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MARGINAL ATTACK RATE,  $k$ -VALUES AND DENSITY DEPENDENCE  
IN THE ANALYSIS OF CONTEMPORANEOUS  
MORTALITY FACTORS

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SUMMARY

1. Procedures for calculating the marginal attack rates and associated  $k$ -values from observed death rates are presented for contemporaneous predators or parasitoids that either do or do not discriminate against previously parasitized hosts.
2. The relationships among previous methods for quantifying contemporaneous mortalities are discussed.
3. Solutions to the problem of calculating marginal rates taken from human survival analysis are given under the assumption of proportional hazards. These calculations are easily extended to three or more contemporaneous sources of mortality.
4. The conditions under which proportional hazards can be expected are discussed.
5. These methods are compared to that of Varley et al., 1973 for assessment of density dependence among contemporaneous predators.

KEYWORDS: marginal rate, apparent mortality, survival analysis, hazard rate, life tables, predation.

INTRODUCTION

The assessment of mortality acting on a population is of major importance in population ecology. Measures of mortality are crucial for life table construction, population modelling, analysis of regulatory or density dependent action of individual factors, and comparison of the impact of mortality factors within and among different populations. One issue which has received relatively little attention in the ecological literature is the estimation of mortality rates for contemporaneously acting factors. Contemporaneous factors are those which act together on a population during the same time interval. Assessing the strength of individual factors which act contemporaneously usually is not possible from the simple analysis of numbers

observed dying from a factor because of the obscuring effect of the action of other contemporaneous factors. This issue has been appreciated by various workers (e.g., Morris and Miller, 1954; Morris, 1965). Varley et al. (1973) suggested that contemporaneous factors be treated as if they had acted in a sequential manner, or by grouping them into a single category, which was left unseparated in the life table. This approach necessarily proves inadequate in many cases for contemporaneous factors, as we discuss below.

Mathematical frameworks describing the action of contemporaneous factors have been given by Royama (1981), Buonaccorsi and Elkinton (1990) and Carey (1989). However, procedures for estimating the mortality rates assignable to contemporaneous factors from population census data have remained largely unutilized. In this paper we review the framework for estimation and analysis of mortality rates for contemporaneous factors introduced by Royama (1981) and elaborated by Buonaccorsi and Elkinton (1990). Further, we offer new solutions adapted from survival analysis and the theory of competing risks which have been developed for the analysis of human mortality and the longevity of industrial products. We attempt to establish the connection between this literature, and the previous contributions of Varley et al. (1973), Royama (1981), Carey (1989) and Buonaccorsi and Elkinton (1990). We consider several specific cases of contemporaneously acting parasitoids and predators, including cases where the predators or parasitoids discriminate between unattacked and previously attacked hosts. We also consider how analysis of contemporaneous mortality factors can affect the expression or detection of density dependence.

#### ANALYTICAL FRAMEWORK

The total proportion of individuals that survive across a generation can be expressed as the product of a series of survivorships:

$$N_s = N_0 * S_1 * S_2 \dots * S_n \quad (1)$$

where  $S_i$  is the proportion of those which entered stage  $i$  and survived to stage  $i+1$ ,  $N_0$  is the number that entered the first stage, and  $N_s$  the number that survived to the last stage.

Varley and Gradwell (1960, 1968) promoted the idea that mortalities occurring in a population can be expressed in terms of  $k$ -values or killing powers which were calculated by taking the negative logarithms of the proportions surviving in each stage

$$K = -\log_{10}(N_s/N_0) = k_1 + k_2 \dots k_n \quad (2)$$

where  $k_i = -\log_{10}(S_i)$ . Royama (1981) showed that  $k$ -values for contemporaneous agents acting within a stage should be calculated from the marginal probabilities of dying, or marginal attack rates, for each contemporaneous agent. The marginal

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attack rate can be defined as the proportion of hosts entering a particular stage that would be attacked and killed by a particular agent in the absence of other contemporaneous agents. Assuming that attacks by each agent are statistically independent, the product of the corresponding proportions surviving (1-marginal attack rate) from each agent equals the total proportion surviving in the stage:

$$S_i = S_{A_i} * S_{B_i} * S_{C_i} \dots \quad (3)$$

or

$$k_i = k_{A_i} + k_{B_i} + k_{C_i} \dots \quad (4)$$

where  $S_{A_i} = 1 -$  the marginal probability of dying from factor  $A$  in stage  $i$ , and  $k_{A_i} = -\log_{10}(S_{A_i})$ .

