

1 **Life tables data collection in entomology: an overview on the differential and the integral representation**
2 **and proposal for a standard electronic file**

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22

23 ***Abstract***

24

25 Life tables are the most common tool to explore the biology of insects and of many terrestrial arthropods, as
26 well as to understand their response to external factors (i.e., temperature, relative humidity, diet, etc.). The data
27 collection process has been partially standardised over the years and life tables results are presented mainly
28 depending on the purpose of the study. In fact, two different representations of the data can be obtained from
29 the raw dataset: a differential and an integral representation. The two representations provide relevant
30 biological information, but they lead to a loss of information (e.g., the stage-duration of each specimen) with
31 respect to the raw dataset. To date, a conceptual explanation of how the two representations can be obtained
32 from the raw data, and of their respective properties, is still missing; moreover, providing the raw dataset as

33 supporting information of the published papers is still not customary by the authors. This paper highlights three
34 main points: *i)* how the two representations are obtained by the life tables raw dataset, *ii)* without raw data it
35 is not possible to switch between the two representations, with a subsequent loss of information, *iii)* why there
36 is the need for a data collection standard. In addition to the conceptual explanation, this work also provides a
37 proposal for a standard data collection spreadsheet that could support data collection, data sharing, and that
38 automatically transform the data in the two representations. We believe that this study is a first step towards a
39 more efficient diffusion of the information among the scientific community, maximising the efforts made by
40 scholars during the experimental and data analysis process.

41

42 **Keywords:** key 1

43

44 **1. Introduction**

45

46 Measurements, data collection, and data representation standards are essential for scientific research, as they
47 ensure the consistency of collected data; this is in turn fundamental to allow the reproducibility of experiments,
48 and coherent data sharing (Mari et al., 2012; Zhan and Xie, 2020). Indeed, there is a high value in collecting
49 and organising data using standardised protocols, allowing for comparability and re-usability of the data (Mons
50 et al., 2017; Stall et al., 2019). Such aspect is particularly important whenever data sharing between research
51 groups is foreseen. It is thus not surprising that all scientific communities that develop and use shared
52 databanks (e.g. NCBI for genetic sequencing <https://www.ncbi.nlm.nih.gov/>) have defined strict standards on
53 how to carry out the experiments and report data (NCBI Resource Coordinators, 2012; Sherry, 2001). In
54 entomology and ecology, the transition towards more quantitative approaches is highlighting the need for
55 defining clear and standard data measurement and representation protocols.

56 Life tables are one of the most recurring laboratory experiments in entomology to explore the biology of the
57 species (of insects and terrestrial arthropods at large) and their reaction to external factors (i.e., temperature,
58 relative humidity, diet, etc.) (Rossini et al., 2024a, 2025). Such factors consist of rearing individuals under
59 controlled conditions and sampling their development at fixed time intervals (Bellows, 1992; Harcourt, 1969;
60 Hsieh, 1991). The resulting dataset from the subject species provides developmental information on a series

61 of important qualitative (e.g., morphological traits) and quantitative (e.g., stage duration, minimum
62 development time, mortality, fertility/egg production) features of the species (Chi and Liu, 1985). Studies are
63 typically carried out under different rearing conditions which may include factors as temperature, humidity,
64 CO₂, nitrogen, diet, or pesticide treatment (Alves et al., 2013; Korpelainen, 1986; Liu et al., 2017; Rossini et
65 al., 2024b; Sánchez-Ramos et al., 2007; Vantornhout et al., 2005; Wen et al., 2020). Even if conditions and
66 goals of the experiments may differ, the procedure is always the same: all experiments determine dead or alive
67 life stages at each inspection and measure qualitative and/or quantitative insect traits depending on the research
68 question (Chi et al., 2023, 2020). This allows researchers to track the life history of the population and define
69 development time, mortality, and fertility quantitatively at different rearing conditions (Chi et al., 2023, 2020;
70 Rossini et al., 2024a). Typically, researchers are interested in analysing differences among various rearing
71 conditions, to validate the hypotheses behind the experiment. However, to reach this goal there is a need for a
72 clear organisation of the dataset that possibly warrants reproducibility of results and application of standard
73 procedures for data analysis (Rossini et al., 2024a).

74 The starting point of this paper is the observation that for this crucial type of experiment, the data collection
75 and data reporting is a process that, to date, is still not univocally defined among entomologists. In fact, if we
76 look at the specific literature, we do not find either the raw data (except in very few cases), or a standardised
77 method for acquisition and reporting of the data (Kareithi et al., 2019; Rossini et al., 2025, 2024a). Currently
78 there are two main representations of the data that have been used in the literature, and whose analysis will be
79 the starting point for this study.

80 The first representation of life tables data records daily changes. This data typically includes recordings of
81 newly developed life stages, dead individuals, and new offspring (eggs) per female (Bieri et al., 1983; De
82 Campos et al., 2020; Genç and Nation, 2008; Moshtaghi Maleki et al., 2016; Nielsen et al., 2008; Samayoa et
83 al., 2018; Southwood, 1978; Tochen et al., 2014; Van Nieuwenhove et al., 2016). The representation leads to
84 a distribution of the development times of each life stage, datasets from which we can obtain descriptive
85 statistics parameters such as the mean value, standard deviation, median, mode, kurtosis, or skewness (Rossini
86 et al., 2024a). Such values are then listed in specific tables as a result and are widely employed in the
87 parameterisation of mathematical models that describe the population dynamics over time (Rossini et al.,
88 2019a, 2020a, 2021a, 2021b, 2025).

89 The second representation was introduced by Chi et al. (Chi, 1988; Chi and Liu, 1985), and consists of
90 developmental life stage, mortality, and fertility matrices containing life stages and age. This framework is
91 inspired by the Leslie matrix (Leslie, 1948, 1945), which however is not suitable to describe insect populations
92 because of the different age-stage division (Chi and Liu, 1985). Elements contained in the matrices depend on
93 their purpose and should contain count of individuals, survival rates, mortality rates, and fecundity. Such data
94 allows scholars to compute some key parameters that characterise the population, such as the intrinsic rate of
95 increase, mean generation time, and age-specific fecundity (Bellows, 1992; Chi et al., 2020, 2023; Rossini et
96 al., 2024a).

97 The two representations can be seen as a “*differential*” representation (the first) and an “*integral*”
98 representation (the second). In this paper we show that these two approaches have benefits and disadvantages
99 and that they are not equivalent: from the differential representation is not possible to recover the information
100 of the integral one and *vice versa*, unless the raw data is available. However, although Chi (Chi, 1988) provides
101 a valuable example of how raw data should be collected (see Table 1 of their study), raw data is not commonly
102 provided in entomology.

