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The multiple decrement life table: a unifying framework for cause-of-death analysis in ecology

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Summary. The multiple decrement life table is used widely in the human actuarial literature and provides statistical expressions for mortality in three different forms: i) the life table from all causes-of-death combined; ii) the life table disaggregated into selected cause-of-death categories; and iii) the life table with particular causes and combinations of causes eliminated. The purpose of this paper is to introduce the multiple decrement life table to the ecological literature by applying the methods to published death-by-cause information on *Rhagoletis pomonella*. Interrelations between the current approach and conventional tools used in basic and applied ecology are discussed including the conventional life table, Key Factor Analysis and Abbott's Correction used in toxicological bioassay.

Key words: Multiple decrement life table – Risk analysis – Demography – Cause of death

The multiple decrement life table is used widely in human actuarial studies to address questions concerning the frequency of occurrence for causes of death and how life expectancy might change if certain causes were eliminated. It can be viewed as a composite of three tools used often in ecology and pest management. The first is the conventional life table (i.e. Deevey 1947; Keyfitz 1982, 1985) that orders and summarizes age-specific survivorship data, the second is Key Factor Analysis (Varley 1947; Varley et al. 1973; Morris 1965, 1959; Harcourt 1969, 1971) which partitions out stage- and cause-specific mortality and the third is Abbott's Correction (Abbott 1925) which provides an arithmetic method to separate two confounded sources of mortality. The multiple decrement life table captures the essence of these tools, each of which is concerned with questions of proven merit in ecology. Therefore, the purpose of the current paper is to introduce multiple decrement techniques to the ecological literature to provide a more cohesive framework for addressing questions concerned with cause-of-death analysis in both basic and applied contexts. I will do this by applying the methods modified from various journal articles and books on human survival analysis (eg. Greville 1948; Krall and Hickman 1971; Schoen 1975; Shryock et al. 1976; Batten 1978; Elandt-Johnson and Johnson 1980; Chiang 1984; Namboodiri and Suchindran 1987) to data generated from observations on cause of death in *Rhagoletis pomonella* populations. The specific fo-

cus will be on cause of death in insect populations but the approach is general.

The multiple decrement life table

Basic concepts

The conventional life table shows the probability of survivorship of an individual subject to the one undifferentiated hazard of death. In multiple decrement tables the individual is subject to a number of mutually exclusive hazards, such as disease, predators or parasites, and is followed in the table only to its exit, as in the ordinary life table. But in the multiple decrement table there is now more than one way of exiting (Preston et al. 1972).

Two probabilities and hence two kinds of tables are commonly recognized in the study of cause of death. One is the probability of dying of a certain cause in the presence of other causes; the other is the probability of dying of a certain cause in the absence of other causes (Preston et al. 1972). The first gives rise to the multiple decrement table proper. The second gives rise to an associated single decrement table and is applied to find the probability of dying if one or more factors were to disappear as a cause of death.

The assumption of the multiple decrement life table is that multiple causes of death act independently and is concerned with the probability that an individual will die of a certain cause in the presence of other causes. The concept itself stems from reliability theory in operations research. Keyfitz (1982, 1985) uses an example of a watch which can operate only as long as all its parts are functioning and that each part has its own life table. The probability that an individual (i.e. the watch) will survive to a given age is the product of the independent probabilities that each of its components will 'survive' to that age. The same notion of probabilities applied to internal components causing the death of a system can also be applied to external components such as disease and accidents in humans or predation and parasitism in insects. The concept here is that the probability of an insect surviving to a certain age (or stage) is the product of all independent risk probabilities.

In general, multiple decrement theory is concerned with basically three questions (Elandt-Johnson and Johnson 1980): i) What is the age (stage) distribution of deaths from different causes acting simultaneously in a given popula-

i) ii) What is the probability that a newborn individual die after a given age or stage from a specified cause? How might the mortality pattern or expectation of life certain causes were eliminated? The first two questions concerned with evaluating patterns and rates of mortality while the last question is concerned with what is termed 'competing risk analysis'. In both cases the analyses are based on three assumptions: i) each death is due to a single cause; ii) each individual in a population has exactly the same probability of dying from any of the causes operating in the population (see Vaupel and Yashin 1985); and iii) the probability of dying from any given cause is independent from the probability of dying from any other source.

