FORUM

Mortality Risk in Insects

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ABSTRACT Understanding how and why insect numbers fluctuate through time and space has been a central theme in ecological research for more than a century. Life tables have been used to understand temporal and spatial patterns in insect numbers. In this study, we estimated cause-of-death probabilities for phytophagous insects using multiple decrement life tables and the irreplaceable mortality analytic technique. Multiple decrement life tables were created from 73 insect life tables published from 1954 to 2004. Irreplaceable mortality (the portion of mortality that cannot be replaced by another cause) from pathogens, predators, and parasitoids was 8.6 ± 7.2, 7.8 ± 4.9, and 6.2 ± 1.6%, respectively. In contrast, the mean irreplaceable mortality from all non-natural enemy mortality factors (mortality from factors other than natural enemies) was 35.1 ± 4.4%. Irreplaceable mortality from natural enemies was significantly lower compared with non-natural enemy factors. Our results may partially explain cases of unsuccessful efficacy in classical biological control, after successful establishment, by showing low irreplaceable mortality for natural enemies, including 5.2 ± 1.6% for introduced natural enemies. We suggest that the environment (i.e., the degree of environmental stability) influences the magnitude of the irreplaceable mortality from natural enemies. Our results lead to several testable hypotheses and emphasize that it is not possible to estimate the effect of any mortality factor without considering its interaction with competing mortality factors, which has far-reaching consequences for population biology and applied ecology.

KEY WORDS risk analysis, multiple decrement life table, biological control, natural enemies, insect demography

Understanding how animals die and why populations fluctuate through time and space has been a central theme in basic and applied ecological research for more than a century. Historically, insects have been the group that has received the greatest emphasis in examining population change, because of their profound ecological significance in terrestrial ecosystems, their importance in agriculture and disease transmission, and their suitability as study organisms.

An important tool in ecology is the life table (Deevey 1947, Southwood 1978, Carey 2001), which was first applied to insect populations by Morris and Miller (1954). Subsequent advances in insect life tables primarily have centered on techniques to estimate the age interval and age-specific mortality factors that have the greatest impact on the population (Morris 1959; Varley and Gradwell 1960; Huffaker and Kennett 1966; Varley et al. 1973; Podoler and Rogers 1975; Southwood 1978; Royama 1981; Carey 1989, 1993; Buonaccorsi and Elkinton 1990; van Driesche et al. 1991; Bellows et al. 1992).

A drawback to many life table approaches is the inability to account for individuals subject to a number of mutually exclusive hazards. However, the multiple decrement life table, 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. The single decrement life table addresses the probability of death from one cause; thus, it does not account for contemporaneous mortality factors operating concurrently on a population (Moriyama 1956, Chiang 1991, Elkinton et al. 1992). The reality of contemporaneous causes of mortality has drawn attention to the limitations associated with key factor analysis (Buonaccorsi and Elkinton 1990, Bellows et al. 1992, Elkinton et al. 1992, Royama 1996). The concept of irreplaceable mortality is an analytic approach that has been used to address this challenge. As its name implies, irreplaceable mortality (also known as indispensable mortality) is the mortality rate from a specific factor that cannot be replaced by another factor (Huffaker and Kennett 1966, Southwood 1978, Carey 1989).

The use of an analytic technique, such as irreplaceable mortality, to estimate the risks of insect death in

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Table 1. Life tables used in the analysis

