenomena in the physical sciences can be explained efficiently by simple formulae. Therefore, some authors have suggested that animal survival is governed by simple laws. Second, it is easier to communicate a function with a few parameters than it is to communicate a life table with several hundred parameters and probabilities. Third, a simple analytical survival function is easily estimated using a few parameters based on the original determination from mortality data. Six of the most frequently used mortality models in demographic and gerontological research are presented in Table 4 along with the corresponding expression for age-specific survival and associated parameters (29).

de Moivre Model

Mortality rate in the de Moivre model (173) equals the inverse of the difference between maximal and current age. Thus, mortality tends to approach unity as age

TABLE 4 Six of the major mortality models used in actuarial research (from Carey 1999)

Model	Description	Notation	Formula
DeMoivre[a]	Mortality model	μ_x	$(\omega - x)^{-1}$
	Survival model	l_x	$1 - \frac{x}{\omega}$
Gompertz[b]	Mortality model	μ_x	ae^{bx}
	Survival model	l_x	$\exp\left[\left(\frac{a}{b}\right)(1 - e^{bx})\right]$
	Mortality doubling time	MDT	$\frac{\ln(2)}{b}$
	Maximal age	$T_{\max}$	$\frac{1}{b}\ln\left\{1 + \frac{b(\ln N)}{a}\right\}$
Gompertz-Makeham[c]	Mortality model	μ_x	$ae^{bx} + c$
	Survival model	l_x	$\exp\left[\left(\frac{a}{b}\right)(1 - e^{bx}) - cx\right]$
Exponential[d]	Mortality model	μ_x	c
	Survival model	l_x	$\exp[-cx]$
Weibull[e]	Mortality model	μ_x	ax^n
	Survival model	l_x	$\exp\left[-\left(\frac{a}{n+1}\right)x^{n+1}\right]$
Logistic[f]	Mortality model	μ_x	$\frac{nx^{n-1}}{g^n + x^n}$
	Survival model	l_x	$\left(1 + \left(\frac{x}{g}\right)^n\right)^{-1}$

[a] ω, oldest age; survival can also be expressed as $l_x = a - bx$ where $a = 1.0$ (radix) and $b = 1/\omega$.

[b] a, initial mortality rate; b, "Gompertz" parameter.

[c] c, age-independent (accidental) mortality.

[d] Constant hazard rate, c.

[e] a, location paramter; n, shape parameter; $n > 0$.

[f] g and n are parameters to be fitted; both parameters control shape and location.

approaches a putative maximum, ω. The resulting survival schedule is a linearly decreasing function of age from 1.0 at age $x = 0$ to zero at age $x = \omega$. The advantage of this model is its simplicity—the model is transparent, easily understood, requires only a single parameter (ω), and produces a linear survival function. The assumption that survival is a linear function of age is often applied over short age intervals.

Gompertz Model

The assumption of the Gompertz model (89) is that mortality beyond the age of sexual maturity (or another predetermined age) is an exponentially increasing function of age. The model contains two parameters—the initial mortality rate, a,

which denotes mortality at the youngest age class in the specified age interval, and the exponential rate of increase in death rate, b. The latter parameter denotes the age-specific slope of the mortality function and is often referred to as the "Gompertz parameter." The mortality trajectory for the Gompertz model is exponential, and its survival trajectory is sigmoidal. The Gompertz model provides two useful formulae (77, 78): mortality doubling time, defined as the time required for the mortality to increase by twofold, and estimated maximum life span, denoted $T_{\max,}$, defined as the age at which a population subject to Gompertzian mortality rates has diminished to one survivor.