103 It is worth remarking that the generation of life tables’ data is characterised by high costs in terms of time and
104 personnel (Kareithi et al., 2019). Given the large effort to generate the data, the fact that the two main
105 representations used in the literature are not comparable nor mergeable is a major issue. This work aims at
106 clarifying the relationship between the common “*differential*” and “*integral*” representation presented in the
107 literature and to suggest a standardised data collection and documentation procedure. This methodology will
108 allow subsequent studies to more effectively determine both population dynamics and cohort representations.
109 In addition, we also propose a standardised spreadsheet template that can support the scientific community to
110 plan experiments and that can be used as supplementary material to first share data during paper submissions,
111 and then after publication. This tool will allow us for a simple and versatile solution that can facilitate open
112 data while not requiring high programming skills, and that may also constitute a basis for the future
113 development of a common database, as already done in other fields of research.

114

115 2. Materials and Methods

116

117 To fully understand the problem of the data collection, the study was structured in two parts. The first one is
 118 more conceptual and highlights the *pros* and *cons* of the most common representations of data for life tables,
 119 and the connections with the raw dataset. The second part introduces our proposal for a standard as well as its
 120 implementation through an electronic spreadsheet file. It is worth pointing out that this study will focus only
 121 on development and mortality, but not on fertility. The two representations, in fact, do not affect the
 122 information on fertility, as this experiment can be conceptually considered as independent. Fertility has been
 123 already well discussed by Chi et al. (Chi, 1988; Chi et al., 2023, 2020; Chi and Liu, 1985) and it is fully inserted
 124 in the framework discussed hereafter.

125

126 **2.1. Background: how do we collect raw data?**

127 Data collection is the starting point of the process, and it is directly related to the experimental trials. The eggs
 128 are placed in climatic chambers at day zero and are usually separated and labelled to maintain their identity.
 129 According to the suggestions of Chi (Chi, 1988), the experimenter should build a table where the lines indicate
 130 the number of the specimen reared (so that the individuality can be maintained) and the columns represent the
 131 sampling time. For the sake of exposition, and with no loss of generality, in this work we consider a sampling
 132 time of one day. The life stages composing the life cycle can be abbreviated with acronyms or letters, as for
 133 instance “E” for “egg”, “L1” or “N1” for first instar larvae or nymphs, until the death, that may be indicated
 134 as “D”. Those acronyms will be the elements of the table, indicating the stage in which the individual “*i*” was
 135 at time *t*: an idea of how this kind of tables should look like is provided in Table 1.

136

137 Table 1: Example of table to report the raw data of life tables experiments. Rows indicate the number of the
 138 specimens, while columns the days. Each label composing the element of the table indicates the life stage: in
 139 this example “E” means *egg*, “L1”, “L2”, and “L3” indicate the *first*, *second*, and *third larval stage*,
 140 respectively, and “D” indicates the *dead*.

	Time (day)												
	1	2	3	4	5	6	7	8	9	10	11	12	...
Specimen													
SP-1	E	E	E	L1	L1	L1	L2	L2	L2	L2	L3	L3	...

SP-2	E	E	L1	L1	L1	L2	L2	L2	L2	L3	L3	L3	...
SP-3	E	E	E	L1	L1	L1	L1	L2	L2	L2	L2	L3	...
SP-4	E	E	L1	L1	L1	L1	L2	L2	L2	L2	L3	L3	...
SP-5	E	E	E	D	--	--	--	--	--	--	--	--	--
SP-6	E	L1	L1	L1	L2	L2	L2	L2	L3	L3	L3	L3	...
SP-7	E	E	E	L1	L1	L1	L2	L2	L2	L3	L3	L3	...
SP-8	E	E	E	L1	L1	L1	L1	L2	L2	L2	L2	L3	...
SP-9	E	E	E	E	L1	D	--	--	--	--	--	--	--
SP-10	E	E	L1	L1	L1	L2	L2	L2	L2	L3	L3	L3	...
SP-11	E	E	E	L1	L1	L1	L1	L2	L2	L2	L3	L3	...
SP-12	E	E	L1	L1	L1	L1	L2	L2	L2	L2	D	--	--
SP-13	E	E	L1	L1	L1	L1	L2	L2	L2	L3	L3	L3	...
SP-14	E	E	L1	L1	L1	L1	L2	L2	L2	L2	L3	L3	...
SP-15	E	E	L1	L1	L1	L1	L2	L2	L2	L2	L2	L3	...
SP-16	E	E	E	L1	L1	L1	L2	L2	L2	D	--	--	--
...

141

142 Typically, these raw data are not published, and they are further analysed or processed. The ways this operation
143 is usually carried out leads to the two different representations that we discuss in Sections 2.2 and 2.3. To fix
144 the ideas, the differential and the cohort representation can be obtained by manipulating the rows and the
145 columns of the Table 1, respectively.

146

147 **2.2. Distribution of the development times for each stage and differential representation**

148 A typical first step to extract information from the raw data is to report the life stage duration of each specimen,
149 i.e. counting how many elements with the same stage label are along each line of Table 1. The values hereby
150 computed are reported in two tables: one accounting for individuals who successfully developed to the next
151 stage, hereafter denoted as *stage-development table* (Table 2), and one accounting for died individuals,
152 hereafter denoted as *stage-mortality table* (Table 3). In other words, this step converts Table 1 into two
153 quantitative tables that can be further processed.

154 Table 2 is an example of stage-development table, where the rows contain the life histories of the individuals,
 155 the columns indicate the life stages, and the elements represent the duration of the stage between life stages.
 156 Table 3 is an example of stage-mortality table, conceptually similar to Table 2 except for the meaning of the
 157 elements, that hereby indicate the duration from the last metamorphosis to death. Adult survival (or longevity)
 158 is part of the stage-mortality table (Table 3) to be coherent with the definition of development, as “survival”
 159 indicates the times between the adult emergence and the death.

160
 161 Table 2: First elaboration of the dataset collected in Table 1 – *Stage-development table*. The rows indicate the
 162 individuals of the population, the columns the life stages, and the elements the duration in days (or other time
 163 sub-units). This table should be read as follows: “*Specimen SP-1 spent 3 days to pass from egg to L1*”, or, as
 164 an alternative “*The duration of the egg stage of the specimen SP-1 was 3 days*”. LN denotes the last preimaginal
 165 stage, while the double dash “--” indicates that the specimen died in the latest stage having numeric values in
 166 the corresponding cell.