We will illustrate how these marginal probabilities, or marginal attack rates, and their corresponding  $k$ -values can be calculated from data typically available during the construction of a life table (and how they differ from the apparent mortality calculated from numbers observed to die from a cause) for four particular cases of contemporaneous factors—two indiscriminate parasitoids, two predators, two discriminating parasitoids and a predator and a parasitoid.

As pointed out by Carey (1989), techniques for quantifying contemporaneous mortalities exist within the statistical literature generally known as survival analysis (e.g., Elandt-Johnson and Johnson, 1980; David and Moeschberger, 1978). Within this literature, the marginal attack rate is termed the net probability of dying, and the death rate is termed the crude probability of dying. For each cause of death, calculation of net rates from crude rates depends upon the assumption that there is some underlying distribution for time to death due to that cause in the absence of all other causes, and that with all causes present these distributions remain the same. Hence, we observe as the cause of death that agent whose time to death is smallest.

#### Contemporaneous Indiscriminate Parasitoids

Suppose that there are two parasitoids, A and B, that together comprise the total mortality that occurs during a particular stage or age interval. Suppose further that the two agents attack hosts indiscriminately and that in a given stage, 80% are attacked by A and 50% by B. As indicated by Royama (1981), this process can be represented by a Venn diagram (Fig. 1) and the proportions attacked (0.8 and 0.5, Fig. 1a) constitute the marginal probabilities of dying or marginal attack rates ( $m_A$  and  $m_B$ , respectively). The proportions of hosts that actually die from A or B ( $d_A$  and  $d_B$  respectively, Fig 1b), usually when the adult parasitoids emerge, depend upon the fate of hosts attacked by both agents and are smaller than the marginal attack rates by an amount which represents a proportion of these multi-parasitized hosts. In many cases competition within the host will result in the survival of only one of the parasitoid larvae, and a proportion  $c$  of multi-parasitized hosts will yield species A and  $(1-c)$  will yield B (Fig. 1b). If this is so, the following equation relates the observed death rates

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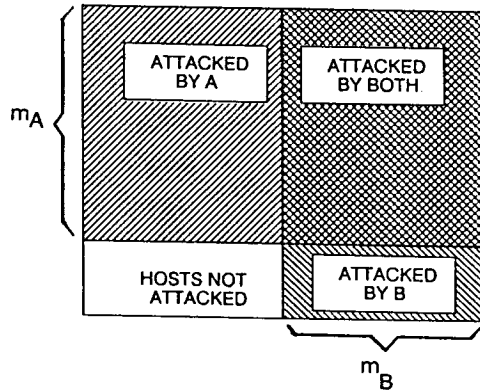
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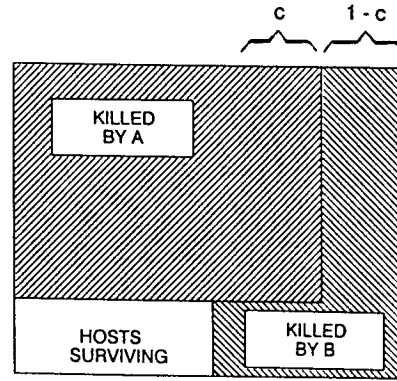


Fig. 1. Venn diagram of proportion of hosts attacked (a) and proportion dying (b) from two hypothetical contemporaneous parasitoids A and B.

to the respective marginal attack rates (Royama, 1981, Eqs. 11, 12):

$$d_A = m_A - (1 - c)m_A m_B, \quad (5a)$$

$$d_B = m_B - c m_A m_B. \quad (5b)$$

Here  $c$  is the proportion of hosts attacked by both A and B from which A emerges. Values for  $m_A$  and  $m_B$  may now be calculated from the observed numbers dying ( $d_A$  and  $d_B$ ) by rearrangement of (5),

$$m_A = \frac{b - ((b^2 - 4cd_A)^{1/2})}{2c}, \quad (6a)$$

$$m_B = d_B / (1 - c m_A) \quad (6b)$$

where  $b = c(d_A + d_B) + 1 - d_B$ .

