Insect Dynamics in Heterogeneous Environments and the Relevance of Retrospective Life Tables and Cyclic Budgets: An Integrated Approach[1]

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Abstract The analysis of cumulative, time-independent survivorship data for insect populations as obtained by using trace methods and their use in constructing retrospective life tables are reviewed. The reliability of the estimates obtained by such methods is examined by placing empirical data in the broader context of a model of the spatiotemporal dynamics of age-structured populations in heterogeneous environments. For the case of stable, average populations, the information contained can be displayed as a cyclic budget quantifying the mortality during development, the sex ratio and the fecundity as key (*k*) factors. Because of the time-independent nature of the display, prereproductive losses of adult females, typically those due to migration and failure to find reproductive resources, can be interpolated. The whole, therefore, can be viewed as a numerical description of a life-history strategy. The mathematical relationship between the "true" mortality function, which in general depends on age, time, population density, and location, and the age-dependent "apparent" mortality as determined from trace methods for a particular sampling area is established. These apparent death rates are then correlated with the *k*-factors appearing in the budget.

Key Words life-history strategy, cyclic budget, life table, trace methods, age-structured population dynamics

Life tables have provided a means to encapsulate the field dynamics of insect populations for nearly 70 yr, although their relationship to what could be called the "normal" dynamics and, hence, life-history strategy (LHS) (Stearns 1992; Den Boer 1968, 1998; Roff and Emerson 2006) of a given species has never been sought rigorously. However, the existence of such a link has been tacitly assumed (Miller 1966, Morris and Miller 1954), mooted as in the generally direct correlation between fecundity and developmental mortality (Cole 1954, Murdoch 1966, Price 1997), even discussed more explicitly (Lawton 1992). On a rather different tack, Southwood (1988) examined LHSs in relation to habitat properties, but he did not bring life tables, to our thinking the numerical core of population dynamics, into the discussion. Nor does he mention Den Boer's concept of risk spreading, to us a basic LHS. While life tables are generally presented as time-dependent processes,

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LHSs are conceived mainly as time-independent properties of species. Freeman (1976) and Freeman and Ittyeipe (1993) made steps toward unification of these aspects with the presentation of the time-independent cyclic budget, an extension of Varley et al. (1973) population budget. According to the extent of its sample base, the cyclic budget seeks the dynamics typical of a given species. But, existing models have insufficient generality to verify its validity, and its accurate application requires a constant mean density for a sufficiently long and representative period. This necessitates assessing dynamic details within the area of distribution of a focal species with due regard to age distribution. Since reference to early workers using life tables has often been omitted, we briefly redress this omission and draw attention to genetic influences, which too are often omitted. We then present a general dynamical model. This is effectively extended in space and time and so can be regarded as the numerical expression of an LHS. Although insect diversity is often envisaged in terms of morphology, diversity in their LHSs is more fundamental; indeed, it drives many morphological features. Just two examples of this effect are modifications of the female reproductive system according to life-history features in ichneumonid wasps (Price 1973) and the evolution of aggressive male weaponry in the scarabaeid genus *Onthophagus* (Coleoptera: Scarabaeidae) (Emlen et al. 2005), driven by natural selection and by sexual selection, respectively.

A Brief History of Life Tables

While time series data have been analyzed increasingly in recent years (Brook and Bradshaw 2006, Turchin 2003), population processes of animals in the field are understood most fully by constructing life tables (Royama 1996, Varley et al. 1973). For biology, Brownlee (1919) noted these tables, but Fisher (1930) presented their theoretical background to biology as a prelude to his fundamental theory of natural selection. “Death tables,” however, would be more fitting, and Fisher warned that life tables were only half the story. He outlined a basic reproduction table, giving the expectation of births from adults surviving to a series of age intervals. But, for natural insect populations at least, more attention has been given to the distribution of mortality than to that of natality. And, we suspect that the extended research time necessary to produce adequate life tables has attracted few young ecologists. Fisher combined the information in both types of table to derive r, his “Malthusian parameter.”

Pearl and Parker (1921) and Pearl et al. (1941) used life tables to analyze the dynamics of *Drosophila* and flour beetle cultures, respectively. Deevey and Deevey (1945) used them for black widow spiders, and Deevey (1947) applied them to empirical field data on the mortality of wild Dall sheep, *Ovis dalli* Nelson, to which we refer below. These early tables did not identify or enumerate mortality factors, they simply described survivorship. More complete tables appeared for the spruce budmoth, *Choristoneura fumiferana* (Clemens), in Canada (Morris and Miller 1954) and the chrysomelid beetle, *Phytodecta olivacea* (Forster), in England (Richards and Waloff 1961). These workers estimated several causes of mortality. Such tables are now better developed as multiple-decrement tables (Carey 2001).

Bias in Traditional Tables

While life tables generally document top-down effects, and occasionally the lateral influence of competition (Price 1997), other factors influencing population dynamics must be incorporated or understanding will be but partial, as Fisher pointed out. A comprehensive plan is required. Bottom-up effects on survival and natality are also critical. In phytophagous insects, mortalities due to plant resistance (Berenbaum 1995, Howe and Jander 2008, Moran and Hamilton 1980) are mentioned rarely, but presumably occur regularly under headings such as "unknown causes." Although the results of poor-quality plant food have been investigated often (Nealis and Regniere 2004, Ohsaki and Sato 1994), such studies are linked infrequently to mortality in life tables. For predatory insects too, the prey may defend themselves chemically, often with compounds derived from plants. Poor food results in longer development, thereby often resulting in an attendant increase in developmental mortality (Williams 1999), ultimately in reduced fecundity in both individuals and the populations they comprise. Prey may also scatter, so affecting density.