Specimen	Stages					
	E	L1	L2	L3	...	LN
SP-1	3	3	4	4	--	13
SP-2	2	3	4	5	...	12
SP-3	3	4	4	5	...	12
SP-4	2	4	4	4	...	12
SP-5	--	--	--	--	...	--
SP-6	1	3	4	5	...	13
SP-7	3	3	3	5	...	13
SP-8	3	4	4	4	...	13
SP-9	4	--	--	--	...	--
SP-10	2	3	4	4	...	13
SP-11	3	4	3	4	...	12
SP-12	2	4	--	--	...	--
SP-13	2	4	3	5	...	12
SP-14	2	4	4	5	...	12

SP-15	2	4	5	4	...	13
SP-16	3	3	--	--	...	--
...

167

168

169 Table 3: First elaboration of the dataset collected in Table 1 – *Stage-mortality table*. Rows indicate the
170 individuals of the population, columns the life stages, and the elements the days from the last metamorphosis
171 to death (D). This table should be read as follows: “*Specimen SP-5 died 4 days after the egg oviposition*”, or,
172 as an alternative “*Specimen SP-9 died 2 days after turning L1*”. The double dash “--” indicates that the
173 specimen successfully developed in the previous stages having numeric values or died before, while AF and
174 AM denote adult males and females, respectively.

Specimen	Stages						
	E-D	L1-D	L2-D	AF-D	AM-D
SP-1	--	--	--	--	...	--	74
SP-2	--	--	--	--	...	--	78
SP-3	--	--	--	--	...	79	--
SP-4	--	--	--	--	...	--	72
SP-5	4	--	--	--	...	--	--
SP-6	--	--	--	--	...	72	--
SP-7	--	--	--	--	...	80	--
SP-8	--	--	--	--	...	--	64
SP-9	--	2	--	--	...	--	--
SP-10	--	--	--	--	...	63	--
SP-11	--	--	--	--	...	--	81
SP-12	--	--	5	--	...	--	--
SP-13	--	--	--	--	...	60	--
SP-14	--	--	--	--	...	74	--
SP-15	--	--	--	--	...	--	70
SP-16	--	--	4	--	...	--	--
...

175

176 It is worth remarking that although this first step of the data analysis does not introduce any loss of information
177 with respects to the raw data (while making them much more readable), it is not customary to report these
178 tables in scientific papers (Kareithi et al., 2019).

179 Indeed, the information listed in the stage-development table (e.g. Table 2) and in the stage-death table (e.g.
180 Table 3) is mostly used as an intermediate step (usually not published) to reach a *differential representation* of
181 life tables data, also known as “*population dynamics representation*”. The differential representation is usually
182 reported as a table or, equivalently, as a family of frequency histograms (an example of the table and of the
183 associated histograms are provided in Table 4 and Fig. 1, respectively) describing the distribution of the stage-
184 development and mortality times of each stage and using bins size coinciding with the sampling time of the
185 experiment. As detailed by Rossini et al. (Rossini et al., 2024a), the stage-distributions of development and
186 mortality can be interpreted as a stage-population dynamics, namely the set of newly emerged (or died)
187 individuals per stage and per sampling unit (e.g., per day). From a mathematical point of view, we can
188 summarise the information of the j -th stage histograms as the column vectors

$$G_D^j = (g_{1j}^D, g_{2j}^D, \dots, g_{ij}^D)^T \quad (1)$$

189 and

$$D_D^j = (d_{1j}^D, d_{2j}^D, \dots, d_{ij}^D)^T, \quad (2)$$

190 where the elements g_{ij}^D and d_{ij}^D denote the number of individuals that spent exactly i days in stage j before
191 passing to stage $j + 1$ or dying.

192

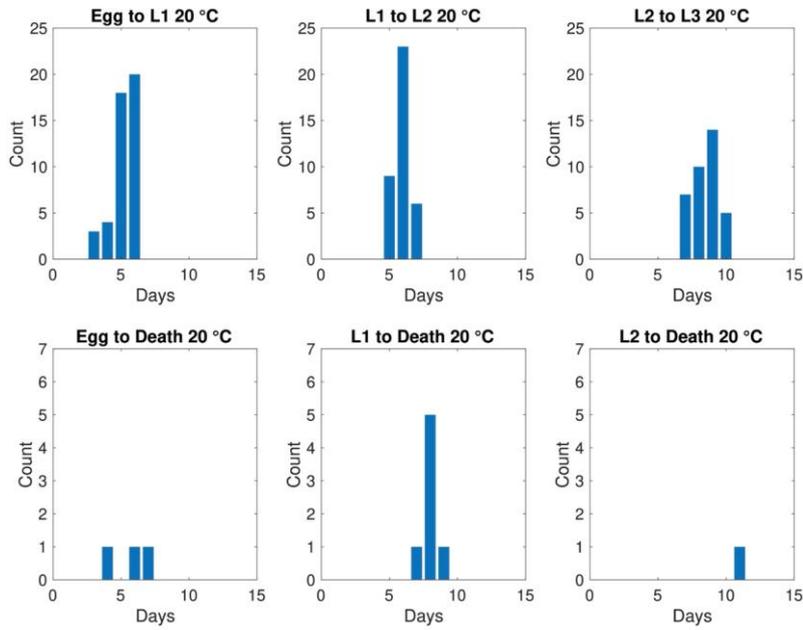
193 Table 4: Example of table data typically resulting from the life tables *differential representation*. The table
194 was made for the sake of exposition using a small portion of unpublished data on *Drosophila suzukii* life tables
195 data at 20 °C. E indicates the egg stage, L1, L2, and L3 indicate the first, the second, and the third larval instars,
196 respectively, and D indicates the death.

Commenté [LR1]: If accepted, cite Baser et al. 2025

Time (days)	Development			Mortality		
	E to L1	L1 to L2	L2 to L3	E to D	L1 to D	L2 to D
1	0	0	0	0	0	0

2	0	0	0	0	0	0
3	3	0	0	0	0	
4	4	0	0	1	0	0
5	18	9	0	0	0	0
6	20	23	0	1	0	0
7	0	6	7	1	1	0
8	0	0	10	0	5	0
9	0	0	14	0	1	0
10	0	0	5	0	0	0
11	0	0	0	0	0	1
12	0	0	0	0	0	0

197



198

199 Figure 1: Example of histogram of the data typically resulting from the life tables *differential representation*.
 200 These plots were made for the sake of exposition using a small portion of unpublished data on *Drosophila*
 201 *suzukii* life tables data at 20 °C.