Species	Insect order	Location of study	Reference
Agromyza frontella	Diptera	Ontario, Canada	Harcourt et al. 1988
Barbara colfaxiana	Lepidoptera	Oregon, USA	Nebeker 1977
Bassaris gonerilla	Lepidoptera	New Zealand	Barron et al. 2003
Ceroplastes destructor	Hemiptera	South Africa	Wakgari and Giliomee 2001
Choristoneura fumiferana	Lepidoptera	New Brunswick, Canada	Morris and Miller 1954
Dendroctonus simplex	Coleoptera	Newfoundland, Canada	Langor and Raske 1988
Diaphania hyalinata	Lepidoptera	Brazil	Gonring et al. 2003
Dioryctria resinosella	Lepidoptera	Wisconsin, USA	Hainze and Benjamin 1985
Euura lasiolepis	Hymenoptera	Arizona, USA	Preszler and Price 1988
Fiornia theae	Hemiptera	Florida, USA	Munir and Sailer 1985
Helicoverpa zea	Lepidoptera	Texas, USA	Teetes et al. 1992
Hylemya brassicae	Diptera	Ontario, Canada	Mukerji 1971
Hypera postica	Coleoptera	Ontario, Canada	Harcourt et al. 1977
Hypera postica	Coleoptera	Virginia, USA	Kuhar et al. 2000
Latoia viridissima	Lepidoptera	Nigeria	Igbinosa 1985
Leptinotarsa decemlineata	Coleoptera	Ontario, Canada	Harcourt 1971
Leptinotarsa undecimlineata	Coleoptera	Honduras	Canas et al. 2002
Neodiprion fulviceps	Hymenoptera	California, USA	Dahlsten 1967
Nezara viridula	Hemiptera	Japan	Kiritani and Hoyko 1962
Operophtera brumata	Lepidoptera	Nova Scotia, Canada	Embree 1965
Ostrinia nubilalis	Lepidoptera	New York, USA	Kuhar et al. 2002
Phoracantha semipunctata	Coleoptera	Malawi	Powell 1982
Pieris rapae	Lepidoptera	Ontario, Canada	Harcourt 1966
Pissodes strobi	Coleoptera	Maine, USA	Dixon and Houseweart 1982
Pleroneura spp.	Hymenoptera	California, USA	Ohmart and Dahlsten 1979
Plutella xylostella	Lepidoptera	Australia	Furlong et al. 2004
Plutella xylostella	Lepidoptera	Ontario, Canada	Harcourt 1963
Recurvaria starki	Lepidoptera	Alberta/BC, Canada	Stark 1959
Rhagoletis pomonella	Diptera	Quebec, Canada	Carey 1989
Siphoninus phillyreae	Hemiptera	California, USA	Gould et al. 1992

the presence or absence of multiple causes, therefore, potentially has far-reaching implications for population ecology. Indeed, causes and intensities of mortality are central components in the fundamental phenomena of biodiversity, ecosystem stability, *r*- and *K*-selection, ecological succession, and life-history evolution (Dobzhansky 1950, MacArthur and Wilson 1967, Pianka 1970, Cornell and Hawkins 1995). Additionally, mortality is central to ecological applications such as biological control and pest management. However, to our knowledge, researchers have not comprehensively estimated cause-of-death probabilities by examining published life tables. Fortunately, many published life table data are suitable for multiple decrement life table analysis and estimation of irreplaceable mortality. Through examining patterns in these data, we discern some surprising insights into causes of insect mortality, suggest testable hypotheses, and discuss their potential relevance to fundamental questions in population ecology.

Analysis of Life Tables

We created multiple decrement life tables from 73 previously published insect life tables. Life tables were obtained and evaluated through conventional library and journal searches and electronic database searches (e.g., Agricola, Biological Abstracts, Biological and Agricultural Index, Web of Science). We used all literature sources that met the following basic criteria for multiple decrement life table analysis. All life tables used in our analysis included multiple age-specific mortality factors (e.g., parasitism, predation, disease, desiccation, freezing, egg infertility) that allowed for placement into multiple decrement life tables and cause-of-death analysis by factor. We did not use life tables that only had two mortality factors (e.g., parasitism and other) because our intent was to compare multiple sources of mortality. The 73 life tables came from 30 publications from 1954 to 2004 (Table 1).

The life tables represented 28 insect species in five orders (43% Lepidoptera, 23% Coleoptera, 13% Hemiptera, 10% Hymenoptera, 10% Diptera). Eleven of the 28 species were non-native. The life table studies were conducted from 43° S to 46° N latitude in several countries on five continents (11 Canada, 11 United States, 1 South Africa, 1 Nigeria, 1 Malawi, 1 Brazil, 1 Honduras, 1 Australia, 1 New Zealand, and 1 Japan). Biomes included temperate forest, tropical rain forest, savanna, desert, taiga, chaparral, grassland, and alpine. Fifty-seven percent of studies were on insects affecting crops within agroecosystems, whereas 37% were on forest insects.