While Birch (1960) drew attention to genetic influences in ecology, these are mentioned infrequently in relation to life tables, although they play a critical role in the evolution of LHSs (Roff and Emerson 2006). Even so, they may constitute further undefined causes of reduced fitness and death. Firstly, there are simply unfit or lethal genes and genotypes (Ford 1975), such as the "curly" and "plum" inversions in *Drosophila melanogaster* Meigan (Mettler et al. 1988) and the dominant lethal gene (RIDL) that acts at the inception of pupation of *Aedes aegypti* (L.) (Yacob et al. 2008). Autosomal killer genes (Medea) are known in *Tribolium castaneum* (Herbst) (Beeman and Friesen 1999). Driving selfish elements either on the autosomes or on dipteran sex chromosomes cause complex population effects (Burt and Trivers 2006). Driving Y-chromosomes cause male-biased sex ratios in some mosquitoes (Hamilton 1967, Hickey and Craig 1966), reducing the reproductive potential of the population and ultimately causing its extinction. In *Drosophila* a driving X-chromosome (Jaenike 2001) has less radical effects until the population approaches total feminization. In diverse insects, male-killing bacteria such as *Wolbachia* (Werren and Windsor 2000) and *Rickettsia* (Majerus and Hurst 1997) similarly skew populations toward spanandry. We cannot always estimate the effects of such factors but must be aware that they might exist and then be significant in population processes.

Types of Life Tables in Insects

Traditional life tables are of two classes (Southwood 1978). Age-specific life tables record the fate of a real cohort, usually of a single generation at a given location. For endopterygote insects the number of individuals entering the egg stage (l_x) and dying in that stage (d_x) and from what factors (d_xF) (Morris and Miller 1954) are recorded, the remainder entering the first larval instar. This sequence continues for the several larval instars, pupae, and emerging adults. Naturally, for exopterygotes there are only eggs, nymphs, and adults. In contrast, time-specific life tables represent a time-section through a population with continuous reproduction and overlapping generations. This approach can be appropriate for stored product pests and many tropical insects.

A further class comprises retrospective or time-independent life tables (Freeman 1976, 1981; Freeman and Ittyeipe 1993) as applied to wasps. They form a series providing increasing information on the mean population dynamics of a species. At simplest, they present data for a single generation from a single habitat (Danks 1971 [for wasps]; Garraway and Freeman 1990 [for bark beetles]). An extension is to continue the study for several generations (Garraway and Freeman 1981, Watmough 1983), combining data on births and deaths through time. These are similar conceptually to tables compiled for mortality in Dall sheep (Deevey 1947). However, as he notes, his data comprise only later mortality, deaths in utero and those of some newly born lambs are unrecorded; whereas, data for the insects estimate both egg and emergence numbers separately. Such samples are weighted automatically, as dense generations contribute more to them than sparse ones do. Finally, data from a representative sample of habitats and several generations can be combined (Freeman 1981, 1982; Freeman and Ittyeipe 1993). Thus, a regional picture of species dynamics and LHS emerges including valid estimates of spatial density dependence (Freeman and Parnell 1973, Richards and Waloff 1961, Walde and Murdoch 1988) and the existence of sink populations (Freeman 1981, Pulliam 1988). We examine formally the validity of such tables here and show they give an efficient, time-saving supplement to traditional time-dependent tables.

Combined Life Tables

Several workers have combined information from life tables, either for single species (LeRoux et al. 1963, Mukerji 1971) or for many species (Cornell and Hawkins 1995, Danks 1971). Surprisingly, Mukerji (1971) and MacPhee et al. (1988) present “summary” tables for single species without noting their potential to yield extra information. Even so, Danks (1971) makes the suggestion, based on data for 12 stem-nesting aculeate Hymenoptera, that compensation for their low mortality must be achieved by the “difficulties of finding suitable [safe] nesting sites.” It follows that there must be high loss during searching. Both Morris (1957) and LeRoux et al. (1963) used these “mean” life tables for some diverse Canadian pest insects, while in a meta-analysis, Peterson et al. (2009) combine data from several life tables for a given species to seek the dynamic effects of indispensable mortality.

As above, the most informative retrospective tables embrace spatiotemporal estimates. Data from several generations and places within the distribution of the focal species are combined, so that a global or metapopulation picture emerges. When they are extensive, a cyclic budget can be developed (Freeman 1976; Fig. 1). This incorporates an estimate of losses during redistribution and the prereproductive life of females, and depends on the premise that the birth rate and death rate are virtually equal when each is averaged over a representative period. We substitute space for time. But, it is onerous using traditional methods to collect such data, while the imprecision of the methods (Bellows et al. 1992) is a further consideration. More efficient and accurate methods are required.