202
 203 The set of vectors (1) and (2) are organised to form the stage-development and the stage-mortality matrices G_D
 204 and D_D , respectively, that assume the following forms:

$$G_D = \begin{pmatrix} g_{11}^D & g_{12}^D & g_{13}^D & \dots \\ g_{21}^D & g_{22}^D & g_{23}^D & \dots \\ g_{31}^D & g_{32}^D & g_{33}^D & \dots \\ g_{41}^D & g_{42}^D & g_{43}^D & \dots \\ g_{51}^D & g_{52}^D & g_{53}^D & \dots \\ g_{61}^D & g_{62}^D & g_{63}^D & \dots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix} \quad (3)$$

205 and

$$D_D = \begin{pmatrix} d_{11}^D & d_{12}^D & d_{13}^D & \dots \\ d_{21}^D & d_{22}^D & d_{23}^D & \dots \\ d_{31}^D & d_{32}^D & d_{33}^D & \dots \\ d_{41}^D & d_{42}^D & d_{43}^D & \dots \\ d_{51}^D & d_{52}^D & d_{53}^D & \dots \\ d_{61}^D & d_{62}^D & d_{63}^D & \dots \\ \vdots & \vdots & \vdots & \ddots \end{pmatrix} \quad (4)$$

206 An interesting property of G_D and D_D is the mass conservation along the columns: by summing all the values
 207 on the columns, we obtain the total number of individuals alive (matrix G_D) or dead (matrix D_D). The matrices
 208 G_D and D_D can also be normalised by dividing each element g_{ij} and d_{ij} by the size of the initial cohort.
 209 Accordingly, the columns can be seen as the impulse response (of the alive or of the dead) as described by
 210 Rossini et al. (Rossini et al., 2024a), which is a convenient way to describe the stage-distributions of individuals
 211 over time. A biological interpretation of the impulse response is the following: the elements of the matrices
 212 indicate the stage-probability that the individuals have of developing (G_D) or dying (D_D) over time.
 213 Matrices G_D and D_D are extremely useful to understand the patterns of development of the population and to
 214 extract synthetic values such as the mean duration of the stage (or from the metamorphosis to mortality), its
 215 standard deviation or standard error, and other parameters that depict the shape of the distribution, namely
 216 median, mode, skewness, and kurtosis. Other useful information that can be extracted from the differential
 217 representation is the minimum and the maximum time before and after which, respectively, no individuals

218 should be expected to develop. This is a biologically meaningful information that is of great importance in
 219 many fields, as for instance in pest control. Knowing the minimum amount of time required by an organism
 220 growing under given conditions (i.e., the *minimum development time*) is fundamental for planning effective
 221 control strategies that possibly target the peak of the population of the life stage more susceptible to the type
 222 of treatment chosen. The differential representation, accordingly, is a very useful tool to analyse the effect of
 223 the rearing conditions on the different life stages.

224 Despite the advantages that the differential representation provides, it is worth remarking that it introduces a
 225 loss of information with respect to the dataset of the stage development and stage mortality matrices (such as,
 226 e.g. Table 2 and 3). Indeed, in this representation the individual story of each specimen is lost, and time is reset
 227 at each metamorphosis. This loss of information is not a minor aspect, and it might hide some important
 228 information about how the development in one stage influences the next one. Furthermore, it might prevent
 229 the detection of anomalies (e.g. to identify sub-populations with different development patterns). To better
 230 understand this fact, let us consider the following example.

231
 232 *Example 1.* This example aims to show, in a simple way, that the differential representation introduces a loss
 233 of information w.r.t. the original *stage-development table* and *stage-mortality table* (and thus to the raw data),
 234 and that this might even hide possible problems in the experiments, hindering the comparability between
 235 results obtained independently. Let us consider a population with only three stages (E, L, A) and a population
 236 of 180 individuals at day 0. The corresponding matrix G_D (3) is reported in Table 5. This example focuses on
 237 a differential representation where the development from E to L is in 1 day for $\frac{1}{2}$ of the population and in 2
 238 days for the rest of the population, and the development from L to A is in 1 day for $\frac{1}{3}$ of the population and in
 239 2 days for the rest of the population.

240
 241 Table 5: Differential representation of the dataset discussed in the *Example 1*.

Time (days)	Development	
	E to L	L to A
1	60	60
2	120	120

242

243 Looking at Table 5, it is possible to see that from this matrix we cannot reconstruct the information contained
 244 in the stage-development table (Table 2): in fact, there are multiple datasets that can give rise to such a G_D . In
 245 Table 6 we report two different *stage-development tables* which both generate Table 5. This example highlights
 246 one of the risks in using only the differential representation to describe life tables experiments. In fact, if we
 247 look at the two datasets, the first one shows a homogenous population where the development in the first stage
 248 does not influence the development in the second stage. *Vice versa*, in the second dataset, there is a full
 249 correlation between the development from E to L and the development from L to A (if they did the first
 250 transformation in 1 day, the second will be in 1 day, if they did the second transformation in 2 days, the second
 251 will be in 2 days). This important information (which might suggest either the presence of some biological
 252 insights or the fact that part of the population had a genetic mutation) is completely lost by only using the
 253 differential approach.

254

255 Table 6: Stage-development tables (a and b) that can be obtained by the differential representation listed in
 256 Table 5.

Specimen	Stage-development table a		Specimen	Stage-development table b	
	E	L1		E	L1
SP-1	1	1	SP-1	1	1
⋮	⋮	⋮	⋮	⋮	⋮
SP-20	1	1	SP-20	⋮	⋮
SP-31	1	2	SP-31	⋮	⋮
⋮	⋮	⋮	⋮	⋮	⋮
SP-60	1	2	SP-60	1	1
SP-61	2	1	SP-61	2	2
⋮	⋮	⋮	⋮	⋮	⋮
SP-100	2	1	SP-100	⋮	⋮
SP-101	2	2	SP-101	⋮	⋮

⋮	⋮	⋮	⋮	⋮	⋮
SP-180	2	2	SP-180	2	2

257

258 **2.3. Cohort (integral) representation**

259 The second representation that can be obtained by the raw dataset in Table 1 is the *integral*, or cohort, form
 260 introduced by Chi et al. (Chi, 1988; Chi and Liu, 1985). While the differential representation observes the
 261 newly individuals that over time are developing towards the next stages, the integral representation provides a
 262 picture of the number of individuals into each stage over time. In this case, accordingly, instead of a density
 263 we obtain the cumulative evolution of the population in each stage.

264 Integral representation datasets can be obtained by the raw data in Table 1 starting from some considerations.
 265 According to its structure, Table 1 lists along the columns the labels (and consequently the life stage) of the
 266 individuals over time. The number of alive individuals in each life stage at time t can be hence obtained by
 267 counting how many times a given label occurs in each column. An example of how the integral representation
 268 looks like is numerically provided in Table 7, while Fig. 2 shows the usual way to plot results. An analogous
 269 process can be carried out for the dead: in this case the process is slightly different, as over time we count the
 270 cumulative number of dead per stage. In case an individual in the stage i dies at time t , the number of dead
 271 corresponding to i will be increased of one unit.

