

Application note

M-DEC: A spreadsheet program for producing multiple decrement life tables and estimating mortality dynamics for insects

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ABSTRACT

In the single decrement life table, an individual exits the table in only one way: through death undifferentiated by cause. In the multiple decrement life table (MDLT), an individual can exit the table through differentiated causes of death. Because of its structure, numerous calculations of demographic importance can be produced from the data in the MDLT, including estimates of the probability of death in the presence or absence of a combination of causes. Producing these life tables using manual calculations can be tedious and time consuming. Therefore, we present here a spreadsheet program, M-DEC, which automatically calculates many of the demographic variables in the MDLT for use with insects.

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1. Introduction

Although the life table is an important tool in human demography and ecology, a disadvantage of several life-table approaches is the inability to account for individuals subject to mutually exclusive causes of death. In the single decrement life table, an individual exits the table in only one way: through death undifferentiated by cause. In the multiple decrement life table (MDLT), an individual can exit the table through differentiated causes of death. In this sense, any life table that differentiates and quantifies more than one cause of death is a MDLT. The MDLT was first developed and used for human demography and it now is also used for situations that might lead to exiting the table in addition to death, such as marriage, divorce, contraception, and pregnancy (Preston et al., 2001). Because of its structure, numerous calculations of demographic importance can be produced from the data in the MDLT. Consequently, the MDLT, which incorporates conventional life table analytic techniques, Abbott's correction for multiple causes of mortality, and aspects of key-factor analysis (Carey, 1989, 1993) is able to estimate the probability of death in the presence or absence of a combination of causes. This consideration is crucial because Carey (1989) and Peterson et al. (2009) showed that for insects it is

not possible to estimate the effect of any mortality factor without considering its interaction with competing mortality factors. These interactions are especially important when estimating the impact of natural enemies for both fundamental and applied questions in population ecology.

Peterson et al. (2009) conducted a large post hoc evaluation of phytophagous insect mortality using MDLT and elimination-of-cause analysis to estimate irreplaceable mortalities. Producing these life tables using manual calculations can be tedious and time consuming. Therefore, to efficiently prepare these MDLT, we developed a spreadsheet-based program in Microsoft Office Excel 2007. Here, we present an updated version of the program, M-DEC (see program in [Electronic Supplementary Material](#)), and explain its use and value. Our examples involve insects, but M-DEC can be modified for any organism with age- or stage-specific life table data.

2. Description of the spreadsheet program

The demographic calculations used by our program are based on those of Carey (1993). The assumptions for a MDLT include: (1) the death of each individual can be attributed to a single cause, (2) each individual has the same probability of dying from any cause, and (3) causes are independent (Carey, 1993). The spreadsheet tool designed to produce MDLT is simple to use and makes entering data and evaluating results efficient. It has the ability to calculate MDLT and elimination of causes for as many as 10 mortality factors and 10 developmental stages (1030 different solutions). Not only can observed data be entered into M-DEC, but also hypothetical

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data can be incorporated easily so the user can evaluate “what-if” scenarios.

The spreadsheet has five tab sheets (Introduction, Mortality Factors and Stages, Form, Tables, Results, and Chart Index). The “Introduction” tab sheet provides brief instructions on the use of the spreadsheet tool, notation definitions, and citations of additional information sources.

The tool uses a three-step process to enter data. First, in the tab sheet “Mortality Factors and Stages”, the user enters mortality factors and stages that are specific to the user’s life table if the factors are not included in the default list (Fig. 1). This list will populate drop-down menus in the next tab sheet.

Second, in the tab sheet “Form”, the user begins construction of a conventional table by selecting the stages and mortality factors from the drop-down menus (Fig. 2). The user selects each listed mortality factor and each life stage independent of each other. For example, if there are a total of four mortality factors (Parasitoid, Predator, Failure to Establish, and Unknown), the user selects each one of those factors from the drop-down menus “MF1”, “MF2”, “MF3”, and “MF4”. Then, if there are a total of five life stages (Egg, Larva I, Larva II, Larva III, and Pupa), the user selects each one of those stages from the drop-down menus “Stage 1”, “Stage 2”, “Stage 3”, “Stage 4”, and “Stage 5”.

Third, in the tab sheet “Tables”, the user will see the mortality factors and life stages selected from the drop-down menus on the conventional life table at the top of the sheet (Fig. 3). The user then enters data that were generated from the user’s life table study. The user enters l_x data (the number of individuals alive at the beginning of the stage) for each stage, and d_x data (the number of individuals dying during the stage) for each stage and cause. Once the data are entered, results can be viewed on the same tab and sheet for

three additional tables. The table titled “Probability of the Cause of Death” describes cause- and stage-specific probabilities of death uncorrected for the proportions of total mortality. The notation for this table is aq_x , the fraction of deaths from all causes in stage x given that the individuals are alive at the beginning of stage x (Fig. 3).