Example of Multiple Decrement Life Table Construction. We provide an example of the construction of an multiple decrement life table from a conventional life table and explain the elimination-of-cause method for combinations of causes of death using the research on *Hypera postica* (Gyllenhall) of Harcourt et al. (1977). Calculation techniques for multiple decrement life tables similar to those discussed below can be found in Spiegelman (1968), Preston et al. (1972), Schoen (1975), Keyfitz (1977), Buonaccorsi and Elkinton (1990), and Elkinton et al. (1992). The conventional *H. postica* life table was converted to a multiple decrement life table using methods described by

Table 2. Conventional life table for alfalfa weevil, *H. postica*

x	k_x	d_x	Cause of death				
			Wasp (d_{1x})	Infertility (d_{2x})	Establishment failure (d_{3x})	Fungal disease (d_{4x})	Rainfall (d_{5x})
Eggs	421	9	1	8	0	0	0
Early larvae	412	106	0	0	106	0	0
Late larvae	306	261	0	0	0	255	6
Prepupae	45	10	3	0	0	7	0
Late pupae	35	4	0	0	0	4	0
Adults	31						

Based on data from Harcourt et al. (1977).

Carey (1993) (Tables 2 and 3). In the conventional life table, the variables are defined as follows: x = the life stage index (i.e., larvae, pupae, adults); k_x = the number at the beginning of each x; d_x = the total number of deaths in each stage; and d_{nx} = the number of deaths attributed to a single cause.

We used an elimination-of-cause method to examine combinations of causes of death in relationship to the absence of other causes and to frame each factor in terms of irreplaceable mortality (Carey 1993). Variables appearing in Tables 3 and 4 are defined as follows: l_x = the number of individuals alive at each x; al_x = the fraction of the cohort living at the beginning of the stage (starting at 1.0 for the first stage and calculated by $al_{x-1} - ad_{x-1}$); ad_{1x} = fraction of deaths attributable to one cause; ad_x = fractions of all deaths from all causes ($ad_{1x} + ad_{2x} + .. + ad_{5x}$); aq_x = stage specific probability of death within that stage calculated by the sum of the probability of dying from all listed causes (d_x/k_x).

An algorithm represented by a quadratic formula for irreplaceable mortality was used to generate mortality solutions for independent mortality factors in the absence of all other factors. Combinations of mortality factors were considered by evaluating the probability of surviving each source of mortality defined by P_x and its complement $(1 - q_x)$, where $(1 - q_1)x \ldots x(1 - q_n)$ is equal to the probability of surviving all mortality factors jointly and $1 - [(1 - q_1)x \ldots x(1 - q_n)]$ is the probability of dying when each variation within the system is considered (Table 5).

The values in Table 5 were calculated as an example from Harcourt et al. (1977) using the abridged results for the elimination of one and two mortality factors. In this case, and in all cases in our paper, all combinations of eliminated causes were considered. In this example, irreplaceable mortality caused by the elimination of a single causal factor ranged from 2.6 to 58.9%, with the largest irreplaceable mortality attributed to fungal disease. If fungal disease was eliminated from the mix of mortality factors, mortality would be reduced by 58.9% because that percentage of mortality cannot be replaced by other factors. For the elimination of two factors, values ranged from 0.7 to 81.8% with large irreplaceable mortality values for the combination of fungal disease with general establishment failure. The utility, however, is not only the identification of a key factor but also irreplaceable mortality when more than one factor is hypothetically removed from the system. When establishment failure is considered with fungal disease, a large proportion of irreplaceable mortality is estimated, indicating the importance of these two factors in determining changes in population levels.

For all life tables, we used percent irreplaceable mortality as a common metric to compare results across tables. By estimating irreplaceable mortality, we could determine how the mortality pattern would change for a population if causes were eliminated or added. Irreplaceable mortality is a key concept in understanding population dynamics because only changes in irreplaceable mortality (immigration and emigration notwithstanding) contribute to changes in final population density.