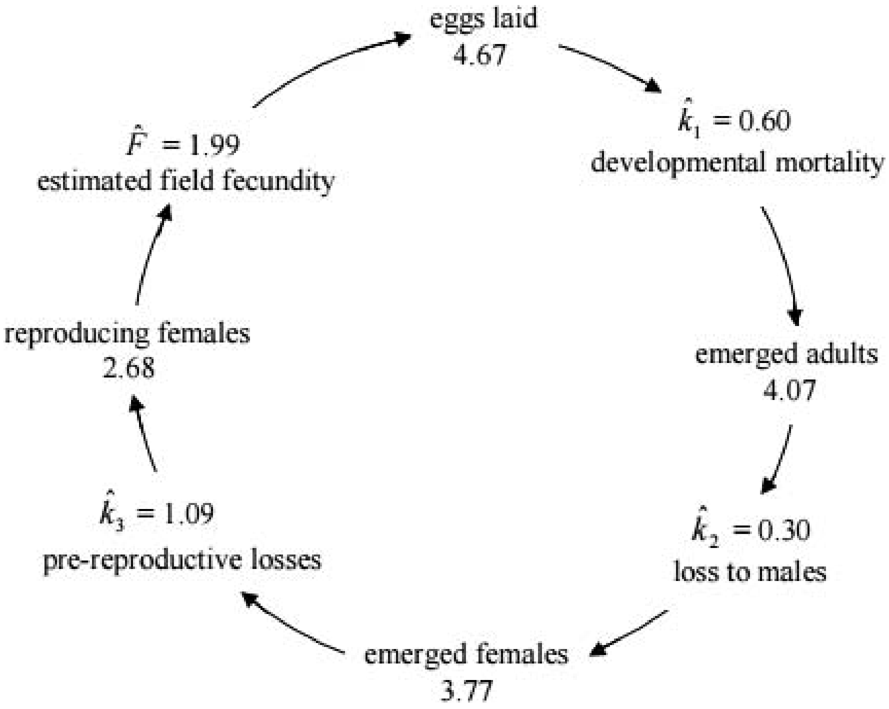

Fig. 1. A cyclic budget for *Asphondylia boerhaaviae* (Möhn) in Jamaica using logarithmic values at each stage. $\hat{k}_1$ = developmental mortality, $\hat{k}_2$ = loss to males, $\hat{k}_3$ = interpolated estimate of the prereproductive mortality of adult females, $\hat{F}$ = estimated field fecundity. This budget is based on numbers sampled at 39 sites throughout Jamaica. Under steady-state conditions, $\hat{F} = \hat{k}_1 + \hat{k}_2 + \hat{k}_3$ (after Freeman and Geoghagen 1989).

Trace Methods

So, it is to G.C. Varley's great credit that he divined a way of circumventing these grave difficulties: the use of trace methods. He chose the tephritid fly, *Urophora jaciana* (Hering) (Varley 1947), specifically because its egg laying caused the growth of a gall, a relatively permanent artifact, facilitating mortality estimates (G.C. Varley, University of Oxford pers. comm. Beaver (1967, 1979), Berryman (1973), Garraway and Freeman (1981, 1990), and many others studied beetles that leave traces of their life history in the bark and wood. Grimble and Knight (1970, 1971) and Togashi (1990) present life tables for cerambycid beetles in dead wood. Redfern and Hunter (2005) and Freeman and Geoghagen (1989) used them to investigate gall midge dynamics. But, the use of traces is not confined to these insects alone.

Holling (1959) adopted this principle to estimate predation by small mammals on sawfly cocoons. For solitary Aculeata, Danks (1971) used traces to study stem-nesting species, and Freeman (1981, 1982), Freeman and Taffe (1974), Freeman and Jayasingh (1975), Taffe (1979), Jayasingh and Freeman (1980), and Ittyeipe and Taffe (1982) used them to study the dynamics of those species that make long-lasting cells. Such methods are very useful in developing retrospective tables. They allow far more accurate estimates than those derived from sampling living insects directly, since at best they provide a record of every entry into every stage of the focal species, and often the cause of each death. The fact that lepidopteran larvae leave semipermanent traces when they consume the leaves of specific food plants gives some idea of their mortality and shows that trace methods have further applicability. For the swallowtail butterfly, *Papilio* (*Pterourus*) *homerus* (F.), the leaves and traces on *Hernandia* trees persist for up to 3 yr and several generations (Garraway et al. 2008). Leaf-mining insects also provide informative traces of population processes (Freeman and Smith 1990, Klug et al. 2008). For forest moths, such as *Lymantria dispar* (L.) (Campbell and Sloan 1976), if cocoons were not removed from the bark by insectivorous birds they would provide an accurate trace of each individual entering the prepupal or pupal stage. Avian predation could be estimated from the torn-open cocoons, as in Holling (1959), while diagnostic exit holes made by adults would provide an accurate estimate of emergence. Potentially, cocoons can reveal entry into two instars: prepupae and adults.

Thus, trace methods are useful to study a variety of species and situations. For solitary Aculeata, leaf miners, and galling insects there is the further advantage that population densities relate to the same area of living space during development. This is quite different from larvae, such as *Pieris* spp., that disperse over the plant as they grow and leave it when they seek sites to pupate. Of course, representativeness of the sample is an additional issue. But, without traces, even if all individuals are in the same stage, as in diapause, estimates will still be negatively biased to an unknown degree because of the mortality that occurs before sampling can begin (Freeman 2019, Harcourt 1969, Partridge and Harvey 1985).