Makeham Model

The Makeham model (127) is also known as the Gompertz-Makeham model because it represents an improvement in the Gompertz model rather than a separate concept. Makeham found that overall mortality levels could be better represented if a constant term for $\mu(x)$ was added to the Gompertz formula to account for causes of mortality not dependent on age (i.e. accidental deaths). There is no analogous transformation for the Gompertz-Makeham equation in which linear regression can be used to estimate the parameter c. Rather, parameter c has been suggested (69) using trial and error after first estimating parameters a and b from the Gompertz regression equation and then adjusting c until the closest approach to a straight line is attained.

Exponential Model

The exponential model is effectively the Gompertz-Makeham model without the Gompertz component. In other words, it accounts for only the accidental deaths, c, and thus assumes age-independent mortality. Because mortality is constant with age in the exponential model, its plot is simply a horizontal line intercepting the y axis at c and extending to the right. The survival function decreases exponentially with age.

Weibull Model

Whereas the de Moivre, Gompertz, and Makeham models were derived in an actuarial context, the Weibull model was developed in the context of reliability engineering (201). The Weibull model is a generalization of the exponential model (117) but, unlike the exponential model, does not assume a constant hazard rate and thus has broader application. The Weibull model has two parameters: the value of n determines the shape of the distribution curve, and the value of a determines its scaling. Note that the Weibull hazard function increases if $n > 0$, decreases if $n < 0$, and is constant if $n = 0$.

Logistic Model

The logistic model was introduced to demography by Pearl & Reed (152), who used it to estimate the ceiling or asymptote of the U.S. population. Wilson (203) showed that the logistic model provided a good fit to the results of the large-scale

medfly study (38). A model comparable to the logistic model is the Perks model (153), which also exhibits leveling-off behavior at older ages.

Fitting Mortality Data to the Gompertz Model

Fitting models to data is useful in several contexts (111)—for smoothing data, thus making the data easier to handle by removing irregularities and inconsistencies; for increasing precision on the assumption that the "real" pattern underlying the observation is a smooth curve; for aiding in drawing inferences from incomplete data, such as interpolation or extrapolation; and for facilitating comparisons between two cohorts using a small number of parameters.

There are two main analytical methods for fitting the Gompertz model [$\mu(x) = ae^{bx}$] (29). In the first method, least-squares fit, the Gompertz equation can be made linear by taking the natural logarithm of each side, yielding $\ln \mu(x) = a + bx$. Thus the slope, b, and the intercept, a, can be estimated by regressing the logarithms of the mortality rates on age using standard linear-regression techniques. An alternative technique is simply to use a nonlinear least-squares statistics program to fit the nonlinear (original) model to the data. The second method is maximum likelihood. The method of least squares is designed to estimate parameter values of a model by minimizing differences between the observed mortality rates and the rates predicted from the mortality model (i.e. hazard schedule) containing these parameters. As described in the previous section, this approach for estimating the parameters of the Gompertz model is based on age-specific mortality rates. In contrast, the maximum-likelihood method for estimating the parameters is based on the age-specific density function of deaths—the frequency distribution of deaths, d_x. Methods for fitting data to the Gompertz model using maximum likelihood techniques are given in references 29 and 84, and sample sizes needed for reliable estimates of the Gompertz parameters are presented in reference 171.

INSECT LIFE SPANS

Life span is more of a biological concept than an actuarial or a statistical one because it refers to the duration of a species' life course rather than to either a probability or an expectation (of life). One of the difficulties with identifying insect life span patterns is that, unlike the literature on mammals and most other vertebrate groups, which contains considerable information on the life spans and mortality patterns of different species (140, 158), the entomology literature contains little insect life span information. Indeed, no database is available on the longevity of adult insects, and none of several mainstream texts on insect ecology (132, 156) address issues concerned with the life spans of adult insects.

Life Span Concepts

Whereas the standard life table functions such as life expectancy, cohort survival, and age-specific mortality are clearly defined and readily measured, life span is

typically characterized in vague, theoretical terms (77) such as "...the limit beyond which, even under the most favorable conditions, the members of a given species cannot survive"; "...its value cannot be easily altered (61); or "the potential number of years an organism might survive if exogenous conditions were ideal" (128). The terms "limit" and "potential years survived" are frequently used synonymously with "maximal life span potential" (5, 174) and are typically estimated using record longevity for the species (i.e. oldest age recorded).