The table titled “Probability for Cause of Death in the Presence of Other Causes” describes the proportional contribution of total mortality by cause. The notations for this table are aq_x (the fraction of deaths from all causes in stage x given that the individuals are alive at the beginning of stage x), al_x (the fraction of survivors at stage x out of original cohort of al_1), ad_x (the fraction of deaths in stage x from all causes). Numerical values for each category of death represent aq_{ix} , the fraction of deaths from cause i in stage x in the presence of all other causes, given that the individual is alive at the beginning of stage x . The total value within each column is the fraction of death by cause across all stages (Fig. 4).

The table titled “Probability for Cause of Death in the Absence of Other Causes” describes the proportion of mortality for one factor in the absence of all other causes. The total value within each column is the fraction of death by specific cause in the absence of all other causes (Fig. 4). Carey (1993) derived a quadratic solution to attribute mortality to each individual factor in the absence of all other factors, and we use his quadratic solution in our spreadsheet. Briefly, elimination-of-cause analysis relies on the probability of surviving each source of mortality (P_x) and its complement ($1 - q_x$) where $(1 - q_1) \times \dots \times (1 - q_n)$ is the chance of jointly surviving a set of mortality factors and its complement, $1 - [(1 - q_1) \times \dots \times (1 - q_n)]$, is the chance of jointly dying from a set of mortality factors. To estimate mortality in the absence of one or more factors, two simultaneous equations with two unknowns must be used. For example, by expressing q_1 in terms of q_2 , D_1 and D_2 (the fraction

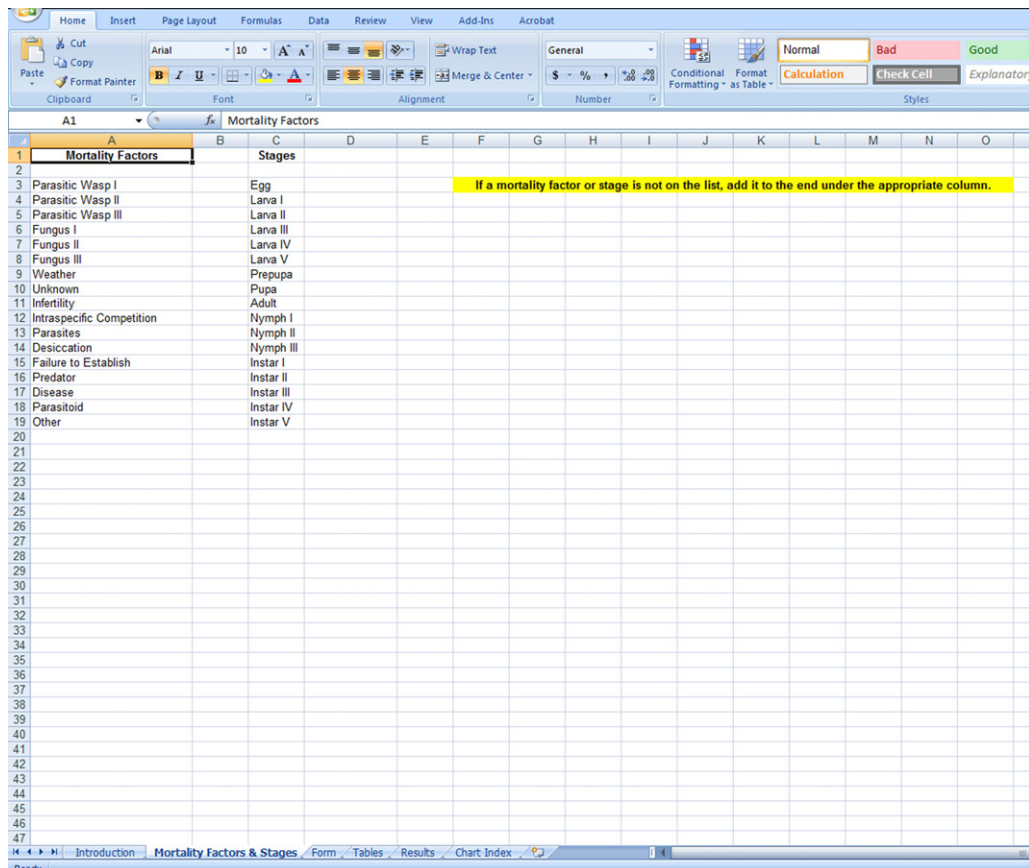


Fig. 1. The tab sheet “Mortality Factors and Stages”.