If the biology of the system were such that we could collect and dissect hosts immediately after oviposition was complete, but before parasitoid emergence commenced (Van Driesche, 1983), we could measure the marginal rate of attack directly. From a sample of 100 hosts in the example given above, on average 80% would contain A, of which 40 would have A alone and 40 both A and B, and 50% would contain B, of which 10 would contain B alone and 40 both A and B. In many studies of insect population dynamics, however, mortality from parasitism or disease is assessed by rearing field collected hosts rather than dissecting hosts to score numbers attacked; such an approach often is the only possible way to score mortality. In these cases, the original marginal rates can be recovered from the emergence rates for the different agents using Eq (6). The value for  $c$  used in Eqs. (5) and (6) could be determined experimentally by rearing hosts parasitized by both A and B, although in field

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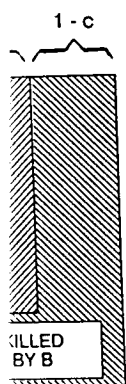
populations the value may vary depending on the temporal distribution of parasitoid attacks. For many hosts and parasitoids, the values for  $c$  will be unknown and some assumption concerning its value will be necessary. It might be reasonable to assume, for instance, that  $c=0.5$ , so that half of the individuals attacked by both A and B yield A and the other half yield B. Buonaccorsi and Elkinton (1990) explore the effect of varying  $c$  on Eqs. (6) and provide solutions for the case in which A or B or both could emerge from hosts attacked by both parasitoids. They also discuss methods for estimating rates for cases when more than two parasitoids act contemporaneously.

We have applied the method outlined above to gypsy moth assuming that  $c=0.5$  for all interactions (Gould et al., 1990). We extended the solutions to the marginal value Eqs. (6a, b) for two interacting agents, to cover interactions between five contemporaneous agents by calculating the proportion that die from each agent in turn versus the combined mortality from all the other agents. Carey (1989) proposes the same procedure to extend an analogous set of equations for two contemporaneous agents to interactions involving three or more agents. It is important to realize that this method of extending equations for two-way interactions to  $n$ -way interactions introduces a small error in the calculation of the marginal values that is proportional to the fraction of host individuals attacked by three or more contemporaneous agents. However, in most populations, this fraction and the resulting error is quite small. Discussion of this issue and a procedure that gives exact solutions for interactions of  $n$  contemporaneous agents is given in Buonaccorsi and Elkinton (1990).

Varley et al. (1973) offered a technique based on dissection of parasitized hosts that under some conditions gave correct estimates of the marginal attack rates (although they did not use this term) and associated  $k$ -values. The technique entailed assuming that the two contemporaneous parasitoids acted sequentially. Applying this technique to our example, we could assume that A went first and thus that 80% of the host were killed by A and then B killed 50% of the remaining 20 hosts. Alternatively, if we assumed that B came first we would say that B killed 50% and then A killed 80% of the remaining 50 hosts. Each of these alternative calculations yield the same marginal probability of attack (and therefore the same  $k$ -values).

#### Contemporaneous Predators

In many populations systems, the impact of predators is difficult to measure directly, but where hosts are sessile it may be possible to record predation of individual hosts. Suppose, for instance, that predation on the pupal stage of a host population could be recorded by scoring the survival of marked pupae. If the remnants of pupae consumed by predator A are distinct from those attacked by predator B, the proportion killed by each of the two agents can be recorded. This example is entirely analogous to that discussed above for parasitoids in which mortality is recorded by rearing parasitized hosts. Some of the pupae that would have been consumed by A are consumed by B first and vice versa. The marginal probability of attacks by each agent



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We would like to estimate the marginal probability of attack for each agent. Suppose, for instance, that 90% of the pupae are consumed, of which 60 were eaten by predator A and 30 by predator B. Calculations employing the suggestions of Varley et al. (1973) in treating these agents as sequential factors would estimate the same total mortality, but would do so by assuming a temporal sequence of action by the two predators. Such assumptions lead to incorrect and conflicting results. If, for example, predator A is deemed to have acted first, it will be credited with consuming 60% of the original host population, while 30 of the remaining 40 (75%) will be assigned to B, with overall survival of  $(1-0.6)(1-0.75)=0.10$ . In this case, however, unlike the case of indiscriminate parasitoids, the answer obtained will be notably different if B is deemed to act first. If B goes first, the resulting mortalities would be 85.7% and 30% for A and B, respectively. If A and B are truly contemporaneous neither of these calculations are correct. The correct value depends on the relative distribution of attacks from the two predators across the given interval. Procedures for obtaining correct estimates can be found in the literature on survival analysis that deals with competing risk (e.g., David and Moeschberger, 1978). Provided that the instantaneous rate of attack by predator A (the hazard rate for A; see Appendix A) over the interval remains proportional to the instantaneous rate of attack by B over the same interval, then the following equation (David and Moeschberger, 1978, Eq. 5.16) holds:

$$m_A = 1 - (1 - d_A - d_B)^{(d_A/(d_A + d_B))} \quad (7a)$$

$$m_B = 1 - (1 - d_A - d_B)^{(d_B/(d_A + d_B))} \quad (7b)$$

In the example given above, in which the observed predation rates ( $d_A$ ,  $d_B$ ) were 0.60 and 0.30, respectively, the calculated marginal rates using (7a, b) are 0.785 and 0.536 respectively. Note that these values are fairly close to those obtained (0.8, 0.5) using (6a, b) and  $c=0.5$  for the parasitoid example given above.

In order to establish the connection between Eqs. (7a, b) and our earlier treatment Eqs. (5), (6), we can solve (7a, b) for  $d_A$  and  $d_B$  (see Appendix B) and determine the resulting value of  $c$ :

$$c = \frac{m_B \ln(1 - m_A) - m_A (1 - m_A) \ln(1 - m_B)}{m_A m_B [\ln(1 - m_B) + \ln(1 - m_A)]} \quad (8)$$

The constant  $c$  in this context expresses the proportion of the pupae that would have been attacked by both A and B, if that were possible, that were eaten by A before they were encountered by B. Of course, there is no reason why one would have to calculate  $c$  in this case, since the marginal rates can be calculated directly from (7a, b).

Assuming proportional hazard rates, Eqs. (7a, b) will also apply in systems for which mortality from parasitoids or disease agents is obtained by rearing and the first

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agent to attack is the one which emerges or causes death. They also will apply in those systems in which the parasitoids avoid attacking hosts that have been previously parasitized by other agents (see below). For these reasons, Eqs. (7a, b) represent a suitable null hypothesis whenever there is no explicit knowledge about the results of competition between agents within a host or about the temporal distribution of attack rates over the interval in which the host stage is present.

Another great advantage of using (7a, b) under the assumption of proportional hazards, is that they are easily extended to multiple contemporaneous sources of mortality:

$$m_i = 1 - (1 - d)^{di/d}, \quad (9)$$

where  $m_i$  and  $di$  are the respective marginal rates and death rates from the  $i$ th cause and  $d$  is the death rate from all causes combined. In contrast, the extension of (6a, b) to multiple interactions discussed in Buonaccorsi and Elkinton (1990) requires an iterative procedure that converges on the correct solution by successive approximation.

Carey (1989) introduced a set of equations similar to Eqs. (6a, b) for calculating marginal rates from contemporaneous mortalities within a system. His formulae did not include an explicit value for  $c$ . Instead, he assumed that the marginal rates were proportional to observed death rates:

$$m_A/m_B = d_A/d_B. \quad (10)$$

This would seem to be a reasonable assumption because, in many cases, the value of the marginal rates will not be very different from the corresponding death rates. However, if we substitute (10) into (5) and solve for  $c$  we find that:

$$c = m_B/(m_A + m_B). \quad (11)$$

In the case of contemporaneous parasitoids, this implies that as attack rates by A increase relative to B, a larger proportion of hosts attacked by both would yield B rather than A. We think this would rarely, if ever, be the case. For predators it implies that as predation rates by A become large relative to B, an increasing proportion of the individuals that would be eaten by both A and B, if that were possible, would be consumed by B first. Instead, we suggest that Eqs. (7a, b) should be employed for analysis of most systems with contemporaneous mortalities, or else Eqs. (6a, b) with  $c=0.5$  or some other fixed value determined by experiment.

In many systems, attack rates by predators and parasitoids may vary during the study interval and will be different for each agent (e.g., Van Driesche and Bellows, 1988), and neither the assumption of complete sequential action nor complete contemporaneity will strictly apply. This problem can be addressed by measuring attack rates over shorter time intervals. If, for example, assessment of predation could be made on a daily basis and daily marginal attack rates then estimated, temporal

changes in attack rates can be noted. The assumption of contemporaneity embodied in the use of (7a, b) could apply for estimation of marginal rates for each daily interval.