These standard definitions of life span are problematic for at least three reasons. First, for no insect species does there exist empirical evidence showing that there is one single age beyond which no individual can live. Thus, maximal age as a life span proxy is ill defined; it is often simply an outlier with little relevance to the ecology and evolutionary biology of the species. Caughley (40) notes that maximal age is an inappropriate general concept because, as he states, "An animal dies before the age of infinity, not because it cannot pass some bounding age but because the probability of its riding out the ever present risk of death for that long is infinitesimal." Second, none of the definitions of life span consider either environmental conditions (e.g. in laboratory or wild) or any of a number of life history characteristics such as the sex, biotype, or caste of the individual. These factors are important because they provide biological and demographic contexts, both of which influence life span. Third, the definitions do not consider the number of individuals ever observed. This is important because records for species in which the life spans of large numbers of individuals have been observed will be significantly greater than the corresponding figure for a species with the same longevity but represented by a few dozen individuals (87).

In short, it is meaningless to consider life span for any species without considering environmental, ecological, and evolutionary contexts, and it is incorrect to believe that life span for any species is a single fixed age. The life span of a monarch butterfly (*Danaus plexippus*) is approximately 2–3 months when it is in the reproductive mode during the summer months but 6–10 months when it is in the migratory mode during the winter months (90). Similarly, the life span of *Drosophila melanogaster* should be considered in the range of 40–60 days in the wild (13) but perhaps 90–120 days in the laboratory (55). Insect life spans are not only indeterminate but also changeable in response to different ecological conditions.

Summary of Insect Life Spans

A summary of the range of life spans in adult insects for the major orders of Insecta and for the Arachnida is presented as a schematic diagram in Figure 1 with the primary data sources cited in the legend. Several aspects of this figure merit comment. First, the between-group variation in life span is enormous. Whereas the life spans of mayflies are typically only a few days (18, 65, 105), the life spans of some species of termite and ant queens, tarantulas, and soft ticks may be up to several decades (204). The 5000-fold difference in the life spans of adult insects