Errors When There Are Traces

Assuming that the sample is representative of the focal population, the accuracy of trace sampling follows ordinary sampling theory, varying as the square root of the sample size. Thus, if we wish to express the probability that a fraction $(1 - p)$ of eggs are infertile and do not hatch, we use the binomial expression:

$$P_n(m) = \frac{n!}{m!(n-m)!} p^m (1-p)^{n-m},$$

the probability that exactly m out of n eggs will hatch if the probability for any individual egg to hatch equals p. For large n, this distribution can be approximated by a normal distribution with mean np and variance $np(1 - p)$. Bear in mind that some insects, such as the mosquito *Aedes aegypti* L., have eggs or like the sawfly *Perga affinis* (Kirby) have pupae, in which a proportion remain in diapause for two or more generations. But, in a given generation or where generations are combined, far more individuals enter the egg stage than the adult stage. Thus, if we have such an estimate for 1,000 eggs laid, 95% confidence limits (95% CL) will be:

$$\hat{p} \pm 1.96\sqrt{\hat{p}(1-\hat{p})/1000} = \hat{p} \pm 0.062\sqrt{\hat{p}(1-\hat{p})},$$

with $\hat{p}$ the fraction of eggs in the sample that hatched. If we estimate that 100 adults emerged, then $\hat{p} = 0.1000$, the 95**%** CL will be: 0.1000 ± 0.019. This logic applies when the number emerging is based on the number entering the egg stage, namely real mortality (Southwood 1978).

Errors When There Are No Traces

Serious difficulties arise without traces. While the numbers present on a given day can be estimated with comparative ease, the total numbers entering a specified instar cannot. Some workers do not appear to understand, or choose to ignore, this basic principle although it has been pointed out repeatedly (Bellows et al. 1992, Freeman 1976, Harcourt 1969, Manly 1989, Morris and Miller 1954, Turchin 2003). We give an example here, and the several references above, since this understanding is crucial for the accurate study of insect dynamics. MacPhee et al. (1988), studying winter moths in Canadian orchards, and in an otherwise valuable 14-yr study, estimated the numbers of first and second instars (young larvae) by the higher of two direct counts made as intensity per leaf cluster. Counts of fourth and fifth instars (mature larvae) were similarly before the prepupae started to drop to the ground. These numbers of larvae entering the small and the large stages are, thus, negatively biased to an unknown degree. For young larvae this is because, as the authors state, not all eggs had hatched on the sampling date, and because, as they do not state, some mortality and emigration of early-hatched larvae must have occurred before sampling. But, the arrival of immigrant larvae on silken threads will have offset this bias partly, again to an unknown degree. The numerical estimates for large larvae suffer similarly.

There are three basic methods by which these difficulties can be reduced: stage frequency analysis, estimation of recruitment to a stage, and death rate analysis. Stage frequency analysis was initiated by Southwood and Jepson (1962) and developed by Manly (1989), but still experiences errors. The direct measurement of recruitment to a stage solves many of these attendant problems, while death rate analysis is another useful approach (Bellows et al. 1992).

The Cyclic Budget

With the conspicuous aid of trace data, an extensive population or metapopulation (called a “large population” below) can be sampled through several generations. As the data become more extensive in space and time, a general picture of the dynamics of the focal species emerges. This database generates a cyclic budget (Fig. 1) comprising logarithmic estimates of all the components necessary to characterize the normal dynamics of a species: fecundity, developmental mortality, sex ratio, and losses to females prior to reproduction (Freeman 1976, 1982; Freeman and Geoghagen 1989). Budgets do not describe classical time-dependent dynamics; they are long-term, time-independent descriptions of events. While *temporal* density dependence cannot be revealed in such data, *spatial* density dependence can be (Freeman and Parnell 1973). Spatial density dependence within a generation can provide information that would be missed otherwise. This is also true for multigenerational data. Thus, one can compare natality and mortality patterns from different areas, that is, those in which density is typically high with those where it is typically low (Andrewartha and Birch 1954, see figs. 1.01 and 1.02; Freeman 1981). In this format, the effects of a shared enemy on two victim species can also be shown (Freeman 1982, Freeman and Jayasingh 1975, Muller and Godfray 1997). This is often called "apparent competition," but we prefer the specific and unambiguous term "trans-specific mortality"; hence, trans-specific predation and trans-specific parasitism.

The assumptions on which cyclic budgets are based are: (1) Over many generations (approximately 30), the dynamics of a large population will not be very different from those in a similar period either before or after the period sampled; (2) Over such a period, the birth rate of the large population will be very nearly equal to the death rate; and (3) Immigration or emigration are for a large population trivial components of its dynamics (Turchin 2003).

Each of these assumptions requires qualification. (1) This is dependent largely on the period of time investigated, longer periods having greater similarity than shorter ones (Lawton 1988), but it is also influenced by the degree of population fluctuation, more stable populations being more similar, that is, if they were at a constant level, the relationship would be exact. (2) This means, of course, that total births very nearly equal total deaths ($b \approx d$; "steady density"). (3) The nature of migration varies greatly between insect species. In those with little migration, such as *Callimorpha dominula* (L.) (Goulson and Owen 1997), the effect is probably trivial. In highly migratory species, such as *Plutella xylostella* (L.) (Chapman et al. 2002), the effect requires further consideration. Now, migration in insects can be a very wasteful process and so dangerous, in fact, that it may often be regarded as a major mortality factor. But, irrespective of the area sampled, losses due to failed migration become incorporated in the cyclic budget under the heading of "prereproductive losses of adult females" ($\hat{k}_3$ in Fig. 1). Such losses are several and the accuracy of estimating them depends upon those of the other components. Losses include: (1) female sterility and failure to mate, and (2) losses during redistribution and failure to find reproductive resources. Those in Group 1 are generally amenable to further study, leaving those in Group 2 a residual group of interest.