Method and data organization

The cause of death in insects can usually be specified by age but seldom by exact age. Therefore the multiple decrement life table must be abridged (i.e. lumped age groups). Insect cause-of-death data may be gathered in one of two ways: i) by recording the number in a *true cohort* that die of particular causes by stage over their life course; ii) by exposing different numbers of individuals at the beginning of each of the stages to the risk of dying by the various causes throughout that single stage. The resulting data is then used to construct what is known as a *synthetic cohort*.

An hypothetical data set for analyzing mortality in a synthetic cohort was derived using average stage-by-cause mortality from 25 life table given in Cameron and Morrison (1977) for Key Factor analysis of *R. pomonella*. The original data were divided into death due to 11 factors—one for egg, four for larval, and six for pupal and adult emergence. The lumped sources into the four categories of predation, parasitism, disease and 'other'. The group within which a cause of death was placed was arbitrary in several cases.

The hypothetical mortality data for the four categories (causes) of death in preadult *R. pomonella* are given in Table 1 where K_x is the number in the cohort aged x , D_x is the total number of deaths in stage x , and D_{ix} is the number of deaths due to cause i in stage x . Note that $D_x = D_{1x} + D_{2x} + D_{3x} + D_{4x}$ and also that the K_x column does not represent the non-normalized survival column. That is, the K_x column gives the number of insects at the beginning of the stage that were exposed to risk through the

Table 1. Deaths from four causes in *Rhagoletis pomonella* populations using an hypothetical data set. The data presented in Cameron and Morrison (1977) were used as guidelines for the relative numbers of deaths by cause

Stage (index)	Number beginning stage	Total deaths	Number deaths due to			
			Pre-dators	Par-asites	Dis-ease	'Other'
x	K_x	D_x	D_{1x}	D_{2x}	D_{3x}	D_{4x}
Egg (1)	977	14	0	0	0	14
Early Larvae (2)	963	810	0	224	0	586
Late Larvae (3)	153	112	100	12	0	0
Early Pupae (4)	435	98	88	0	10	0
Late Pupae (5)	351	206	133	0	19	54
Adult (6)	-	-	-	-	-	-

stage. This is not the same as the number that would be exposed to risk in a true cohort where the numbers would decrease from stage to stage.

General framework and notation

The notation for all functions in the multiple decrement table correspond to the single decrement cases except: i) the prefix a is added to denote 'in presence of all causes'; and ii) the symbol x is used to denote the stage index rather than the age interval. Therefore let:

$a_{1,x}$ = fraction of original cohort living at stage x that ultimately die from cause i .

$a_{1,x}$ = denote the fraction of survivors at stage x out of original cohort of $a_{1,1}$.

$a_{d_{ix}}$ = fraction of deaths in stage x from cause i among $a_{1,x}$ living at stage x .

a_{d_x} = fraction of deaths in stage x from all causes ($= a_{d_{1x}} + a_{d_{2x}} + \dots + a_{d_{kx}}$).

$a_{q_{ix}}$ = probability of death from cause i in stage x in the presence of all other causes, given alive at beginning of stage x .

a_{q_x} = probability of death from all causes in stage x , given that individual is alive at stage x ($= a_{q_{1x}} + a_{q_{2x}} + \dots + a_{q_{kx}}$).