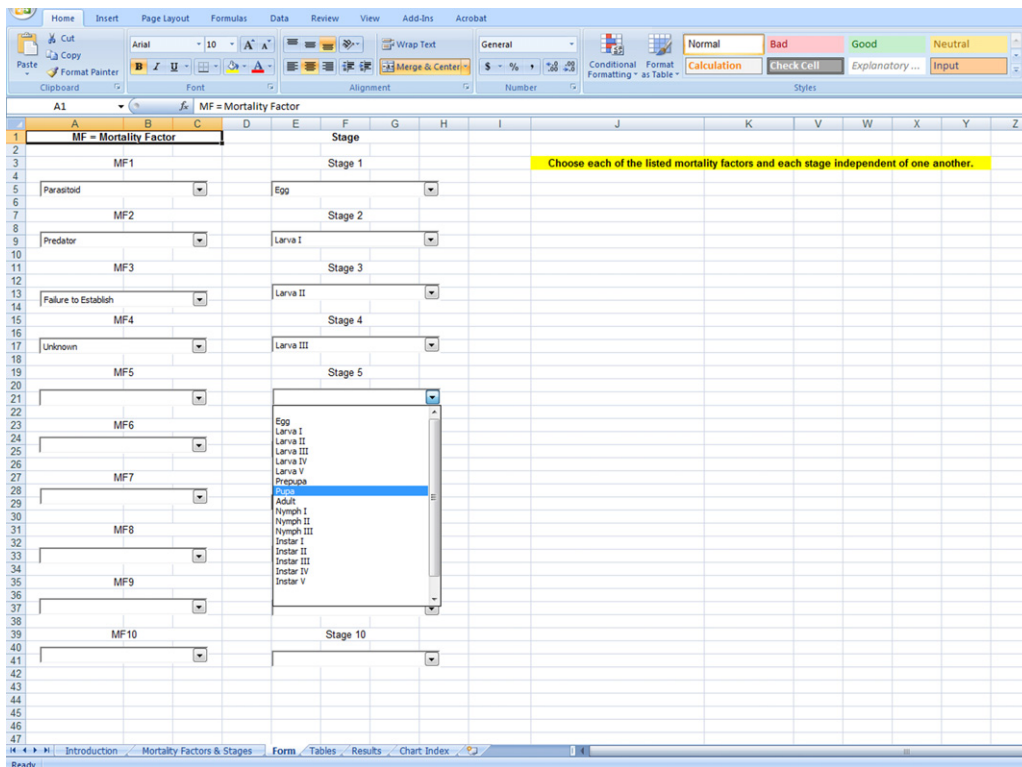


Fig. 2. The tab sheet “Form”. The user begins the construction of a conventional life table by selecting the stages and mortality factors from the drop-down menus. Stage 5 is in the process of being selected.

Enter the conventional life table data. Then you can view results.

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Conventional Life Table							
x	lx	dx	Parasitoid	Predator	Failure to Establish	Unknown	
Egg	4220	963	532	247	0	184	
Larva I	5665	5288	0	453	4016	819	
Larva II	3170	2146	391	94	23	1638	
Larva III	1631	1253	850	67	0	336	
Pupa	540	123	102	12	0	9	

Probability of the Cause of Death (uncorrected for proportion of total mortality)							
x	lx	aqx	Parasitoid	Predator	Failure to Establish	Unknown	
Egg	4220.0000	0.2282	0.1261	0.0585	0.0000	0.0436	
Larva I	5665.0000	0.9335	0.0000	0.0800	0.7089	0.1446	
Larva II	3170.0000	0.6770	0.1233	0.0297	0.0073	0.5167	
Larva III	1631.0000	0.7682	0.5212	0.0411	0.0000	0.2060	
Pupa	540.0000	0.2278	0.1889	0.0222	0.0000	0.0167	

Fig. 3. The tab sheet “Tables”. In the first table, the user enters the data that were generated from her or his study.