Relationships between Spatiotemporal Age-Structured Population Dynamics, Retrospective Life Tables, Cyclic Budgets, and LHS

The cyclic budget provides a special case and empirical description of the fate of a large population of insects through time in a heterogeneous environment. Since the area occupied by a species is never constant, neither is the relationship between its numbers and its population density. A given number can be spread out thinly or be concentrated in a single area. This difficulty exists at all spatial levels: patch, habitat, and landscape. So, density dependence can be estimated empirically only if number and density are closely correlated. We, therefore, initially formulate a comprehensive description of the behavior of population density and age structure at an arbitrary location (x, y) as described in terms of the quantity $n(x,y,t,\tau)d\tau$, to be interpreted as the number of individuals (females) of age between τ and $\tau + d\tau$ per unit area at location (x, y) and at absolute chronological time t.

The density function $n(x,y,t,\tau)$ varies locally at a rate $\frac{\partial n}{\partial t}$, which is the result of three contributing factors:

(i) Aging of individuals. This proceeds at a rate $-\frac{\partial n}{\partial \tau}$ and follows from the momentary local age distribution;
(ii) Mortality, which is a function of age, place, time, and density. The rate at which individuals of age τ die at the given location, per unit area, equals μn;
(iii) Migration. The net rate of change due to this process is given by minus the divergence of the migration flux, which is the vector quantity $\vec{J} = (J_x, J_y)$.

In many cases, this can be modeled by a diffusion process, with age-, position-, and time-dependent mobility (“diffusion coefficient”) D (Webb 2008). The underlying assumption is that individuals move down a density gradient specific to their age. According to Fick’s first law of diffusion, $\vec{J} = -D\vec{\nabla} n$. When applied to the distribution $n(x,y,t,\tau)$ for fixed age τ, the corresponding contribution to $\partial n/\partial t$ is:

$$-\vec{\nabla} \cdot \vec{J} = -\frac{\partial J_x}{\partial x} - \frac{\partial J_y}{\partial y} = \frac{\partial}{\partial x}\left(D\frac{\partial n}{\partial x}\right) + \frac{\partial}{\partial y}\left(D\frac{\partial n}{\partial y}\right) \equiv \vec{\nabla} \cdot (D\vec{\nabla} n)$$

The assumption can be made less restrictive by replacing the driving force of diffusion–migration by the gradient of the net population density,

$$n(x,y,t) = \int_0^\infty n(x,y,t,\tau)d\tau.$$

Combining these results yields the equation that governs the spatiotemporal dynamics of an age-structured population:

$$-\frac{\partial n}{\partial t} = \vec{\nabla} \cdot \vec{J} + \frac{\partial n}{\partial \tau} + \mu n. \tag{1}$$

For this equation, which simplifies to the McKendrick–von Förster equation if the distribution is uniform in space (in which case $\vec{J} \equiv 0$), to have a unique solution one must also specify initial and boundary conditions. We assume that the age distribution is known for every location at time $t = 0$:

$$n(x,y,0,\tau) = f(x,y,\tau). \tag{2}$$

A general and important boundary condition comes from the birth rate, which determines the density of individuals of age $\tau = 0$,

$$n(x,y,t,0) = \int_0^\infty bn(x,y,t,\tau)d\tau, \tag{3}$$

where b denotes the birth rate (fertility) of an average female at age τ, at location (x, y), and at time t. Other boundary conditions must be imposed to render the solution unique, for example, the population may be confined to a finite area A, such as an island. In that case, the normal component of the migration flux for each age group equals zero along the boundary L of such an area.

As a consistency check, we integrate $n(x,y,t,\tau)$ and (1) with respect to x, y, and τ, to obtain the differential equation that determines the time dependence of the total population $N(t) = \iint_A dxdy \int_0^\infty d\tau n(x,y,t,\tau)$ contained within a finite area A.

As a consequence of the above set of equations, $N(t)$ satisfies the familiar differential equation

$$\frac{dN}{dt} = (\bar{b} - \bar{\mu})N = rN, \tag{4}$$

(which is subject to the initial condition $N(0) = \iint_A dxdy \int_0^\infty d\tau f(x, y, \tau)$), with the Malthusian parameter r defined as the difference between the per capita birth and death rates.

To show this, the population density for a particular age group, $n(x,y,t,\tau)$, must be solved from the boundary value problem (1–3). Furthermore, the condition $J_n = 0$ is imposed for all points (x, y) along the boundary L, where J_n denotes the component of $\vec{J}$ along the outward normal to the boundary at the point where it is evaluated.

Integrating (1) with respect to x, y, and τ yields

$$-\frac{dN}{dt} = \int_0^\infty d\tau \iint\limits_A dxdy \vec{\nabla} \cdot \vec{J} + \iint\limits_A dxdy \int_0^\infty d\tau \frac{\partial n}{\partial \tau} + \int_0^\infty d\tau \iint\limits_A \mu n dxdy \tag{5}$$

The first term on the right side vanishes on account of the divergence theorem in two dimensions in combination with the condition along L, according to which

$$\iint\limits_A dxdy \vec{\nabla} \cdot \vec{J} = \int\limits_L dL J_n = 0. \tag{6}$$

The second term can be evaluated based on boundary condition (3)

$$\begin{aligned} \iint\limits_A dxdy \int_0^\infty d\tau \frac{\partial n}{\partial \tau} &= \iint\limits_A dxdy \Big(n(x, y, t, \infty) - n(x, y, t, 0) \Big) \\ &= \iint\limits_A dxdy \Big(0 - \int_0^\infty d\tau b n(x, y, t, \tau) \Big) \\ &= -\bar{b} N(t), \end{aligned} \tag{7}$$

defining the average fertility per female, $\bar{b}$.