We modified the irreplaceable mortality values by standardizing the number of life tables per study to avoid bias because some studies presented multiple life tables, whereas others had only one table. For example, if a study presented eight life tables that varied only over location and year, we determined the mean values from these tables so that they could be

Table 3. Multiple decrement life table for alfalfa weevil, *H. postica*

x	aq_x	al_x	ad_x	Fraction of deaths attributed to each cause				
				Wasp (ad_{1x})	Infertility (ad_{2x})	Establishment failure (ad_{3x})	Fungal disease (ad_{4x})	Rainfall (ad_{5x})
Eggs	0.021	1	0.021	0.002	0.019	0	0	0
Early larvae	0.257	0.979	0.252	0	0	0.252	0	0
Late larvae	0.853	0.727	0.620	0	0	0	0.606	0.014
Prepupae	0.222	0.107	0.023	0.007	0	0	0.016	0
Late pupae	0.114	0.084	0.010	0	0	0	0.010	0
Adults		0.074						
Total			0.926	0.009	0.019	0.252	0.632	0.014

Based on data from Harcourt et al. (1977).

Table 4. **Elimination of mortality causes for alfalfa weevil, *H. postica***

x	l_x	Total q_x	Probability for cause of death in the absence of other causes				
			Wasp	Infertility	Establishment failure	Fungal disease	Rainfall
Eggs	421	0.021	0.002	0.019	0	0	0
Early larvae	412	0.257	0	0	0.257	0	0
Late larvae	306	0.853	0	0	0	0.85	0.02
Early pupae	45	0.222	0.07	0	0	0.164	0
Late pupae	35	0.114	0	0	0	0.114	0
Eggs to adults		0.926	0.072	0.019	0.257	0.889	0.02

Based on data from Harcourt et al. (1977).

compared with a study that only presented one life table. However, some studies examined life tables under different treatments (e.g., releases versus no releases of parasitic wasps). In those cases, mortality data from each table were considered separately. For comparisons, therefore, most life table data were expressed in a "per unique life table" statistic.

Causes of mortality were grouped into major categories to broadly compare among life tables. The major categories common to most studies were predators, parasitoids, pathogens, and non-natural enemy factors. We also created other groupings of interest for comparisons. These included all natural enemies and insect natural enemies (i.e., natural enemies of insects that are insects). Some causes of mortality were not sufficiently common across the life tables to group together for analysis (e.g., egg infertility, desiccation, freezing). The non-natural enemy factor category represented mortality factors that were mostly abiotic (according to respective life table study observations) but also included some genetic and host plant quality factors. If researchers could not differentiate between natural enemy and non-natural enemy factors (e.g., differentiate between predators and abiotic factors), the respective life table was not included in the analysis. Surprisingly, there were only five life tables that could not differentiate certain natural enemies from non-natural enemy factors.

We conducted several post hoc statistical tests on the irreplaceable mortality data generated from our analyses. Where possible, mortality data were transformed to meet assumptions of normality (Proc TRANSREG, Box-Cox transformation) and evaluated using analysis of variance (ANOVA) with contrast statements (Proc GLM, $\alpha = 0.05$; SAS Institute 2003). Because of the need to transform several data sets, data were also analyzed using nonparametric techniques (Proc RANK and NPAR1WAY, Wilcoxon scoring; SAS Institute 2003). It is important to note that these statistics were not determined for a single population of inference, but rather from evaluation of 73 life tables representing a variety of species, locations, data collection techniques, and research questions. Therefore, results should be interpreted cautiously. Meta-analyses were not possible because life table papers rarely report SDs or SEs.

Results and Discussion

The mean (±SE) overall mortality, typically egg to adult, from all causes was 87.2 ± 1.7%. The mean irreplaceable mortality from all natural enemies was 16.6 ± 4.1% (median = 6.1). The irreplaceable mortality from pathogens, predators, and parasitoids was 8.6 ± 7.2 (median = 0.9), 7.8 ± 4.9 (median = 1.33), and 6.2 ± 1.6% (median = 1.9), respectively. The irreplaceable mortality from all insect natural enemies was 13 ± 3.6% (median = 4.3). In contrast, the mean irreplaceable mortality from all non-natural enemy mortality factors was 35.1 ± 4.4% (median = 33.7; Fig.