The fraction of a cohort that survives from x to $x+1$ is given by

$$(K_x - D_x)/K_x.$$

The numerator in this equation is the total number alive at stage x minus the number dying before reaching stage x . This net total by the original starting number, K_x , gives the fraction surviving. Therefore the complement of this fraction is the fraction dying in the interval, designated a_{q_x} . That is

$$a_{q_x} = 1.0 - [(K_x - D_x)/K_x]$$

The fraction of the cohort age x dying in stage x due to cause i is given by

$$a_{q_{ix}} = 1.0 - [K_x - D_{ix}]/K_x]$$

For example, no deaths occurred in the egg stage due to predators, parasites or disease. Thus

$$a_{q_{1,1}} = a_{q_{2,1}} = a_{q_{3,1}} = 0.0$$

However 14 of 977 eggs died of 'other causes' therefore

$$\begin{aligned} a_{q_{4,1}} &= 1.0 - [K_1 - D_{4,1}]/K_1] \\ &= 1.0 - (977 - 14)/977 \\ &= 1.0 - 0.98567 \\ &= 0.01433 \end{aligned}$$

and

$$a_{q_1} = a_{q_{4,1}} = 0.01433$$

since 'other causes' was the only source of death. The complete table of death probabilities based on the mortality data of Table 1 is given in Table 2. The computation of these rates is necessary for completing the full multiple decrement analysis. Note in Table 2 that the stage- and cause-specific mortality rates derived from the data are now expressed as per capita probabilities. Two aspects of this table may be noted: i) the highest death rate is due to late larval

Table 2. Cause-specific probability of death from specified causes in the presence of all causes for *R. pomonella* using hypothetical data presented in Table 1

Stage (index)	Total	Cause of death			
		Pre-dators	Parasites	Disease	'Other'
<i>x</i>	aq_x	aq_{1x}	aq_{2x}	aq_{3x}	aq_{4x}
Egg (1)	0.01433	0.00000	0.00000	0.00000	0.01433
Early Larvae (2)	0.84112	0.00000	0.23261	0.00000	0.60851
Late Larvae (3)	0.73203	0.65359	0.07842	0.00000	0.00000
Early Pupae (4)	0.22529	0.20230	0.00000	0.22990	0.00000
Late Pupae (5)	0.58690	0.37892	0.00000	0.05413	0.15385
Adult (6)	1.00000	-	-	-	-

predation; and ii) the highest stage-specific mortality occurs in early larvae and is due to both predation and 'other' causes.

Table construction

The main multiple decrement table uses the aq_{ix} -values in Table 2 to determine schedules for the fraction of the starting cohort dying in stage *x* due to cause *i* ($ad_{i,x}$), the total fraction dying in stage *x* due to all causes (ad_x) and the fraction of newborn surviving to stage *x* (al_x). These are computed as follows:

Step 1. Compute survival to stage *x* subject to all causes. We set $al_1 = 1.0$ and compute progressively

$$al_{x+1} = al_x(1.0 - aq_x).$$

For example

$$\begin{aligned} al_2 &= al_1(1.0 - aq_1) \\ &= 1.0(1.0 - 0.0143) \\ &= 0.9857 \end{aligned}$$

$$\begin{aligned} al_3 &= 0.9857(1.0 - 0.8411) \\ &= 0.1566 \end{aligned}$$

Step 2. Compute the fraction of newborn dying in stage *x* due to all causes. This is computed as

$$ad_x = al_x - al_{x+1}.$$

For example

$$\begin{aligned} ad_1 &= al_1 - al_2 \\ &= 1.0 - 0.9857 \\ &= 0.0143 \end{aligned}$$

Step 3. Compute the fraction of newborn dying in stage *x* due to cause *i*. We use the formula

$$ad_{i,x} = al_x(aq_{i,x}).$$

For example

$$\begin{aligned} ad_{4,1} &= al_1(aq_{4,1}) \\ &= 1.0(0.0143) \\ &= 0.0143 \end{aligned}$$

$$\begin{aligned} ad_{1,3} &= al_3(aq_{1,3}) \\ &= 0.1566(0.65359) \\ &= 0.1024 \end{aligned}$$

Values for the various relationships are given in Table 3. This table reveals relations that were not evident from Table 2. For example, nearly 83% of all deaths occur in the early larval stage, only about 4% of all newborn survive to the pupal stage, nearly 62% of all deaths are a result of 'other' causes and disease accounted for less than 1% of all deaths.