The last integral can be written formally as

$$\int_0^\infty d\tau \iint\limits_A \mu n(x, y, t, \tau) dxdy = \bar{\mu} N(t), \tag{8}$$

where $\bar{\mu}$ is the average mortality per female. Substitution into (5) gives (4).

If the per capita birth and death rates are independent of density, (4) predicts exponential growth if $\bar{b} > \bar{\mu}$, and exponential decrease for $\bar{b} < \bar{\mu}$, thus: $N(t) = N(0)e^{rt}$.

A further check can be performed to show that (1) implies other well-known results under certain very restrictive conditions. If we were to assume a uniform environment and a focal population existing for a sufficiently long period under conditions such that density dependence of mortality and fertility are negligible, the Malthusian scenario predicts exponential time dependence of the overall population, as indicated by (4), without any reference to demographic details. "Stability" of a population in a demographic sense, however, requires the *relative* numbers of individuals in different age groups to be time independent. We are, therefore, seeking solutions of (1), with the spatial dependence suppressed, of the form

$$n(t,\tau) = v(\tau)e^{rt}. \tag{9}$$

Under these conditions, and for given fertility and mortality rates that only depend on age, the parameter r follows from the Euler–Lotka equation:

$$\int_0^\infty d\tau b(\tau)l(\tau)e^{-r\tau} = 1, \tag{10}$$

where $l(\tau)$ is the probability at birth that an individual will survive to age τ, which is related to the mortality function via the "rate equation"

$$\frac{dl(\tau)}{d\tau} = -\mu(\tau)l(\tau). \tag{11}$$

That the equation for r follows from the dynamic equation (1) can be seen most easily by inserting the trial solution (9) into (1) and reorganizing the result into

$$\frac{dv}{d\tau} = -(r+\mu(\tau))v(\tau). \tag{12}$$

In this case, the boundary condition (3) assumes the form

$$v(0) = \int_0^\infty b(\tau)v(\tau)d\tau. \tag{13}$$

The first equation can be readily integrated, using separation of variables, to yield

$$v(\tau) = v(0)l(\tau)e^{-r\tau} = \left(\int_0^\infty b(\tau')v(\tau')d\tau'\right)l(\tau)e^{-r\tau}. \tag{14}$$

The Malthusian parameter r for a population with known birth and death rates, depending only on age, can be found by multiplying this equation by $b(\tau)$, followed by integration with respect to τ on both sides, and canceling the common factor (the bracketed integral expression), leading to (10).

No exact closed-form analytical solution for r in terms of the functions $b(\tau)$ and $l(\tau)$ exists, but some approximate generic solutions have been proposed, one of the most accurate being

$$r \cong \frac{\ln R_0}{T_c} + \frac{\sigma^2(\ln R_0)^2}{T_c^3} \tag{15}$$

(May 1976), where the *net reproductive rate* R_0 is defined as

$$R_0 = \int_0^\infty d\tau b(\tau)l(\tau). \tag{16}$$

The parameters T_c and σ are similarly defined in terms of integrals involving $b(\tau)$ and $l(\tau)$ and have straightforward interpretations:

$$T_c = \frac{\int_0^\infty d\tau \tau b(\tau) l(\tau)}{R_0} \tag{17}$$

is the *generation period*, which has variance

$$\sigma^2 = \frac{\int_0^\infty d\tau \tau^2 b(\tau) l(\tau)}{R_0} - T_c^2. \tag{18}$$

When dropping the restrictions on spatial uniformity, of particular interest are *stationary* solutions, $n(x,y,\tau)$, with the property that local density and age structure are time independent. Under the right conditions, this turns out to be the limiting solution for very long times ($t \to \infty$). These stationary solutions are obtained, in principle at least, by solving the system (1–3) after setting $\partial n/\partial t = 0$ in (1). From the corollary, (4), it is already obvious that such a solution will be unstable, as it would require that, at least, $\bar{b} = \bar{\mu}$, which is usually not the case, unless some stabilizing mechanism is built into the model.

The formulation of the problem has been kept sufficiently general to allow for inclusion of effects of spatial heterogeneity, time, age, and population density on the model parameters D, b, and μ. So, for example, μ can be made to also depend on $n(x,y,t)$ (Freeman and Parnell 1973). Density dependence of b and μ leads typically to the introduction of a carrying capacity $K(x,y,t,\tau)$ (i.e., the stable, equilibrium population density). Destabilizing effects are: seasonality of physical factors and food resources, predator–prey interactions (as in the Lotka–Volterra model), and time delays. All of these tend to produce oscillations and/or formation of spatial patterns (Murray 2002).

The simplest mathematical form of the dependence of b and μ on the net local density $n(x,y,t)$ assumes a linear relationship for both, thus

$$b(x,y,t,\tau) = b_0(x,y,t,\tau) - \alpha n(x,y,t), \tag{19a}$$

$$\mu(x,y,t,\tau) = \mu_0(x,y,t,\tau) + \beta n(x,y,t), \tag{19b}$$

where b_0 and μ_0 are the values of b and μ in the low-density limit, and α and β are positive constants.