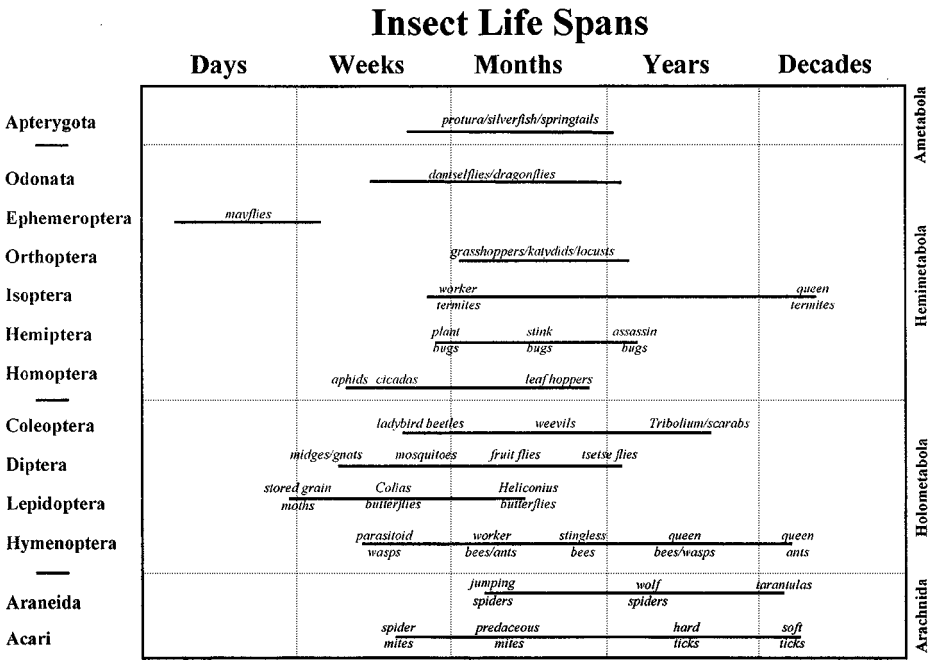

Figure 1 Longevity of insects and selected acarina (1, 3, 6, 7, 11, 14, 16–23, 44–46, 50, 53, 54, 56, 59, 60, 62, 64–68, 71, 76, 82, 85, 86, 88, 90, 91, 97–100, 102, 105, 110, 116, 118, 119, 122, 124, 131, 133–136, 142, 143, 154, 155, 162, 164, 165, 167–169, 175, 177, 178, 180, 183, 185, 187, 191, 192, 200, 202, 204–207).

can be contrasted with the 60-fold difference in the life spans of mammals—from small rodents that live $\leq$2 years to humans that live $\leq$120 years (77).

Second, the phylogenetic legacy of a species has an important bearing on its potential life span. This is apparent from the lack of extreme longevity in any species of Ephemeroptera, which live $\leq$1–2 weeks, or of Lepidoptera, which typically live no more than a few weeks (although some *Heliconius* species can live $\leq$5–6 months). Presumably the frail adult body plan of mayflies, butterflies, and moths and the inability of most species to acquire protein food preempt the possibility of extreme life spans. In contrast, most species of Coleoptera are relatively long-lived, with some life spans exceeding 3–4 years. The heavy sclerotization and chewing mouth parts for acquiring protein food apparently preadapt beetles for extended longevity.

Third, parental care, monogamy, and eusociality (at least for queens) are all strongly associated with extended life spans. For example, the life span of brood-caring, monogamous dung beetles (Scarabaeidae) is >3 years (23, 66), and the life span of species of subsocial beetles (Passalidae) is >2 years in the wild and 5 years in captivity (168). Insect queens in general (e.g. *Apis* spp.) but subterranean insect

queens in particular are extraordinarily long-lived—both ant queens and termite queens hold longevity records for all insects, with life spans exceeding 30 years for some species (14, 99, 154). Many species invest heavily in parental care and thus have extraordinarily low lifetime reproduction (70), including tsetse flies (*Glossina* spp.), which can live >8–10 months (185), and sheep keds (Hippoboscidae), with life spans of >5 months (118).

Fourth, species that are subject to uncertain environments frequently exhibit extended longevity. Examples include the satyrine butterfly, *Mycalesis perseus*, in Australia, which remains reproductively dormant for >5 months in 1 year to wait out a dry period (16); many tick species with life spans of 10–20 years (76, 205); and some species of primitive spiders, including the orthognath purse-web spider, *Atypus*, which can survive 7 years, and large tarantulas, which can live to >20 years (17, 82). Long life span as an adaptation for increasing fitness in uncertain environments is supported by empirical evidence in other groups (184) as well as by mathematical models (188, 189)—at least some individuals must be capable of surviving long, unpredictable spells of unfavorable conditions to ensure population replacement.

Fifth, species that must find food sources or seek out hosts that are scarce and/or widely dispersed tend to be long lived. For example, the life span of cave species of ground beetles range from 1–4 years, with one cave-inhabiting species (*Laemostenus schreibersi*) living up to 6.5 years (124); the life span of many species of *Heliconius* butterflies, which must seek out widely-dispersed host plants while laying only a few eggs at a time, is extraordinarily long for lepidopterans, sometimes exceeding 4–6 months (68, 88). Euglossine bees that must forage great distances for widely dispersed host plants or food sources are capable of living for 6–8 months (103, 165). Many species of polyphagous tephritid fruit flies exhibit extended longevity tailored to resources that are unpredictable in time and space (80, 81). Most blood-feeding hemipterans that are subject to conditions of unpredictable food resources are also quite long-lived, including the cimicids (bed bugs) and the reduviids (assassin bugs). Many species in these groups are capable of living up to 18 months (22, 118).