272

273 Table 7: Example of table data typically resulting from the life tables *integral representation*. The table was
 274 made for the sake of exposition using a small portion of unpublished data on *Drosophila suzukii* life tables
 275 data at 20 °C. E indicates the egg stage, L1 and L2, indicate the first and the second larval instars, respectively,
 276 and D indicates the death.

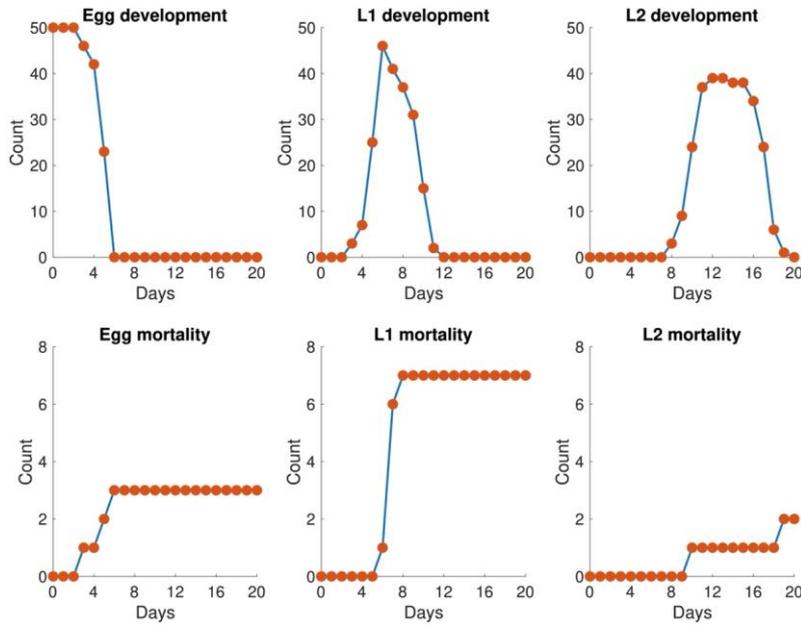
Commenté [LR2]: If accepted, cite Baser et al. 2025

Time (days)	Development			Mortality		
	E	L1	L2	E to D	L1 to D	L2 to D
1	50	0	0	0	0	0
2	50	0	0	1	0	0
3	46	3	0	1	0	0
4	42	7	0	2	0	0

5	23	25	0	3	1	0
6	0	46	0	3	6	0
7	0	41	3	3	7	0
8	0	37	9	3	7	0
9	0	31	24	3	7	1
10	0	15	37	3	7	1
11	0	0	39	3	7	1
12	0	0	39	3	7	1
13	0	0	38	3	7	1
14	0	0	38	3	7	1
15	0	0	34	3	7	1
16	0	0	24	3	7	1
17	0	0	6	3	7	1
18	0	0	1	3	7	2
19	0	0	0	3	7	2
20	0	0	0	3	7	2

277

278



279
 280 Figure 2: Example of plot of the data typically resulting from the life tables *integral representation*. These
 281 plots were made for the sake of exposition using a small portion of unpublished data on *Drosophila sukukii*
 282 life tables data at 20 °C.

283
 284 This procedure led us to obtaining the matrices G_C and P_C already described by Chi et al. (Chi, 1988; Chi and
 285 Liu, 1985) mathematically defined as follows:

$$G_C = \begin{pmatrix} g_{11}^C & g_{12}^C & g_{13}^C & g_{14}^C & \dots \\ g_{21}^C & g_{22}^C & g_{23}^C & g_{24}^C & \dots \\ g_{31}^C & g_{32}^C & g_{33}^C & g_{34}^C & \dots \\ g_{41}^C & g_{42}^C & g_{43}^C & g_{44}^C & \dots \\ g_{51}^C & g_{52}^C & g_{53}^C & g_{54}^C & \dots \\ g_{61}^C & g_{62}^C & g_{63}^C & g_{64}^C & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix} \quad (5)$$

286 and

$$P_C = \begin{pmatrix} p_{11}^C & p_{12}^C & p_{13}^C & p_{14}^C & \dots \\ p_{21}^C & p_{22}^C & p_{23}^C & p_{24}^C & \dots \\ p_{31}^C & p_{32}^C & p_{33}^C & p_{34}^C & \dots \\ p_{41}^C & p_{42}^C & p_{43}^C & p_{44}^C & \dots \\ p_{51}^C & p_{52}^C & p_{53}^C & p_{54}^C & \dots \\ p_{61}^C & p_{62}^C & p_{63}^C & p_{64}^C & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix} \quad (6)$$

287 The matrices (5) and (6) are composed of the column vectors

$$G_C^j = (g_{1j}^C, g_{2j}^C, \dots, g_{ij}^C)^T \quad (7)$$

288 and

$$P_C^j = (p_{1j}^C, p_{2j}^C, \dots, p_{ij}^C)^T, \quad (8)$$

289 where the elements g_{ij}^D and p_{ij}^D indicates the number of individuals (dead or alive) in the life stage j at time i .

290 Unlike the differential representation, where the sum of the elements on the columns of the matrices (3) and
 291 (4) provides the total number of individuals into each life stage, in the matrix (5) and (6) the sum of the elements
 292 on the rows provides the total number of individuals alive (5) or dead (6) at time i . This property is further
 293 underlying the different focus that the two representations have: the differential representation is always
 294 centred on the stage, while the integral representation on the whole life cycle.

295 Before going ahead, it is worth remarking two important aspects. In this paper we are not going to recall the
 296 overall methodology of Chi et al. (Chi, 1988; Chi and Liu, 1985) as it has well explained in several works over
 297 the years (Amir-Maafi et al., 2022; Chi et al., 2023, 2020), but instead we are providing a connection between
 298 the differential and the integral representation. Accordingly, we have maintained the same notation of Chi et
 299 al. (Chi, 1988; Chi and Liu, 1985) for the matrices (5) and (6), even if the mortality matrix P_C has been indicated
 300 in a slightly different way. Chi et al. (Chi, 1988; Chi and Liu, 1985) in fact, do not cumulate the daily values
 301 of the dead, as carried out for the stage-development in the matrix (5), but they just report the number of new
 302 died individuals per day. In this study we are conceptually separating the differential from the integral
 303 representation, this is the reason why for the sake of coherence it would be better to express the matrix (6) as
 304 daily cumulative values. This however does not limit further analyses, as the datasets hereby represented
 305 provide the necessary information to fully apply the framework of Chi et al. (Amir-Maafi et al., 2022; Chi,
 306 1988; Chi et al., 2023, 2020; Chi and Liu, 1985).