Elimination of cause

Concept

Farr (1875) apparently was the first to ask the question: "What would be the effect on life expectancy if a certain disease were eliminated as a cause of death?" This question is particularly germane to pest management since if it possible to gain an understanding of the effect on life expectancy of eliminating a particular source of death, it follows that the same methods could be used to determine the impact of adding a source of death.

The only definitive method for determining the effect on expectation on life in arthropod populations of eliminating a certain cause of death is through experiment (Luck et al. 1988; DeBach and Huffacker 1971). However, experimentation is sometimes either not possible or the only data available is natural history. Therefore it is necessary to mathematically approximate the effect of eliminating a cer-

Table 3. Life table deaths from specified causes at given stage of *R. pomonella* (data from Table 1)

Stage (index)	Probability of death	Fraction living at beginning of interval	Fraction of all deaths	Fraction deaths due			
				Predator	Parasites	Disease	'Other'
<i>x</i>	aq_x	al_x	ad_x	ad_{1x}	ad_{2x}	ad_{3x}	ad_{4x}
Egg (1)	0.0143	1.0000	0.0143	0.0000	0.0000	0.0000	0.0143
Early Larvae (2)	0.8411	0.9857	0.8291	0.0000	0.2293	0.0000	0.5998
Late Larvae (3)	0.7320	0.1566	0.1146	0.1024	0.0122	0.0000	0.0000
Early Pupae (4)	0.2253	0.0420	0.0095	0.0085	0.0000	0.0010	0.0000
Late Pupae (5)	0.5869	0.0325	0.0191	0.0123	0.0000	0.0018	0.0050
Adult (6)	-	0.0134	-	-	-	-	-
Totals*	-	-	0.9866	0.1232	0.2415	0.0028	0.6191

* Apply only to the total mortality to the adult stage (i.e. ad_x) and the totals for each of the four mortality causes (i.e. $ad_{i,x}$'s)

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tain cause. One such approach is described as follows. Suppose the probability of surviving factor A alone is p_A and factor B alone is p_B . Then the probability of surviving both independent causes together, denoted p_{AB} , is given as

$$p_{AB} = p_A p_B \quad (1a)$$

or

$$p_{AB} = (1 - q_A)(1 - q_B) \quad (1b)$$

where q_A and q_B are complements of p_A and p_B , respectively. If D_A and D_B denote the fraction of all individuals observed that died of cause A and B, respectively, then

$$p_{AB} = 1 - (D_A + D_B) \quad (1c)$$

and

$$1 - (D_A + D_B) = (1 - q_A)(1 - q_B). \quad (1d)$$

The objective is to obtain values for q_A and q_B since we would like to determine mortality in the absence of one or the other factor. It is necessary to specify a second equation since Eq. (1d) has two unknowns. By assuming that the ratio of numbers dying due to factor A to the numbers dying due to factor B equals the ratio of probability of dying due to factor A to the probability of dying due to factor B, we can obtain the second equation. That is:

$$\{q_A \ q_B\} = \{D_A/D_B\}. \quad (2)$$

Therefore Eqs. (1d) and (2) represent two simultaneous equations in two unknowns (q_A and q_B). By expressing q_A in Eq. (2) in terms of q_B , D_A and D_B and then substituting this expression in Eq. (1d) yields the quadratic equation

$$a q_B^2 + b q_B + c = 0 \quad (3)$$

where $a = D_A$, $b = -(D_A + D_B)$ and $c = D_B(D_A + D_B)$.

The value of q_B is found by substituting a , b and c into the quadratic formula

$$q_B = \frac{-b - \sqrt{b^2 - 4ac}}{2a}.$$

Elandt-Johnson and Johnson (1980), Namboordiri and Suchindran (1987) and Preston et al. (1972) present alternative approaches for finding the solutions to the independent risk probabilities.