The factors that appear to favor the evolution of extended longevity in insects can be grouped into two broad categories and several subcategories (Table 5):

1. Environmental: This category includes insects whose life histories involve scarce food and/or widely dispersed habitats (e.g. *Heliconius* butterflies, orchard bees, and cave species), uncertain resource availability, and/or environmental conditions that are predictably adverse part of the time (many blood-feeding insects and desert species);

2. Kinship and cooperation: This category includes species that exhibit extensive parental investment (e.g. tsetse fly, *Glossina palpalis* and louse flies, *Hippobosca variegata*), extensive parental care [e.g. the burying beetle, *Nicrophorus vespillo*, (48, 204)]; progressively provisioning wasps such as *Bembix* (73, 74, 169), kin-selected nonsocial species such as

TABLE 5 Classification of factors that favor the evolution of extended life span in insects and arachnids and selected example species or groups

Factors	Examples
Environmental	
Food scarce or widely dispersed	*Heliconius* spp., cave dwellers, orchid bees (Euglossidae)
Uncertain or adversity	*Polistes* queens, soft ticks, treehole mosquitoes, *Tribolium*, monarch butterflies (migratory phase), *Locusta*, tarantulas, cimicids (bed bugs)
Kinship and cooperation	
Parental care/monogamy	Tsetse fly, dung beetles, ambrosia beetles, *Bembix* spp. (progressive provisioning wasp)
Nest helpers/kin selection	*Polistes* spp., aposematic saturniid moths, bumble bees, primitive ants
Primary reproductives (eusocial)	Queen termites, ants, bees, wasps

aposematic saturniid moths that experience a long postreproductive period (12), and primary reproductives in eusocial species [e.g. ant and termite queens (110, 204)].

GENERAL BIODEMOGRAPHIC PRINCIPLES

This section summarizes the general actuarial patterns and describes some of the key concepts concerning insect mortality, longevity, and life span, many of which were taken from studies on the Mediterranean fruit fly summarized in references 28 and 34 with methods described in references 33 and 38.

Mortality Slows at Older Ages

The results of the study described in reference 38 on 1.2 million medflies revealed that mortality slowed at older ages and therefore that mortality was distinctly non-Gompertzian. Mortality deceleration at older ages also was reported in the companion article on mortality in *D. melanogaster* Meigen by Curtsinger et al (55), as well as in a number of subsequent *Drosophila* mortality studies (47, 84, 159, 182) and in the cowpea weevil, *Callosobruchus maculatus* (179, 181). That mortality slows at older ages is important because it reveals that the Gompertz model is not universal and it forces biologists to revisit the definition of senescence as an ever-increasing probability of death with age, suggesting that a species-specific maximal age does not exist.

Female Longevity Advantage Is Not Universal

Many biologists, including ecologists, gerontologists, and biodemographers, believe that the female advantage in life expectancy is a universal law of nature

(95, 96, 186). Carey & coworkers (37) tested whether a female longevity advantage exists for *C. capitata* and discovered that the answer was not straightforward—males exhibited a higher life expectancy at eclosion, but females were fourfold more likely than males to be the last to die (37). They concluded that there were at least three reasons why it is impossible to state unequivocally that either males or females are longer lived (31, 32, 37): (*a*) although longevity can be characterized in different ways (e.g. life expectancy at eclosion, life expectancy at day 30, age when 90% of the original cohort is dead [life endurancy], and maximal life span), one measure of longevity often favored one sex whereas another measure favored the other sex; (*b*) considerable between-cohort variation existed for a given longevity measure; for example, neither male nor female longevity was greater in all of the cages regardless of the measure used; (*c*) relative longevity for the two sexes depended on the environment in which they were maintained or the treatment to which they were subjected; for example, expected life spans for males and females were similar if flies were maintained in solitary confinement but favored males if the flies were maintained in grouped cages. In short, sex-specific mortality responses and, in turn, male-female life expectancy differences cannot be predicted a priori—a female longevity advantage is not universal.