Table 5. **Irreplaceable mortalities for alfalfa weevil, *H. postica***

Combination of causes	Percent mortality	Eliminated causes	Percent irreplaceable mortality
Wasp + infertility + failure + fungus + rain	92.6	—	—
Wasp + infertility + failure + fungus	92.5	Rain	0.2
Wasp + infertility + failure + rain	33.8	Fungus	58.9
Wasp + infertility + fungus + rain	90.1	Failure	2.6
Wasp + failure + fungus + rain	92.5	Infertility	0.1
Infertility + failure + fungus + rain	92.1	Wasp	0.6
Wasp + infertility + failure	32.4	Fungus, rain	60.2
Wasp + infertility + fungus	89.9	Failure, rain	2.8
Wasp + infertility + rain	10.8	Failure, fungus	81.8
Wasp + failure + rain	32.5	Infertility, fungus	60.2
Wasp + fungus+ rain	89.9	Infertility, failure	2.7
Infertility + failure + fungus	91.9	Wasp, rain	0.7
Infertility + failure + rain	28.6	Wasp, fungus	64.0
Infertility + fungus + rain	89.3	Wasp, failure	3.3
Failure + fungus + rain	91.9	Wasp, infertility	0.7

Based on data from Harcourt et al. (1977).

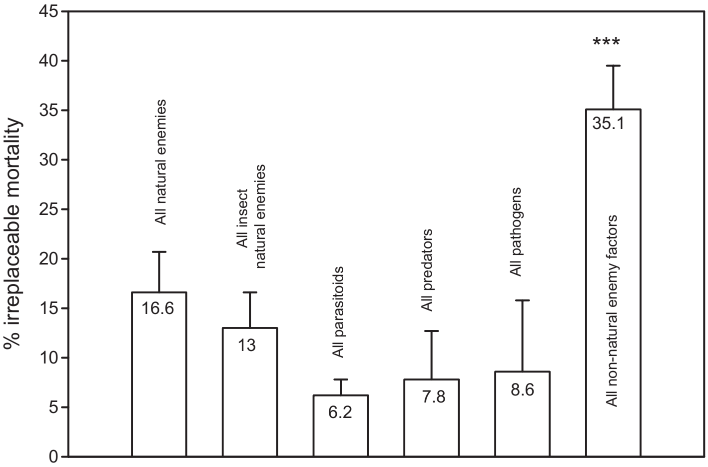

Fig. 1. Irreplaceable mortalities by mortality type. The number within each bar is the mean (***$P < 0.0001$).

1). The percent irreplaceable mortality from non-natural enemy factors was significantly greater than for all types of natural enemy mortality factors (parametric: model, df = 5,414; contrast, df = 1,414; F = 1,650; $P < 0.0001$; nonparametric: $P < 0.0006$). In addition to means, quartiles clearly showed the relatively low irreplaceable mortality associated with natural enemies, especially predators and parasitoids (Table 6).

The irreplaceable mortality from introduced insect natural enemies was 5.2 ± 1.6% (n = 16). Only two introduced natural enemies had irreplaceable mortalities >10%. The parasitoids, *Bathyplectes* spp., for alfalfa weevil, *H. postica,* and the parasitoid, *Dacnusa dryas* (Nixon), for the alfalfa blotch leafminer, *Agromyza frontella* (Rondani), had irreplaceable mortalities of 19 and 19.4%, respectively. Not only were those irreplaceable mortalities the highest for introduced natural enemies, but those enemies are considered to be effective at suppressing the respective pest populations below economic levels (Harcourt et al. 1988, Kuhar et al. 2000).

For non-native insects (n = 13), irreplaceable mortality was 15 ± 5.8% for all natural enemies and 35.6 ± 7.2% for non-natural enemy mortality factors. For native insects (n = 17), irreplaceable mortality from all natural enemies was 20.9 ± 6.8 and 20.5 ± 5.1% for non-natural enemy factors. Differences in irreplaceable mortality between native and non-native species were not statistically significant.