As an example, suppose that of 1000 individuals observed over their preadult lifetime, 20 remained alive (i.e. 2%), 370 died due to natural enemies and 610 died of 'other' causes. Therefore set $D_A = 0.37$ and $D_B = 0.61$. Substituting these values into Eq. (3) yields $a = 0.37$, $b = -0.98$ and $c = 0.598$. Therefore

$$q_B = [0.98 - \sqrt{(0.98)^2 - 4(0.37)(0.598)}] / 2(0.37) = 0.953$$

and

$$q_A = q_B D_A / D_B = (0.953)(0.37) / 0.61 = 0.578$$

A graphical interpretation of the analysis is presented in Fig. 1. The results state that if factor A were completely eliminated as a source of mortality, factor B alone would still kill 95.3% of the original cohort. This is a substantial

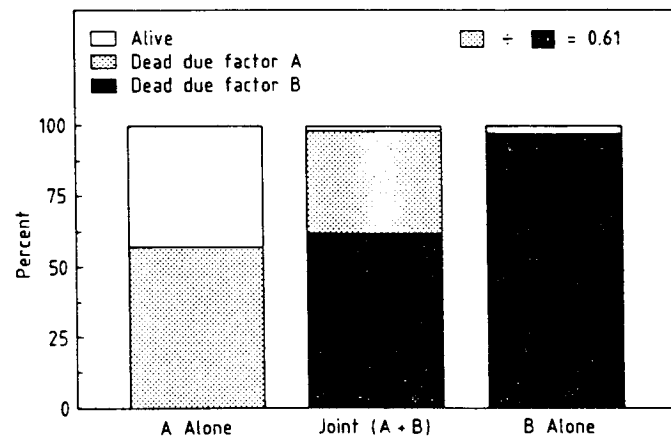


Fig. 1. Illustration of the concept of competing risk in hypothetical cohorts subject to mortality factors A alone, B alone and A and B jointly. Note that the ratio of those dead to A alone (q_A) and B alone (q_B) equals the ratio of the cause-specific mortalities when the two factors act jointly (i.e. D_A & D_B). That is, $\{q_A/q_B\} = \{D_A/D_B\} = 0.61$

increase from the 61% mortality due to this factor in the presence of factor A. On the other hand 57.8% would die if factor A alone accounted for deaths. In short, adding factor A as a cause of mortality when B is already present would increase mortality from 95.3 to 98% or less than 3%. However, by adding factor B as a cause of mortality when factor A is already present would increase mortality from 57.8 to 98% or by over 40%. These differences are referred to in the ecological literature as indispensable (or irreplaceable) mortality (Huffaker and Kennet 1965; Southwood 1971).

Note that computationally the concept of double decrement given here embraces all the issues of multiple decrement (Preston et al. 1972). That is, no matter how many causes are considered, the probability of dying from each can be computed by considering the one in question versus 'all others'.

Application to data

The data presented in Table 1 are used to compute the independent stage-by-cause probabilities of dying, q_{ix} 's. Note from this table that the egg stage has a single risk ('other'), early larvae, late larvae and early pupae have two competing risks each and late pupae have three competing risks. Thus for the egg stage we have:

$$q_{11} = q_{21} = q_{31} = 0$$

and

$$q_{41} = 1 - (963/977) = 0.0143$$

The independent probabilities for the two risks in each of the next 3 stages can be computed using the same relationships described in the earlier example with the quadratic equation. For example, 224 of 963 individuals were parasitized in stage 2 (early larvae) and 586 died of 'other' causes. Therefore let D_A denote the fraction of the total that died of parasites

$$D_A = 224/963 = 0.2326$$

Table 4. Stage and cause-specific probability of death for *R. pomonella* in the absence of all other causes. Totals computed prior to rounding

Stage (index)	Total	Cause of death			
		Pre- dators	Par- asites	Dis- ease	'Other'
<i>x</i>	q_x	q_{1x}	q_{2x}	q_{3x}	q_{4x}
Egg (1)	0.014	0.000	0.000	0.000	0.014
Early Larvae (2)	0.842	0.000	0.296	0.000	0.775
Late Larvae (3)	0.733	0.708	0.085	0.000	0.000
Early Pupae (4)	0.225	0.207	0.000	0.023	0.000
Late Pupae (5)	0.587	0.458	0.000	0.065	0.186
Egg to adult	0.987	0.874	0.356	0.087	0.762

and let D_B denote the fraction that died of 'other'

$$D_B = 586\ 963 = 0.6085.$$

Substituting these values in Eq. (3) yields values for $q_{22} = 0.296$ and $q_{42} = 0.775$. Probabilities for the three causes in stage 5 (i.e. predators, disease & 'other') are determined by applying the quadratic to three 2-cause cases: i) predators vs. (disease + 'other'); ii) disease vs. (predators + 'other'); and iii) 'other' vs. (predators + disease).