To see that these assumptions naturally lead to the notion of carrying capacity, we first assume that both the habitat and the population distribution are spatially uniform. Combining different age groups at any location, that is, integrating $n(t,\tau)$ with respect to τ, we are dealing with the uniform time-dependent density function $n(t)$. If we now integrate (1) we obtain, with the aid of (3), an expression similar to (4):

$$\frac{dn(t)}{dt} = (\bar{b}(t) - \bar{\mu}(t))n(t). \tag{20}$$

Here, $\bar{b}(t) = \bar{b}_0(t) - \alpha n(t)$ and $\bar{\mu}(t) = \bar{\mu}_0(t) + \beta n(t)$ denote the per capita birth and death rates, with $\bar{b}_0(t)$ and $\bar{\mu}_0(t)$ their “zero-density” limiting values. Substitution of these relations into (20) and subsequent rearrangement gives rise to the differential equation

$$\frac{dn(t)}{dt} = r_0(t)n(t)\left(1 - \frac{n(t)}{K(t)}\right), \tag{21}$$

where

$$r_0(t) = \bar{b}_0(t) - \bar{\mu}_0(t), \tag{22}$$

representing a, possibly time-dependent, “zero-density” growth rate (i.e., the Malthusian parameter proper), and

$$K(t) = \frac{r_0(t)}{\alpha + \beta}, \tag{23}$$

which defines a (time-dependent) carrying capacity since (21) has the same form as Verhulst’s logistic equation. Hence, if K is not time dependent, $n(t)$ will approach K asymptotically in the limit of long times. Once the general solution of the above problem is known, so that an explicit form of the density function $n(x,y,t,\tau)$ is available, its average across a large enough sampling area A can be calculated for any time (t) and age group (τ). This average density will be denoted by

$$n(t,\tau) = \iint_A dxdyn(x,y,t,\tau)/A, \tag{24}$$

and the overall average population density by

$$n(t) = \int_0^\infty d\tau n(t,\tau). \tag{25}$$

Mortality (death rate) is assumed to depend on age τ (aging, genetic effects), chronological time t (seasonal variation of available food resources, predation, parasitism, catastrophic events, etc.), and total density $n(t)$, which follows from the previous analysis of population dynamics in the given habitat. Thus, $\mu = \mu(\tau,t,n(t))$.

Next, we define the *survivorship function* $l(\tau,t)$ as the probability that an individual born at time $t - \tau$ survives to time t (the “present”) when the mortality function is known. Equation (11) already introduced this concept in the case of the absence of an explicit t-dependence, when l only depends on age τ, in which case it essentially summarizes the information contained in life tables.

With explicit time dependence, the problem is more subtle, since we are now dealing with a population in a dynamic environment where chances of survival depend not only on an individual’s current age but also on prevailing conditions at time t, including population density. From the definition of $l(\tau,t)$, it must be equal to $1 -$ (probability of death between $t - \tau$ and t). In mathematical terms, this becomes

$$l(\tau,t) = 1 - \int_0^\tau d\tau' \mu(\tau', t-\tau+\tau', n(t-\tau+\tau')) \cdot l(\tau', t-\tau+\tau'). \tag{26}$$

Taking the derivative of this equation with respect to τ, we obtain for the left side $\frac{dl}{d\tau} = \frac{\partial l}{\partial \tau} + \frac{\partial l}{\partial t}\frac{\partial t}{\partial \tau} = \frac{\partial l}{\partial \tau} + \frac{\partial l}{\partial t}$, since $\frac{\partial t}{\partial \tau} = 1$ (age increases at the same rate at which time progresses). The τ-derivative on the right side reduces to $-\mu(\tau,t,n(t))l(\tau,t)$. The survivorship function $l(\tau,t)$ is, therefore, the solution of the first-order partial differential equation

$$\frac{\partial l(\tau,t)}{\partial \tau} + \frac{\partial l(\tau,t)}{\partial t} = -\mu(\tau,t,n(t))l(\tau,t), \tag{27}$$

which obviously generalizes the conventional result (11), obtained if μ and l depend exclusively on τ. The function $l(\tau,t)$, furthermore, has the property $l(0,t) = 1$ for all t.

In constructing a *retrospective life table*, one uses cumulative data on mortality over a period T that extends over many generations. Let $D_T(\tau)d\tau$ represent the total number of individuals in the age range $(\tau,\tau + d\tau)$ that died during time T, as determined for wild Dall sheep (Deevey 1947) by simply counting the number of skulls for each age group. With the definition (24) and the mortality function $\mu(\tau,t,n(t))$, this quantity can be identified as:

$$D_T(\tau)d\tau = A\int_0^T \mu(\tau,t,n(t))n(t,\tau)dt \cdot d\tau. \tag{28}$$

Alternatively, this may be formulated as $-B(T)\frac{dl_T(\tau)}{d\tau}d\tau$, where $B(T)$ is the total number of individuals that existed in the sampling area A during the period T (equal to the total number of births in the absence of migration), and $l_T(\tau)$ an "apparent" survivorship function that forms the basis for constructing a retrospective life table.