307 Unlike the differential representation, the vectors (7) and (8) of the integral representation report the
 308 information in absolute time, namely by setting the time reference on the oviposition day for all the stages. On
 309 the other hand, there is a loss of information with respect to Table 2 and 3, as already showed for the differential
 310 representation. As conclusion of this Section, we discuss the *Example 2*, that shows the consequences of the
 311 loss of information in case of a dataset collected in integral form.

312
 313 *Example 2.* This example aims to show that the integral representation leads to a loss of information with
 314 respect to Table 2 and 3. For the sake of simplicity, let us consider a population composed of three individuals,
 315 whose eggs are laid at time $t = 0$. Moreover, let us focus on the egg (E) and larva (L) stage only. By observing
 316 the stage development on the following days, we can write the dataset as shown in Table 1. From the raw data
 317 (Table 8), we assess that: *i)* the specimen SP-1 dies on day two, *ii)* the specimen SP-2 develops to larva on day
 318 three, and *iii)* the specimen SP-3 is still in the egg stage on day four. Accordingly, from Table 8 we can know
 319 who the individuals involved in the aforementioned scenario are.

320
 321 Table 8: Raw dataset discussed in the *Example 2*. Rows indicate the number of the specimens, while columns
 322 the days. “E” indicates *egg*, “L” *larvae*, and “D” the *dead*.

Specimen	Time (day)					
	1	2	3	4	5	...
SP-1	E	E	D	--	--	...
SP-2	E	E	E	L	L	...
SP-3	E	E	E	E	E	...

323
 324
 325 From Table 8, we can obtain the integral representation by counting how many individuals are in each stage
 326 on day two, three, and four (Table 9): *i)* on day two we have 1 individual dead and 2 individuals in the egg
 327 stage, *ii)* on day three we have one egg and one larva, *iii)* on day four we have one egg and one larva.

328
 329 Table 9: Integral representation of the dataset discussed in the *Example 2*.

Time (days)	Development		Mortality	
	E	L	E	L
1	3	0	0	0
2	2	0	1	0
3	1	1	1	0
4	1	1	1	0
⋮	⋮	⋮	⋮	⋮

330

331 Table 9 shows that we are losing, with respect to Table 8, the following information: *i)* the specimen one died
332 on day two, *ii)* the duration of the egg stage of the individual two was three days, *iii)* the duration of the egg
333 stage of the individual four is 4 days. As already discussed for the differential representation in the *Example*
334 *1*, there might be different combinations of Table 9 that leads to the original configuration shown in Table 8.

335

336 **2.4. Spreadsheet file for standard of data collection**

337

338 The two representations described in Section 2.2 and 2.3 are complementary to each other and allow an overall
339 understanding of the biology of the species. During this study, we analysed the whole process of data collection
340 and transformation, highlighting the importance of data sharing to maximise the information that life table
341 studies provide to the scientific community. To pursue this aim, we hereby propose a simple solution, namely
342 an electronic spreadsheet file where scholars can insert data and automatically obtain the differential and the
343 integral representation as a result. The idea behind this choice comes from our experience: experimenters are
344 used to collecting life tables data directly on electronic spreadsheets, often organised according to their
345 personal needs. As a consequence, it is extremely difficult, for third people, to understand the logic behind the
346 data collection, as well as to retrieve the main information needed to fully reproduce the results of the
347 experiments. Further calculations to reach the differential or the integral representation are then carried out by
348 transforming and/or reshaping the data, a very time-consuming operation that further slows down the overall
349 experimental process.

350 The main goal of the spreadsheet we are proposing is either to standardise the data collection or to guide
351 scholars in set up their experiments such that the reproducibility of the results and the reusability of the data is
352 warranted. Data elaboration is not the only disadvantage of the experimental process, as data are usually
353 collected and analysed at the end of the trial. An online processing of the data, instead, may be helpful to
354 understand if there are anomalies or adjustments needed in the experimentation. As a last motivation of our
355 choice, we can say that it is not worthy, at this stage, to build an *ad hoc* software without having a well-defined
356 standard, forcing the potential users to install and get familiar with it. An electronic spreadsheet can further be
357 uploaded on online platforms that extrapolate the data and store them as already common in gene banks.

358 The development of the spreadsheet hereby proposed is based on the following logic process. The file should
359 be self-explanatory for external readers; accordingly, the first tab should contain a detailed resume of the data
360 about the species, the experimental conditions explored, and the acronyms that denote the life stages.
361 Moreover, it would be extremely helpful if the researchers report additional details, such as the main aim of
362 the experiment and the rearing protocol, besides citations to helpful literature. From our experience, a clear
363 summary of all the information in a single file will speed up the manuscript writing process as well, as the
364 spreadsheet can be considered, *de facto*, an electronic logbook. The overview tab is also a first important step
365 to give credit to the research group.

366 The second part of the file concerns the data acquisition. We may use a single spreadsheet for each constant
367 condition experiment; however, this is not practical for data sharing and further analysis. This concept, can be
368 explained with a practical example: let us consider that we aim to explore the thermal response of a given
369 insect species; to do that, we should repeat the rearing at different constant temperatures. If the dataset
370 corresponding to the different experiments is included in a single spreadsheet, it is possible to easily compare
371 the overall results. For this reason, the spreadsheet proposed consider 15 tabs, corresponding to 15 independent
372 rearing carried out under different conditions. The number of tabs is just a compromise, as in the average the
373 conditions explored (e.g., temperature, humidities, diets, treatments) is around 6–10 and, in the best of our
374 knowledge, there are no cases that exceed 15. Each tab allows the experimenter to collect life history data of
375 up to 1000 individuals: data obtained from multiple experiments under the same conditions can be grouped in
376 the same tab and analysed together. Moreover, we foreseen a textbox in each tab, as it can be helpful either to
377 take personal notes or observations to share with third people.

378 The third part of the file, instead, should automatically calculate the differential and the integral representation
379 of each dataset, so that they are ready to be copy/pasted for further analyses that depends on the aim of the
380 research. Note that since the calculations are automated, the spreadsheet is uploaded as soon as a new data is
381 inserted somewhere in a tab, an operation that allows to double check if the ongoing experiment shows
382 anomalies and/or unexpected behaviours of the population that need further investigation. The two
383 representations can be obtained by transforming the raw data according to the procedure detailed in Section
384 2.2 and 2.3.

385 The fourth part of the file is the life tables statistics and plots, reported in two corresponding tabs. The life
386 tables statistics are computed from the differential representation and provide a summary of the stage durations
387 under the different rearing conditions. More specifically, the mean and the standard deviation of the stage
388 duration and the moments of the distribution (median, mode, skewness, and kurtosis) are automatically
389 computed for each rearing condition. The plot tab, instead, plots the distributions coming from the different
390 rearing conditions, grouped by stage, for quick and intuitive comparison of the results.