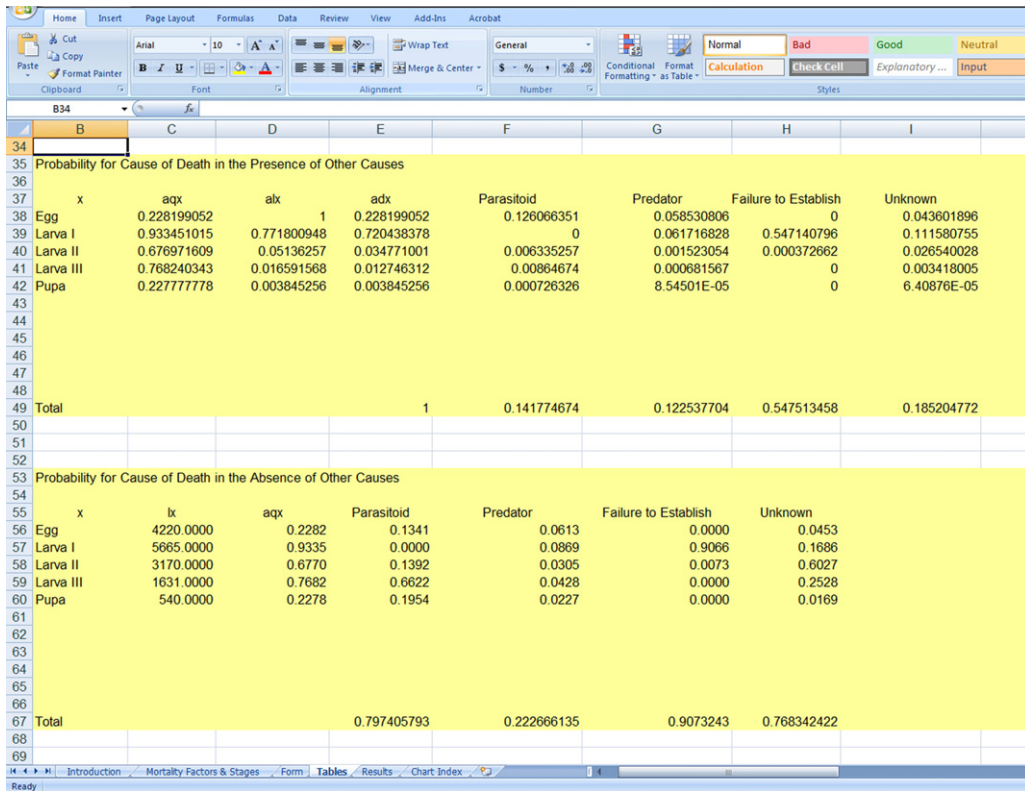


Fig. 4. The tab sheet “Tables”. The two tables shown are multiple decrement life tables with values automatically calculated and displayed by M-DEC.