So, in conclusion,

$$\begin{aligned} l_T(\tau) &= 1 - \frac{A}{B(T)}\int_0^\tau d\tau' \int_0^T dt\mu(\tau',t,n(t))n(t,\tau') \\ &= 1 - \frac{\int_0^\tau d\tau' \int_0^T dt\mu(\tau',t,n(t))n(t,\tau')}{\int_0^\infty d\tau' \int_0^T dtb(\tau',t,n(t))n(t,\tau')}, \end{aligned} \tag{29}$$

which can be used to define an apparent mortality function as (compare with [11])

$$\mu_T(\tau) = -\frac{1}{l_T(\tau)}\frac{dl_T(\tau)}{d\tau} = -\frac{d\ln l_T(\tau)}{d\tau}. \tag{30}$$

Losses due to mortality factors acting during different stages of development were expressed traditionally as k values. The k value for stage i is denoted by $\hat{k}_i$ (which should include "losses" to males) and is defined as the difference between the $\log_{10}$ of the number of females entering and that of the number surviving to the end of that stage, as originally suggested by Haldane (1949) and used by Varley et al. (1973). These are employed in a modified form in the cyclic budget. While the use of k values to find key factors in empirical studies has now been superseded (Royama 1996), this does not affect their application in a cyclic budget. Assuming a population that has maintained a constant average number and density of females during the period T $(r = 0)$, the net reproductive rate of a representative female,

$$R_0 = \int_0^\infty d\tau b_T(\tau)l_T(\tau), \tag{31}$$

can be taken to be equal to one, in which case the life table can be represented by a cyclic budget.

For retrospective life tables, the definition of $\hat{k}_i$ implies a simple relation with the apparent mortality rate, as follows:

$$\hat{k}_i = \int_{\tau_{i,1}}^{\tau_{i,2}} \mu_T(\tau) d\tau / \ln 10, \tag{32}$$

where $\tau_{i,1}$ and $\tau_{i,2}$ are a female's age at the start and end of stage *i*, respectively.

To ensure that $R_0 = 1$, fecundities $\hat{f}_i = \log_{10}$ (total number of eggs produced per female during stage *i*) must be such that

$$\sum_{j=0}^{\infty} \mathrm{antilog}_{10}(\hat{f}_j - \sum_{i=0}^{j} \hat{k}_i) = 1, \tag{33}$$

which is equivalent to this condition.

If, and only if, reproduction occurs during a single stage, *m*, (33) reduces to the criterion

$$\hat{f}_m = \sum_{i=0}^{m} \hat{k}_i, \tag{34}$$

which corresponds to the estimated fecundity $\hat{F}$ required to "break even" (Freeman and Geoghagen 1989). As implied by (34), nonreproducing females beyond stage *m* are excluded from the budget.

Discussion

Fully developed cyclic budgets (Freeman 1976) record retrospective estimates of the major logarithmic components of the dynamics of a large population. These components are considered as a quantifiable whole. While their drivers, for example a parasitoid complex (Klug et al. 2008), often vary between regions, separate budgets applied to such areas may be similar; the play may be familiar, but the supporting actors have changed. Put another way, the LHS is similar, but the details vary. In organismal science, we do not expect identity but often find similarity. Thus, high fecundity is often associated with high developmental mortality (Price 1997), and the prereproductive loss of adults in migratory species is often a major component of their dynamics (Freeman and Ittyeipe 1993, Ward et al. 1998).

As we saw previously, the mode of application of the budget as a tool in population dynamics very much depends on the extent of redistribution in the focal species, a feature that is highly variable among species. Where migration is restricted, as for example in scarlet tiger moth, *Callimorpha dominula* (L.) (Goulson and Owen 1997), many small Tipulidae such as *Paradelphomyia senilis* (Haliday) (Freeman and Adams 1972, table 3), and pests such as Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Boiteau et al. 2008), and gypsy moth, *Lymantria dispar* (L.) (Elkinton and Liebhold 1990), budgets from habitats not far distant from each other will be validly comparable. Indeed, the global distributions of most species are much wider than the redistributive distances of the individuals comprising them. But, for wide-ranging species like *Plutella xylostella* (L.), *Choristoneura fumiferana* (Clemens) (Harvey 1996), *Nilaparvata lugens* (Stål) (Kisimoto and Sogawa 1995), and numerous cereal aphids, budgets must embrace the extensive migratory ambit of the species. In addition, metapopulations (Hanski 1991) would be better understood by employing cyclic budgets. When applied to harsh and benign sections of an insect's distribution, because they are time independent, they usefully reveal the extent of a sink habitat (Dias 1996, Freeman 1981).

At first sight it might appear that a cyclic budget provides an adequate description of an insect's LHS. Fecundity, mortality, sex ratio, and losses during redistribution, should it occur, are all estimated. But, there are some omissions. Firstly, being time-independent the budget fails to include the time to first reproduction that Cole (1954) showed to be a critical parameter. Secondly, an individual's size, which usually correlates with time to first reproduction (see Klingenberg and Spence 1997) and which varies by a factor of more than a million in insects (Hamilton 1995), is not taken into account. Even so, budgets for large and small insects could be compared.

Den Boer's (1968, 1998) concept of risk spreading is often not included in studies of LHS. One of its ecological aspects in insects is egg distribution. Single-batch layers, such as in gypsy moths (above), deposit a higher proportion of their maximum than do those that seek different locations for several smaller batches (Courtney 1984). They invest their metabolic reserves directly into reproduction not into redistribution and resource seeking for themselves and their progeny. The corollary is that when egg batches are distributed, although a chancy business for females, many of the progeny avoid local catastrophe. But, this aspect too would not be recorded clearly in a cyclic budget, only in a life table. Even so, cyclic budgets could be made showing several causes of developmental mortality.

A further application of these budgets is to use them to compare the life strategy and dynamics of related species and members of a guild sharing the same landscape or region. This has been done for two *Sceliphron* species of the same subgenus (*S. asiaticum* (L.) and *S. fistularium* (Dahlbom)) throughout Trinidad (Freeman 1982). But, for a rigorous comparison, methods must be developed to estimate the significance of the differences in the two budgets. This will form the subject of a future paper.

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