391

392 **3. Results**

393

394 The theoretical considerations discussed in this study lead us to organise the spreadsheet for life tables data
395 collection such that the information is standardised and complete of the details needed to reproduce the
396 experiments. The datasheet can be downloaded at the following GitHub page
397 <https://github.com/lucaros1190/LifeTables-StandardSpreadsheet>, where it is also possible to notify further
398 improvements or report bugs. Two versions of the datasheet are available: a “user” version, protected to avoid
399 accidental modifications of the formulas in the different cells, and a “developer” version, free and ready to be
400 modified or improved according to special needs. The web page contains a detailed guide of the datasheet, and
401 will be enriched with some examples based on real experiments carried out over the years by our research
402 group and collaborators, as well. Let us now discuss the details of each tab, to show how the theoretical aspects
403 have been implemented.

404

405 *DatasetOverview*: The first page of the file contains details about the species, the credits to the research group
406 that carried out the experiment, the definitions that will be further provided as input to the other tabs, and a
407 text box where the rearing protocols and the aim of the experiment should be reported. For the sake of
408 generality, the rearing conditions are indicated by “Cond-1, ..., Cond-15”, the same name indicated on the raw
409 data tabs. In this first page, it is possible to assign names/acronyms to the different “Cond-”, that will be
410 automatically propagated along the spreadsheet.

411 A second general trait concerns the number of life stages and the sex division. We are aware that the number
412 of stages can vary among the species, and this is the reason why they have been exceeded on purpose: in case
413 the species under study has less preimaginal stages, the exceeding ones can be skipped by indicating “--” as a
414 label. The same reasoning is applied to parthenogenetic species: if there are only females in the populations,
415 the adult males’ cell can be skipped by indicating “--”, as well.

416
417 *LifeTables-Statistics*: This tab provides a summary of the data inserted, by exploiting the differential
418 representation from the *Differential-Rep* tab. Here, users can either have real-time overview/synthesis of the
419 experimental data, helpful during the trials, or the life tables values ready to be used elsewhere (e.g., in a
420 manuscript/report). This tab provides life tables statistics of the different life stages and experimental
421 conditions explored, according to the indications of Rossini et al. (Rossini et al., 2024a). This tab provides a
422 textbox as well, helpful to write notes for third people or for the experimenter himself.

423
424 *Plots*: After the numerical synthesis is carried out in the *LifeTables-Statistics* tab, a graphical summary follows
425 as well. This tab provides a plot of the differential representation, coming from the *Differential-Rep* tab. The
426 stage-populations corresponding to the different rearing conditions are grouped together in the same plot, so
427 that users can easily see differences and insights of their studies. For the sake of completeness, plots are
428 extended to mortality tables as well.

429
430 *Cond-1, ..., Cond-15*: These tabs are the core of the datasheet file, as the data collected for each rearing
431 condition should be directly inserted here to produce the Table 1 of this study. Even if the sampling time is
432 usually set to one day, this is not generally true, as some species develop more rapidly (above all at optimal

433 temperatures), requiring multiple inspections per day. For this reason, each tab provides for a cell where the
434 sampling time (expressed in hours) should be indicated. Once defined, the times corresponding to that
435 experimental conditions are automatically converted in days (or fraction of days) in the overall spreadsheet.
436 For the users' convenience, a list indicating the labels defined in the *DatasetOverview* is provided on top of
437 the tab.

438 The table, instead, is organised in columns indicating the time step of each sampling, and in rows indicating
439 the individuals: note that in this way it is possible to uniquely identify the individuals, taking track of the life
440 history of up to 1000 specimens. It may be possible that, to reach a statistically significant number of reared
441 individuals, the experimenter should rear many cohorts under the same conditions. In this case, the data can
442 be pooled together in the same tab, as they are independent repetitions of the same experiment, and the different
443 rearing sessions can be indicated in the textbox. An example at hand can be: "Specimens 1-50 correspond to
444 the rearing session 1, Specimens 51-100 correspond to the rearing session 2".

445
446 *Individual-LifeHistory*: This tab contains the first summary of the data, more precisely it transforms each raw
447 dataset in the stage-development table (Table 2), according to the procedure described in Section 2.2. For each
448 individual, in fact, this tab counts how many cells (corresponding to a single time step increase) contain the
449 same label. The same is carried out for mortality, obtaining the stage-mortality table (Table 3). The stage-
450 development table contains only the preimaginal stages, as adult survival is included in the stage-mortality
451 table.

452
453 *Differential-Rep*: This tab contains the second summary of the data, namely the differential representation.
454 Calculations are carried out according to the procedure described in Section 2.2, organising the dataset as in
455 Table 4. Since the differential representation is providing us the number of individuals that *complete* the stage
456 (or that exit from the stage because they die) over time, adult males' and females' survival should belong to
457 mortality table. This is the reason why the differential representation tables related to development include
458 only the preimaginal stages.

459

460 *Integral-Rep*: This tab contains the third summary of the raw data, namely the integral representation. The
461 tables report, for each experimental condition, the number of individuals that over time are into the different
462 life stages (Table 7), this is the reason why this time the adults are present in both development and mortality
463 tables.

464

465 **4. Discussion**

466

467 Standardising data collection is fundamental to endorse open science and reproducibility of experiments and
468 results. We contributed to this goal in the case of life table experiments in entomology, widely used to explore
469 the biology and the response of insect populations to different external conditions. Besides providing a possible
470 solution, this study wanted to also revise the theoretical background behind life tables experiments, to better
471 clarify which are the procedures that lead to the two different representations of the data.

472 The differential and the integral representation have been used since long time by the community of
473 entomologists working in life tables experiments but, to the best of our knowledge, there are no in-depth studies
474 that discuss their connection and their advantages. The differential representation, for instance, provides the
475 distribution of the development times of the individuals that develop under different external conditions
476 (Carey, 2001; Harcourt, 1969; Rossini et al., 2024a; Southwood, 1978). From those distributions it is possible
477 to carry out different analyses: the most common one is the calculation of the synthetic values listed in
478 *LifeTables-Statistics*, as they provide a direct idea of the impact of the conditions on the different life stages of
479 the species. More accurate analyses of the differences between the experimental datasets, instead, can be
480 carried out through statistical tests, such as Generalised Linear Models (GLM), classical parametric tests (e.g.,
481 analysis of the variance ANOVA) or non-parametric tests (e.g., Kruskal-Wallis test). The common process of
482 data analysis provides for an intermediate step of data preparation, usually by organising the data in .csv or
483 .xlsx files, that is regardless of the software used. By experience, this phase is extremely time consuming and
484 slows down the overall analysis and the further manuscript preparation process. The datasheet provided with
485 this study automatically prepares the dataset for the most common software utilised by the community (e.g.,
486 R, SAS, custom Python scripts, or Matlab), endorsing the researchers to easily get their results. Future studies

487 will focus on the development of scripts that automatically analyse the data, providing an additional benefit
488 for the scientific community.