Our results may have been influenced by several factors. First, insect sampling methods among the studies were highly variable. Second, determining cause of death was often difficult for many of the studies. This was especially true for predation and abiotic causes because of the difficulty in directly observing predation and disappearance of individuals. Third, Preszler and Price (1988) and Price et al. (1990) have argued that most life tables have not incorporated the effects of host plant quality and host plant defensive compounds on herbivore mortality. Therefore, life tables most likely underestimate the mortality from this potentially important factor, especially in natural ecosystems. We recognized this by grouping all non-natural enemy mortality factors together rather than trying to distinguish non-natural enemy biotic mortality factors from abiotic factors. Although previous life table researchers may have underestimated the effects of host plant quality, mortality from plant quality would not have been placed by researchers in a natural enemy category. Therefore, our comparisons of non-natural enemy and natural enemy factors would not be complicated by a failure to assess host plant quality mortality. Finally, the use of irreplaceable mortality to evaluate mortality factors discounts the potential influence of density dependence in changing percent mortality; however, based on simulations we conducted, density dependence only substantially changes the irreplaceable mortality if the

Table 6. Irreplaceable mortality by mortality factor, percentile, and mean

Mortality type	Percentile				Mean	SE	N
	25	50	75	100			
Non-natural enemies	11	33.7	54.3	74.9	35.1	4.4	32
All natural enemies	1.5	6.1	23.1	90.9	16.6	4.1	34
Insect natural enemies	0.8	4.3	14.5	90.9	13	3.6	35
Parasitoids	0.6	1.9	6.7	37	6.2	1.6	33
Predators	1.1	1.3	5.6	86.1	7.8	4.9	17
Pathogens	0.2	0.9	3.2	58.9	8.6	7.2	8

largest mortality factor is eliminated (unpublished data).

Conclusions about population regulation may be limited because each life table typically represented a single generation. Population trends over multiple generations are needed to determine which causes of mortality are most important in determining changes in population size (Harcourt 1963, Varley et al. 1973), but even these approaches have substantial limitations (Royama 1981, Cornell and Hawkins 1995, Royama 1996). Our inclusion of 73 life tables provides a cross-section through many species, population levels, times, and habitats. Therefore, we believe our results provide a direct indication of the importance of mortality factors in determining within-generation populations and an indirect indication of between-generation population trends.

Our results suggest that irreplaceable mortality from natural enemies is significantly lower than that from other factors. In particular, irreplaceable mortality values were very low for parasitoids and predators. These results support previous observations (although expressed differently) of the lack of impact of natural enemies on insect populations (Andrewartha and Birch 1954, Milne 1957, Dempster 1983, Hassell 1986, Hawkins et al. 1999). However, in a review of life tables for holometabolous insect herbivores, Cornell and Hawkins (1995) concluded that natural enemies were the most frequent mortality source for immature herbivores. It is important to note that their analysis was based on researcher rankings and tabulated frequencies of the major sources of mortality rather than actual sampling measurements of mortality from different sources. Our estimates of irreplaceable mortality were dependent on life tables that had actual measurements of mortality. Furthermore, our approach considered contemporaneous mortality factors.

Importantly, the breadth of our conclusions depends on the systems studied. Because available data for multiple decrement life table analysis emphasize temperate and agricultural ecosystems, the importance of natural enemies in natural and tropical (or less climatically variable) ecosystems is unclear (Cornell and Hawkins 1995). Indeed, we believe the most interesting point from our analysis is the potential importance of ecosystem stability on irreplaceable mortality.

Although we were able to include only a few studies from subtropical and tropical habitats, the greatest irreplaceable mortality from insect natural enemies across all studies occurred in tropical areas (generalist predators in Brazil and Nigeria). This observation is also supported by two recent studies on *Bemisia tabaci* (Gennadius) in Arizona and Uganda, which reported that the largest irreplaceable mortalities were from predators and parasitism, respectively (Naranjo and Ellsworth 2005, Asiimwe et al. 2007). Indeed, classical biological control (the introduction of natural enemy species from the geographic origin of an introduced pest) has been most successful in more moderate climates and perennial crops, such as orchards (DeBach 1964, Southwood 1978, Pedigo 2002).