Cost of Reproduction

Cost of reproduction refers to the concept that an increment in reproduction at some age may result in a decrement in expected reproduction and an increase in mortality at later ages (160). Although a trade-off between reproduction and survival has been shown to exist in virtually all insect studies (8, 163), most of the systematic research in this context has been done with fruit flies. Three examples of cost of reproduction follow. First, Partridge (144) showed that high rates of early reproduction in males shorten their life spans. This was used to develop the concept of reproductive risk (149)—an individual that reproduces at an elevated rate incurs an increased probability of death at the time of reproduction but suffers no lasting harm. Reproductive risk contrasts with an acceleration of aging, for which future reproductive prospects are permanently damaged (144, 145). Second, considerable research has also been conducted on the cost of reproduction in *Drosophila* females, including (*a*) production of eggs (148) and (*b*) nonmating exposure to males (146). Both of these factors reduce life expectancies of females (83, 147). Sperm appear not to be involved, because the cost of mating for females is the same in females mated to mutant spermless males (41). The entire cost of mating for females is instead caused by receipt of protein components of the male seminal fluid at mating (41). Third, recent research on *C. capitata* aging (36) revealed that females may experience two physiological modes of aging with different demographic schedules of fertility and survival: a waiting mode, in which both mortality and reproduction are low; and a reproductive mode, in which mortality is low at the onset of egglaying but accelerates as eggs are laid. *C. capitata* that switch from waiting to reproductive mode due to a change in diet (from sugar to full protein diet) survive longer than those kept in either mode exclusively. The switch from

waiting mode to reproductive mode initiates egglaying and reduces the level of mortality but increases the rate of aging.

Mortality Trajectories Are Facultative

The term "facultative" is used in biology to describe life history traits that are affected by environmental conditions. For example, clutch size in some birds, diapause in insects, and diet selection in many animals are all considered facultative. I suggest that the term also applies to mortality patterns in the medfly and most other species because there exists no unique pattern—the specific trajectories frequently depend on the environmental conditions. One of the most compelling findings emerging from the collection of life table studies on the medfly, and one that was not evident even after the first large-scale study was completed (38), is that the female mortality patterns are extraordinarily plastic. The reason this plasticity was not evident from the first series of studies is because none involved manipulations that altered the physiology and/or behavior of the flies. It is now apparent that manipulations that affect components of a fly's life history, such as irradiation, diet, or mating, have a profound effect on the trajectory of mortality in females and less of an effect on male trajectories (35, 138). Thus, it is doubtful that the mortality pattern for any species exhibits either a characteristic "signature" (141) or an "irreducible" mortality component (190)—a component of mortality that can never be reduced by any means.

Demographic Selection Shapes Mortality Trajectory

As populations age, they become more selected because groups with higher death rates die out in greater numbers than those with lower death rates, thereby transforming the population into one consisting mostly of individuals with low death rates (31, 198). The concept of subgroups endowed with different levels of frailty is known as demographic heterogeneity, and the winnowing process as the cohort ages is referred to as demographic selection. The actuarial consequence of cohorts consisting of subcohorts, each of which possesses a different level of frailty, is that the mortality trajectory of the whole may depart substantially from Gompertz rates even though each of the subcohorts is subject to Gompertz mortality rates. Vaupel & Carey (196) fitted an observed *C. capitata* mortality pattern with mixtures of increasing Gompertz curves and demonstrated that 12 subgroups were sufficient to capture the observed pattern of medfly mortality using a range of frailty values and initial proportions of subcohorts. The point is that demographic selection winnows the frail and leaves the robust and thus shapes the mortality trajectory as cohorts age.