#### Discriminating Parasitoids

We earlier assumed that parasitoids A and B were indiscriminate, that is, they were as likely to attack hosts previously parasitized by the other species as unparasitized hosts. In some cases this assumption may not be appropriate because of the parasitoid's ability to detect and avoid hosts that have been previously parasitized. When parasitoids discriminate against hosts that have been previously attacked by the other species, the assumption of independence of attacks by A and B is violated. Royama (1981) suggested an approach to this problem which entailed redefining the marginal rates to refer to the proportion of hosts encountered rather than the proportion of hosts actually attacked by contemporaneous parasitoids or predators. Encounters, by definition, are restricted to those which would result in lethal attacks by the predator or parasitoid in hosts that had not been previously parasitized. Such a restriction retains the original definition of the marginal attack rate as the proportion of hosts attacked and killed by an agent in the absence of other contemporaneous agents. Encounters are further assumed to be statistically independent. The proportion of hosts actually attacked reflects the relative preference by either A or B for hosts that have been previously parasitized by the other species compared to unparasitized hosts. In systems where discrimination is total, that is where parasitoids completely avoid attacking hosts which have been previously attacked by other agents, the proportion of hosts attacked has the same relationship to the proportion of hosts encountered as the proportion of hosts dying ( $d_A$ ,  $d_B$ ) has to the marginal attack rates ( $m_A$ ,  $m_B$ ) given above for nondiscriminating predators or parasitoids. Thus, if we can measure the proportion of hosts attacked by dissection, we can use the same mathematics Eqs. (6a, b) or (7a, b) to estimate the marginal encounter rates. In systems with contemporaneous predators, encounters include contacts with hypothetical prey that would have been present had they not been eaten by the other predator first.

In many systems, the degree of discrimination would be partial, and some host individuals would be attacked by both agents. To determine whether there was partial discrimination, the proportion of individuals actually multi-parasitized (determined by dissection) could be compared with that expected from the case of no discrimination (the product of the calculated marginal rates ( $m_A$ ,  $m_B$ )). If the null hypothesis (no discrimination) was rejected, calculations for marginal rates would have to incorporate assumptions concerning the degree to which each parasitoid would avoid attacking hosts previously parasitized by the other species. Equations describing the action of partially-discriminating parasitoids may be found in Royama (1981, Eqs. 14-17); solutions to these equations for the estimation of marginal rates and a discussion of the limitations under which they can be solved are given by

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Buonaccorsi and Elkinton (1990). These solutions also apply in the situation in which parasitism is determined by rearing and adult parasitoids attack indiscriminately, but the outcome allows both A and B to emerge from some of the hosts attacked by both species (Buonaccorsi and Elkinton (1990).

#### Contemporaneous Predator and Parasitoid

The case of nondiscriminating predator (one which attacks parasitized and unparasitized hosts with equal probability of success) and a parasitoid acting contemporaneously is a particularly simple one. It is analogous to the case of indiscriminate parasitoids where  $c=1$  (assuming the predator is agent A). The predator always "wins" in any host attacked by both the predator and parasitoid. In this case the marginal attack rate for predation is the same as the death rate and is observed directly, ( $m_A=d_A$ ). The marginal attack rate for the parasitoid (B) is  $m_B=d_B/(1-m_A)$ .

In the case of discriminating predators (predators that avoid or preferentially attack previously parasitized hosts), Eqs. (5a, b) still apply, but  $c$  will take on values that reflect the preference for parasitized versus unparasitized hosts. Unlike the case with contemporaneous parasitoids,  $c$  is not constrained to values less than 1.0. Values of  $c > 1.0$  occur when the predator prefers parasitized to unparasitized hosts. Suppose the degree of preference could be represented by a constant ( $p$ ) and could be measured experimentally by exposing parasitized and unparasitized hosts and determining their relative rates of consumption by the predator:

$$p = \text{Parasitized hosts attacked} / \text{Healthy hosts attacked.}$$

For example, if the predator, upon encountering the host, is twice as likely to consume a parasitized versus an unparasitized individual, then  $p=2.0$ . The following relationship holds between  $p$  and  $c$  (see Appendix C):

$$c = p + s - sp \tag{12}$$

where  $s$  is the proportion of prey that would have been attacked by both agents in which the parasitoid (A) came first and is equivalent to  $c$  given in (8) for the case when there is no discrimination. Unfortunately (12) does not give rise to an explicit solution for  $m_A$  and  $m_B$  as a function of  $d_A$ ,  $d_B$ ,  $c$ ,  $p$  and  $s$ . However, in many cases it may be reasonable to assume that  $s=0.5$ , to determine  $p$  experimentally, calculate  $c$  from (12) and use (6a, b) to calculate  $m_A$  and  $m_B$ .