Although the post hoc statistics presented here should be interpreted cautiously, our analysis of irreplaceable mortality suggests that the environmental stability may influence the magnitude of mortality from natural enemies. This effect also has been theorized or observed by Dobzhansky (1950), Southwood and Comins (1976), Price and Pschorn-Walcher (1988), Price (1991), Hawkins (1994), Cornell and Hawkins (1995), and Hawkins et al. (1999). Although not statistically significant, in their review of life tables, Cornell and Hawkins (1995) observed trends suggesting that mortality from natural enemies was greater in tropical versus temperate systems and mortality from weather was more frequent in temperate versus tropical systems. Beyond developing and analyzing data sets from diverse ecosystems—especially natural ecosystems—a more definitive assessment of this hypothesis might come from comparing life table data and resulting irreplaceable mortalities for the same insect species across widely different environments.

The practical implication of these results is that the suitability of classical biological control may be limited by environmental variability. Although classical biological control of insects has had several important successes, it is well known that most attempts have not been successful (Greathead and Greathead 1992, Pedigo 2002). Our results support this observation by showing low irreplaceable mortalities for natural enemies, including a mean of only 5.2% for introduced natural enemies. Increasing evidence points to the need for biological control programs to incorporate ecological methods to evaluate target and nontarget effects (Follett and Duan 2000, Louda et al. 2003); because of its relative ease in estimating irreplaceable mortality and its adherence to robust ecological theory, the multiple decrement life table could be used to improve decision making within biological control.

A demonstration of the potential value of estimating irreplaceable mortality in biological control can be seen with the European corn borer, *Ostrinia nubilalis* (Hübner), and its introduced egg parasitoid wasp, *Trichogramma ostriniae* (Peng and Chen) (Kuhar et al. 2002). Releases of *T. ostriniae* increased egg mortality from 4 to 34% in field corn, *Zea mays* L. However, the action of contemporaneous mortality factors was not considered. If the life tables are converted to multiple decrement life tables, the results show that the irreplaceable mortality from releases of *T. ostriniae* would have been only 5.1%, an increase of just 1.1% over the population with no releases. According to irreplaceable mortality results within a cause-of-death analysis, a seemingly large increase in mortality from a release of *T. ostriniae* would be replaced almost completely by contemporaneous mortality factors if the egg parasitoid were not released (specifically, the egg mortality would be replaced by neonate larval mortality so the replaceable mortality factor would still prevent damage to the field corn). Therefore, incorporation of irreplaceable mortality could have greatly influenced cost-benefit analysis of releases of *T. ostriniae.*

Although percentages of irreplaceable mortality were significantly lower for natural enemies compared with non-natural enemy factors in our study, this does not mean that low irreplaceable mortalities are necessarily meaningless. From a pest management perspective, if the percent mortality prevents economic injury, it is sufficient. Also, if a specific mortality factor for an injurious larval stage is replaced only by another mortality factor after the larval stage, the injury to the crop already has occurred. It is clearly important to understand irreplaceable mortality within and among insect developmental stages.

It has long been recognized that although theory suggests the possibility for significant impact of natural enemies on insect populations, empirical data have been lacking (Milne 1957, Dempster 1983, Hassell 1986, Hawkins et al. 1999). Also, it has been hypothesized that in temperate regions, abiotic mortality factors may be more important than biotic factors (Dobzhansky 1950, Southwood and Comins 1976). Because our results show that it is not possible to interpret the effect of any mortality factor without considering its impact in the presence or absence of other mortality factors, there is a need for a systematic, rigorous analytic basis for better understanding the effect of mortality factors on insect populations. The multiple decrement life table is ideally suited for this because it is both an organizational and conceptual tool and inherently possesses a uniformity of existing, well-established model concepts. Carey (1989) argued for the importance of the multiple decrement life table and irreplaceable mortality to ecology, and our study has shown how they can be used to show the potential impact of specific mortality factors on insect populations by examining numerous published life tables. They also can be used to provide valuable information to the longstanding debates on animal population biology and address hypotheses such as those discussed above. The answer to the question of how insects die and how mortality is distributed in populations can only be answered meaningfully by consideration of competing mortality; thus, the fundamental concept of irreplaceable mortality should be incorporated widely and used as a discerning filter in basic and applied ecological research.

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