Life Span Is Indeterminate

One of the most compelling concepts in ecology and demography is maximal length of life. The validity of this concept is viewed by many as self-evident because different species exhibit different life expectancies. All individuals eventually die

before the age of infinity, and therefore each of the different species must possess unique and finite maximal ages. Kannisto (107, 108) noted that the problem with this concept is that our knowledge of the nature of mortality makes it difficult to accept the notion that there is a single age that some individuals may reach but that none has any chance of surviving. He views the only valid alternative as the existence of an asymptote which the probability of dying approaches and that may or may not be near 100%. Manton & Stallard (130) noted that declines in the rate of increase of mortality with age for male and female cohorts in the United States are inconsistent with a fixed life span limit. In general, studies of *C. capitata* suggest that this species and most likely other species as well do not appear to have a characteristic life span. Indeterminacy is a concept fundamentally different from limitlessness, and therefore insect life spans should be considered over a range of ages rather than as a single age.

Longevity Is Adaptive

In evolutionary biology, an adaptation is a characteristic of organisms whose life history traits are the result of selection in a particular functional context. Just like different birds' beaks are adaptations for exploiting different niches that must be balanced with the other traits, such as body size and flight propensity, the longevity of an animal is also an adaptation that must be balanced with other traits, particularly with reproduction. The variations in the relationship between reproduction and longevity can make sense only when placed within the context of such factors as demographics, duration of the preadult period, number of offspring, and the species' ecological niche—the organism's overall life history strategy. Indeed, the longevity potential of members of a species is not an arbitrary or random outcome of evolutionary forces but rather an adaptive one that must fit into the broader life history of the species.

IMPLICATIONS

Whereas many new developments in disciplines such as statistics, genetics, and computer science are often quickly integrated into entomological research, this has not been the case for the use of new demographic and actuarial concepts in entomology during the last 4–5 decades. This is unfortunate because many entomological subdisciplines, such as medical entomology, pest management, and insect ecology, rely on basic actuarial concepts. Therefore, both researchers and practitioners could benefit from a greater awareness of biodemographic principles. Several examples of novel and innovative ways in which biodemographic techniques could be used in different entomological contexts will serve to underscore this point.

Vector Biology

The vectorial capacity of an arthropod is strongly affected by its longevity—the longer a vector lives, the greater the expectation that it will become infective

and transmit the disease (63, 126). Whereas the standard formula for computing vectorial capacity assumes constant (age-independent) mortality, a new formula could be developed that incorporates a more realistic and potentially important component of age-dependent mortality. It is virtually certain that incorporating an age dynamic into the vectorial capacity concept will have important implications in vector biology. For example, a leveling off or decrease in age-specific mortality at older ages will imply that a long survival tail may be creating a small but important reservoir for infected vectors. Alternatively, a rapid rise in vector mortality early in adult life might significantly decrease the expectation of life and consequently reduce the probability of pathogen transmission by arthropods in that population.

Estimation of Field Mortality

A new technique for estimating the mortality of insects in the field might be developed that involves the use of mark-recapture studies of different ages of cohorts to create a "synthetic cohort" (172). Mortality rates could be derived from recapture rates of released individuals of different ages measured over a short time period (e.g. 1–2 days). For example, a study might involve the simultaneous release of 20 cohorts ranging in age from young to old and differing in age in 1- or 2-day increments. Differences in observed mortality patterns between individuals of different ages that are released simultaneously and subsequently recaptured after 24–48 h would be more reliable than estimates based on the recapture rates through time of individuals of the same age released all at once, as is the current standard practice. The use of synthetic cohorts is standard practice for creating so-called "current" life tables for contemporary human populations (15).