The results of this analysis are given in Table 4 where the q_{ix} 's denote the probability of dying in stage x of cause i in the absence of all other causes of death. These relations show that if a single cause of death were retained in the population, predation alone would reduce the cohort by over 87% while 'other' causes would reduce it by around 76%. This ranking of importance differs from the mortality data in the presence of all causes given in Table 3. From this perspective, predators appear to be less important in the presence of all causes since they attack later stages. Thus earlier causes of death reduced the number at risk in the stages susceptible to predation.

The q_{ix} -values in Table 3 were used to compute the effect of various combinations of factors on total mortality. For example, the effect of predators+parasites on total mortality was computed by: i) determining the probability of surviving each source in the absence of other sources over all stages. That is $(1 - q_{1x})$ and $(1 - q_{2x})$; ii) obtaining the product of the two survival probabilities within each stage: and iii) computing the product of these products over all stages. Since this gives total survival, 1 minus this value yields total mortality. The computations for this two-cause case are: $[(1 - 0)(1 - 0)] \times [(1 - 0)(1 - 0.296)] \times [(1 - 0.708)(1 - 0.085)] \times [(1 - 0.207)(1 - 0)] \times [(1 - 0.458)(1 - 0)] = 0.081$. This represents the fraction surviving to adulthood. Thus $(1 - 0.081) = 0.919$ gives the total preadult mortality.

The results of the complete analysis are given in Fig. 2. Several aspects of these results merit comment. *First*, the effect of simultaneously eliminating multiple cause-of-death agents from the population cannot be inferred from observing the effect of eliminating each individually. The total contribution to mortality exceeds the sum of the individual components of total mortality (Preston et al. 1972). *Second*, while predators alone would kill 87% of an original cohort, predators plus 'other' would reduce the population by

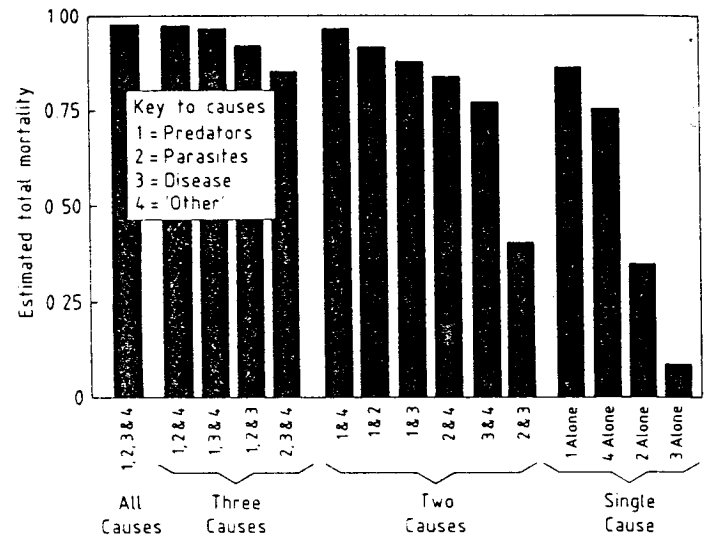


Fig. 2. Estimated total mortality in *R. pomonella* cohorts for different cause-specific combinations (see text)

nearly 98%. Thus the effect of adding parasites and disease to the system in the presence of the other two factors is negligible. *Third*, any pair-wise combination of parasites, disease and 'other' causes, as well as all three causes combined, would reduce the population less than would predation alone. Conversely, adding or subtracting predation as a source of mortality affects total mortality much greater than adding or subtracting any other single source.