#### THE ANALYSIS OF DENSITY DEPENDENCE

One of the major uses for mortality assessment is in the search for density-relatedness in mortality factors. A critical issue for tests of density-relatedness is the correct assessment of mortality. In cases with contemporaneous factors, improper

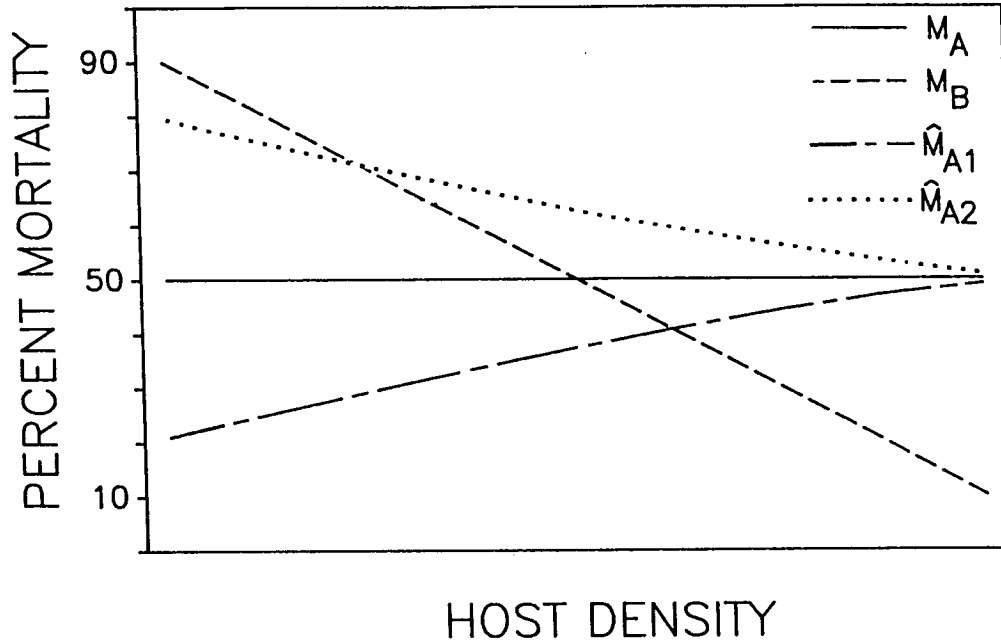


Fig. 2. Marginal attack rates of a density independent predator plotted against host density as calculated by the methods outlined in this manuscript ( $m_A$ , eq. 6a) and by the method of Varley et al. (1973) assuming that it preceded ( $\hat{m}_{A1}$ ) or followed ( $\hat{m}_{A2}$ ) another density dependent contemporaneous agent (B).

calculation can lead to errors in mortality estimation which can lead, in some cases, to spurious relationships between mortality and density.

As an example, we consider a system with two contemporaneous predators A and B acting on a series of populations that vary in density. Predator A attacks 50% of hosts in a population regardless of density (i.e., is density independent), while predation by B is 90% at low densities and decreases to 10% at high densities (i.e., is inversely density dependent, Fig. 2). If we employ the assumption that the predators acted sequentially (as proposed by Varley et al. (1973) for contemporaneous agents), we could assume either that predator A acted before ( $\hat{m}_{A1}$ ) or after ( $\hat{m}_{A2}$ ) predator B. The results from either approach suggest strongly that mortality caused by A is density dependent (Fig. 2). Only the proper calculation of marginal rates employing the assumptions of contemporaneous action Eqs. (6a, b) or (7a, b) provides the correct answer (density independence).