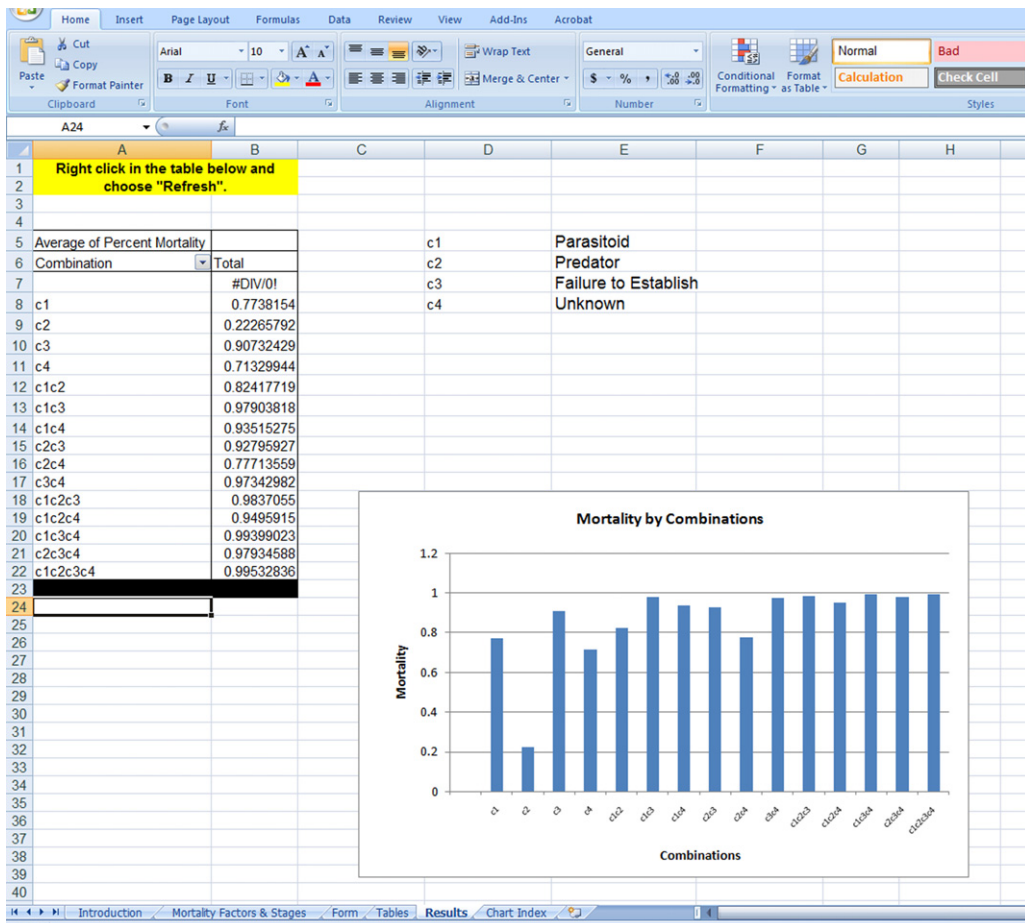


Fig. 5. The tab sheet “Results” includes all outcomes from the elimination-of-cause analysis.

of all individuals observed that died of cause 1 and 2), this yields the quadratic equation $aq_2^2 + bq_2 + c = 0$, where $a = D_1$, $b = -(D_1 + D_2)$ and $c = D_2(D_1 + D_2)$. The value of q_2 can be found by substituting a , b , and c into the quadratic formula (Carey, 1989, 1993).

A valuable aspect of the MDLT is the ability to estimate mortality in the absence and presence of a combination of causes. Therefore, the “Results” tab sheet includes all outcomes from an elimination-of-cause analysis, both numerically and graphically, for every possible combination of mortality factors from the “Tables” sheet. The user must first right-click on the table on the “Results” sheet, then select the “Refresh” option (Fig. 5). The resulting display which includes the estimation of total mortality for all combinations of mortality factors will be displayed.

An important extension of the MDLT is the ability to estimate irreplaceable mortality (also known as indispensable mortality), which is the mortality rate from a specific factor that cannot be replaced by another factor (Huffaker and Kennett, 1966; Southwood, 1978; Carey, 1993). To estimate irreplaceable mortality for any cause or combination of causes, the remaining causes must be subtracted from the total mortality from all causes. For example, to estimate the irreplaceable mortality from “Parasitoids” in the scenario described above, the mortality from “Predators, Failure to Establish, and Unknown” is subtracted from the total mortality from all four causes. The remainder is the irreplaceable mortality from parasitism.

The final tab and sheet is “Chart Index”, which is used to provide the data for populating the graph on the “Results” sheet. “Chart Index” does not require any user input.

2.1. Example

The user has a total of four mortality factors (Parasitoid, Predator, Failure to Establish, Unknown) and five life stages (Egg, Larva I, Larva II, Larva III, Pupa), so he selects each one of those factors from the drop-down menus “MF1”, “MF2”, “MF3”, and “MF4” and each life stage from the drop-down menus “Stage 1”, “Stage 2”, “Stage 3”, “Stage 4”, and “Stage 5” in the tab sheet “Form” (Fig. 2). The user proceeds to the tab sheet “Tables” where he will see that both the life stages and mortality factors are listed on the tables. He then enters the l_x data for each stage and d_x data for each mortality factor by stage (Fig. 3). All other values for the three tables below the conventional life table are automatically calculated by M-DEC (Figs. 3 and 4). Note that in the table “Probability for Cause of Death in the Presence of Other Causes”, the mortality from par-

asitism in the Larva III stage is 0.9% of the overall mortality even though parasitism accounts for 52% of the total mortality in that stage. Total mortality from parasitism is 14% in the presence of all other causes, but is 80% if parasitism is present in the absence of all other causes (Fig. 4). In tab sheet “Results”, note that the total mortality is 99.5% (c1c2c3c4) (Fig. 5). Above that value, all combinations are presented. From these combinations, irreplaceable mortalities can be estimated. For example, even though parasitism accounts for 14% of total mortality, the irreplaceable mortality from parasitism is only 1.6% (c1c2c3c4–c2c3c4). This means that all but 1.6% of the mortality from parasitism would have been replaced by other factors if parasitism was not present. This can be seen in the graph as well. The bar on the far right of the graph shows the total mortality with all factors. The other bars to the left show the mortalities when causes are removed.

The example above shows the value of M-DEC for addressing questions of effectiveness of natural enemies in biological control. In addition, M-DEC can be used for many other basic and applied problems in population ecology, including preservation of endangered or threatened populations, conservation of species, and management of floral and faunal species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.compag.2010.12.009.

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