Discussion

Multiple decrement theory embraces most of the major concepts and techniques currently used in insect mortality analysis. These include those mentioned earlier – conventional life table, Abbott's Correction and Key Factor Analysis – as well as others such as tests for joint chemical toxicity (eg. Hewlett and Plackett 1959, 1961, 1964; Sun and Johnson 1960; Robertson et al. 1984 a, b) and Probit Analysis (i.e. Finney 1964). The interconnections of these tools and multiple decrement theory are described as follows:

1. The independent variable for each is time, age, stage or dose. And for chemical tests such as Probit Analysis, dose and age are interchangeable in that age can be viewed as a dose of time. Thus Probit Analysis and life table analysis are conceptually and statistically identical (see Carey 1986). Abbott's Correction is simply a double decrement, single time step life table and tests of joint toxicity are essentially multiple decrement, one time step life tables. Key Factor Analysis orders events by stage as well as causes of death within a stage and is therefore a type of sequential risk life table.

2. All of the techniques either explicitly or implicitly rely on the assumption of competing risk. That is, the removal of one of several mortality factors within a stage or prior to the stage will change the number of individuals exposed to the risk of the cause in question. Thompson (1955) labelled these contemporaneous mortality factors and Huffaker and Kennett (1966) referred to the non-additive changes in mortality on removal of one of several competing risk as compensatory mortality. In the conventional single decrement life table, death at early stages is 'competing'

death at later stages. That is, a small fraction of total deaths occur at older ages simply because most have not yet attained old age. This is a form of sequential peting risk.

Most of the techniques are based on the assumption of independence. In conventional life table analysis it is assumed that the probability of surviving from age x to $x+1$ is independent of the probability of surviving from $x-1$ to age x and also independent of density. This assumption is explicit in Abbott's Correction or in the tests for joint toxicity where one chemical does not change the logical effect in the presence of another chemical. Likewise, in multiple decrement life tables it is assumed, for example, that if an insect is infected with a pathogen it is no more susceptible to predation than if it were not infected and that the associated probabilities of dying of either are density independent. Although it is commonly understood that few mortality factors are totally independent of the presence of other factors or of density, efforts at measuring and modelling these aspects have been less than satisfactory.

Because of the interrelationships with standard techniques for evaluating mortality in ecology, the current approach is felt to have applications beyond ones like the example given for *R. pomonella*. This work is felt to be especially relevant to research that develops quarantine treatment protocols in that there is currently a strong movement toward 'multiple-stage treatments'. Single stage chemical treatments are generally too damaging to the commodity and possibly to the consumer (T. Batchelor, per com). Another potential application may be in measuring mating competitiveness in male mass rearing programs for sterile release (Carey 1988). That is, a female can exit from current virgin state via one-of-two competing risks-fer-versus sterile males.

Despite the fact that demographers concerned with humans originated the life table that was introduced to the biological literature by Deevy (1947) and is now viewed as conventional, ecologists have subsequently resisted drawing from the human demographic and actuarial literature analytical techniques concerned with survival. The reason most frequently given for this provincialism concerns differences in the quality of the data. While the data on causes of death and death rates in plant and animal populations may be less accurate than human vital statistics, concepts for data evaluation are identical in both cases. Even the concepts involved in cause of death (eg. Moriyama 1956; Anon. 1962; Kitagawa 1977) or differences in susceptibility to death (eg. Vaupel and Yashin 1985, 1987) have direct bearing on coding, classifying and interpreting mortality patterns in, for example, insect populations (eg. van den Bosch and Messenger 1973; Sturm and Sterling 1986). Distinguishing between the underlying cause of death and contributory causes of death is often as difficult in humans as it is in animals. And estimating the effect on life expectancy by eliminating a major source of mortality is as important for policy in human populations as it is for conservation policies when dealing with endangered species (eg. Arnold 1983).

Although a few new perspectives on interpreting field mortality data have been presented recently (eg. Knipling and McGuire 1968; Royama 1981a, b, 1984; van Driesche 1983), no new broad approaches for evaluating mortality have been set forth since Varley (1947). Thus the applica-

tion of multiple decrement theory to plant and animal survival analysis is felt to be well overdue.

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