Combining Laboratory and Field Studies

Many field entomologists consider life table studies in the laboratory of little value because the insects are maintained under "unrealistic" conditions. Yet it is extraordinarily difficult to make even crude estimates of the age-specific mortality rates of natural populations of insects in the field (125), much less attempt to identify any of the nuances in age-related patterns. Thus, another innovative approach for estimating age-specific mortality trajectories in the field could involve creating a "family" of mortality schedules adjusted (via scaling models in Table 3) to the levels consistent with the life expectancies and/or cohort survival schedules observed in mark-recapture or field cage studies. This kind of hybrid method of estimating field mortality rates would capture both the inherent age-dependency patterns of mortality observed in laboratory studies and the mortality levels to which field populations are subjected.

Sterile Insect Technique

The sterile insect technique is a biological pest control method in which sterilized members of a target insect species are released into an infested region in order

to dilute the wild population's reproductive capacity (114). This technology is inherently demographic (39, 121) inasmuch as the release rate represents a cyclical "pulse" of a particular cohort (release) and each sterile cohort is subject to an age-specific mortality rate. Populations of sterile insects will then peak on the release days and, due to attrition, drop exponentially through time until the next release day. A demographic framework for the sterile-insect technique would include (*a*) periodicity of sterile release (e.g. weekly or biweekly), (*b*) number of insects per release cycle, and (*c*) age-specific mortality in the field, which would allow computation of (*d*) the estimated number of insect days per release cycle (i.e. standing crop). An estimate of the number of insect days per release cycle would complement the standard measures of fly quality because this measure combines two rates—factory production and field survival.

Demography of Social Insects

Despite the recognized importance of demography in understanding the biology of social insects (204), there is a paucity of research involving the use of formal demographic techniques in analyzing individual and colony properties. Demographic methods can be used to estimate the average death rate of workers (d_w) from their life expectancy, e_0, (i.e. $d_w = 1/e_0$) and, in turn, the number dying each day that need to be replaced ($N \times d_w$) (26). A number of parallels also exist between the demographic theory of kinship from demography and the demography of social insects from entomology. These include concepts and analytical tools for addressing questions concerning the probabilities of living ancestors (e.g. mothers and grandmothers) and colineal kin (sisters and aunts) or the length of time a pair of individuals (founding king and queen termite) will both be alive (113).

Age as Order; Dose as Age; Death as Metaphor

Many demographic concepts can be generalized, and therefore tools such as life table techniques can be brought to bear on a wide range of seemingly unrelated biological problems. For example, the concept of "event histories" can be applied to all age patterns of occurrences of similar life history events (e.g. reproduction, mating, and death) and all events can be classified as recurrent (reproduction) or nonrecurrent (death). However, recurrent events such as reproduction can be reclassified as nonrecurrent events by specifying order—just as an individual cannot pass to age 2 without first experiencing age 1, an individual cannot transition from parity 2 without first experiencing parity 1. Thus, parity can be substituted for age, and a parity-specific life table can be constructed (75). Chemical dose is also an age analog, and therefore probit analysis used in toxicology is conceptually identical to life table analysis (24). Similarly, life table methods can be used to analyze any data in which a change of state is dichotomous, including from virgin to mated, from noninfected to infected, and from nondiapausing to diapausing. This underscores the unity of the cohort concept in particular (166) and demographic methods in general (93).

CONCLUSION

Demographic studies of insects can both benefit from and contribute to developments in the emerging field of biodemography. Mortality, survival, longevity, and life span are all concepts that have long histories in the discipline and will certainly maintain their empirical and conceptual primacy in organismal biology in the future. Indeed, the whole organism is considered by many to be the quintessence of biological relevance—every discovery at lower levels of biological organization (molecular and physiological) that is concerned with insect control, aging, or ecology must ultimately be tested at the level of the whole organism. Thus, the future of entomological research focusing on manipulation of insect populations should belong to a strategy founded on explaining the biological mechanisms that influence insect vital rates and linking this understanding to the fundamental actuarial and demographic properties of populations.

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