489 There is the same advantage for the integral representation, even if the data analysis in this case has been better
490 discussed and organised by Chi et al. (Chi et al., 2023, 2020). While the differential representation focuses
491 more on how the rearing conditions affect the single stage populations, the integral one provides an overview
492 of the overall life cycle. This aspect is also underlined by the different time scales considered: as discussed in
493 Section 2.2 and 2.3, the absolute time scale (the time zero set to the oviposition day for each life stage
494 population) is typical of the integral representation, while the differential one entrusts on a relative time scale
495 (the time zero is set at the beginning of each life stage). For this reason, the integral representation is more
496 suitable to calculate parameters such as the age-stage specific survival rate, distribution of the mortality, age-
497 specific survival rate, net reproductive rate, intrinsic rate of increase, finite rate of increase, age-stage life
498 expectancy, and reproductive value (Chi, 1988; Chi and Liu, 1985). Given the higher complexity of this
499 analysis with respect to the differential representation, Chi et al. introduced an *ad hoc* software, TWSEX-
500 MSChart (<http://140.120.197.173/Ecology/prod02.htm>). TWSEX-MSChart provides for an input that is
501 close to the *Individual-LifeHistory* tables: even in this case our datasheet shows its utility to speed up the data
502 analysis process, besides supporting the data sharing.

503 The suitability of the data for third parties' software is not the only advantage of the spreadsheet introduced
504 with this study, as it can be useful as a guide for researchers approaching to life tables experiments. The data,
505 in fact, should be inserted in the same way, independently from the species or from the rearing conditions: the
506 logic behind the datasheet and its structure provides instructions on how to carry out the experiments.
507 Additionally, as every dataset contains information in the same format and units, it can endorse the constitution
508 of a common database, as in the case of gene banks. Our wish for the future is that the datasheet starts to be
509 used to collecting the data, and further uploaded on web databases (with specific identifiers). Even if this
510 hypothesis is still remote, the advantage would be great, as datasets obtained under the same experimental
511 conditions can be combined and available to the scientific community with the observations and notes reports
512 as well.

513 Open science practices are going to be supported and, in some cases imposed, by always more institutions,
514 journals, and funding agencies worldwide (Mons et al., 2017). This willingness led to the constitution of the

515 Findable, Accessible, Interoperable, and Reusable (FAIR) policies (Stall et al., 2019), adopted for instance by
516 the European Union, where “*open science is at centre of European research policy*” ([https://research-and-](https://research-and-innovation.ec.europa.eu/strategy/strategy-2020-2024/our-digital-future/open-science_en)
517 [innovation.ec.europa.eu/strategy/strategy-2020-2024/our-digital-future/open-science_en](https://research-and-innovation.ec.europa.eu/strategy/strategy-2020-2024/our-digital-future/open-science_en)). FAIR policy
518 endorses the transparency of the experiments while offering the right protection of the data (they might be
519 openly accessible, or before proper requests) and credit for the authors (Mons et al., 2017). This tendency
520 should further motivate the standardisation of the data collection (even if FAIR policies do not impose
521 standards) and analysis, so as everyone from the scientific community can easily understand what the data and
522 the results mean without going through further explanations contained in *readme* files or published papers. On
523 the other hand, the scientific literature associated with the data will be the reference only for the objectives,
524 rearing conditions, and results.

525 However, we should clarify that standardisation of the data collection is not a fast process, as it needs to be
526 discussed by the scientific community before being accepted. What this study introduces is a proposal that can
527 be tested and further improved by the scientific community, as it still contains limitations. For instance, we
528 focused on the different representations and to an easy way to collect the data about insect (and terrestrial
529 arthropods at large) life cycles, discarding reproduction aspects. We are aware that this is an important aspect,
530 but we should also recognise that the method introduced by Chi et al. (Chi, 1988; Chi and Liu, 1985) is already
531 suitable to deal with egg production. What we suggest to the researchers focusing on this specific part of the
532 life tables study, is to recall the cited literature, as including this aspect in our framework would be just a
533 repetition of something that already exist and that has been widely accepted by the community. Under this
534 point of view, our proposal is an extension and a clarification of the works of Chi et al. (Chi, 1988; Chi et al.,
535 2023, 2020; Chi and Liu, 1985) above all concerning the theoretical aspects on the differential representation,
536 that to date has never been discussed properly.

537 Raw data of life tables experiments are extremely important, above all in the current age of the entomological
538 research. Besides the biological information and their implication in many fields as, for instance, insect pest
539 control or edible insect industry, they are also the basics of parameter estimation for mathematical models
540 (Buffoni and Pasquali, 2007; Castex et al., 2018; Damos and Savopoulou-Soultani, 2012; Gutierrez et al.,
541 1981, 2012; Ikemoto and Kiritani, 2019; Quinn, 2017; Rossini et al., 2019a, 2019b, 2020a). Modelling insect
542 populations is one of the hot topics of the modern research, as they can potentially provide predictions on

543 future population trends (Grimm et al., 2020; Rossi et al., 2019; Rupnik et al., 2019; Zhai et al., 2020). There
544 are many proposals, to date, based on different mathematical frameworks, but the common starting point is
545 laboratory data that allows the parameter estimation (Rossini et al., 2025, 2020b). Therefore, the unavailability
546 of data can be a strong limitation to this field of research, as not all the researchers involved in this kind of
547 studies have access to experimental data, or connections with groups specialised in life tables experiments.
548 Additional aspect, not negligible in many cases, is the budget constrain: climatic chamber experiments require
549 specialised laboratory with proper equipment and experienced personnel, and this is one of the main limitations
550 that affect several research groups worldwide (Kareithi et al., 2019). Multidisciplinary research can be
551 endorsed by open data and by collecting data according to standards, as the interpretation of the dataset can be
552 easier for researchers coming from different fields.

553

554 **5. Conclusion**

555

556 This work dealt with the conceptual clarification and standardisation of the data collection process of life tables
557 in entomology. We have provided a conceptual explanation of the different representations that can be obtained
558 from the raw data, underlying why only sharing the experimental dataset provides the complete information to
559 the scientific community. We are aware that this is just a first step that needs further adjustments and feedback
560 from the insiders, but we strongly believe that this can be carried out in the very next future. Our hope is that
561 the scientists working with life tables experiments will adopt our data collection protocol and shares the data
562 in public repositories, enriching the knowledge on many topics that are relevant for the current and future
563 challenges of research.

564

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568

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