#### DISCUSSION

These examples make it clear that tests for density dependence or, indeed, any comparison of levels of mortality between populations, should only be made using the marginal attack rates or  $k$ -values calculated from marginal rates and not based on

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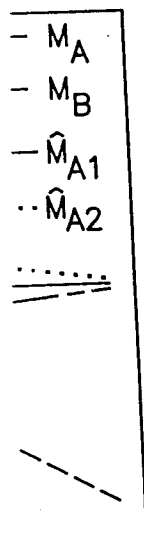
proportions dying. Most life tables include data on the number dying ( $d_x$ ) and the apparent mortalities or proportion dying ( $q_x$ ) of those individuals that entered the stage or age interval. Some life tables also include  $k$ -values, but for contemporaneous mortalities these are only correct if they are calculated from the marginal attack rates. The death rate or apparent mortality will be the same as the marginal rate of mortality if and only if it is either the only source of mortality in an interval or stage or else it is the first of a sequential series of factors acting within the interval or stage. The level of apparent mortality is influenced by the presence of contemporaneous mortalities acting in a stage, and thus becomes an ambiguous measure of mortality in the presence of contemporaneous factors. The marginal attack rate of a factor has a value which is independent of the value of other contemporaneous mortalities. Many life tables in the literature do not provide information in sufficient detail to permit the proper calculation of the marginal attack rate and thus are of limited value for comparisons with other systems or for seeking generalities among different systems concerning the impact of specific agents.

The use of (7a, b) requires that hazard rates from contemporaneous predators or parasitoids be proportional over the interval on which data is collected. Proportional hazard rates occur under specific temporal distributions of attacks. For instance, if the hazard rate (the instantaneous rate of attack) remains constant, the number of attacks per unit time declines exponentially over the interval as hosts are removed. This will occur when attack rates are determined by the ability of predators to find prey and they search at a constant rate over the interval (see Appendix A). Constant search rates are typically assumed in theoretical models of predation and parasitism (e.g., Rogers, 1972). On the other hand, if the number of hosts consumed or attacked by two or more predators per unit time remains constant, the hazard rates increase with time, because this number represents a greater and greater proportion of the remaining hosts. Such cases might occur when rates of predation are determined by predator appetite and not by difficulty in finding prey. In such cases the ratio of the hazard rates does not remain constant. In this case however,  $c=0.5$  and Eqs. (6a, b) should be used to calculate the marginal attack rates (see Appendix D).

Various approximations to the marginal attack rate have been offered in the survival literature. One of these (Elandt-Johnson and Johnson, 1980, Eq. 11.21):

$$m_A = d_A / (1 - 0.5d_B) \quad (14)$$

is used in several widely used statistical packages: SPSS\* SURVIVAL (SPSS\* User's Guide, 1986) and BMDP1L (BMDP Statistical Software, 1983). These programs are used to calculate survival functions and hazard rates for data in which subjects are observed over some interval and times of death from specific causes are noted. Death from contemporaneous causes other than the specific cause under study are known as censored cases and treated as if they had withdrawn from the study. They are lumped into  $d_B$  above. It is important to note that the result obtained from (14) is only



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approximate. For instance, if the observed death rates were  $d_A=0.60$  and  $d_B=0.30$ , as in the examples given above, then the calculated marginal rates using (14) would be  $m_A=0.706$  and  $m_B=0.429$ . The product of the corresponding estimated marginal rates (0.168) is not equal to the total survival (0.10).

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同時死亡要因の解析における周辺攻撃率,  $k$ -値, および密度依存性

J. S. ELKINTON · J. P. BUONACCORSI · T. S. BELLOWS, JR · R. G. VAN DRIESCHE

複数の捕食者や寄生者が同時死亡要因として働いている場合に, 観測された死亡率から周辺攻撃率 (真の要因別攻撃率) およびそれに基づく  $k$ -値を計算する方法を, 攻撃者が既寄生寄主を識別する場合としない場合のそれぞれについて提案し, 同時死亡要因の評価のために従来用いられてきた諸方法との関係を論じた. 特に, ヒトの生存率解析における competing risk の扱いとの関係について詳しく考察した. また, 同時に攻撃する捕食者間の密度依存性の評価の問題も, Varley et al. (1973) の方法と対比させながら論じた.

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## APPENDIX A

Here we briefly describe the hazard rate. Consider a random variable  $T$  which denotes the time of attack by an agent. Denote the cumulative distribution function by  $F(t) = P(T < t)$  and assume it has density function  $f(t)$ . The hazard rate which is a function of  $t$  is defined by

$$\lambda(t) = \frac{f(t)}{1 - F(t)}$$

$$= \lim_{\Delta t \rightarrow 0} \frac{P(\text{attack is in } (t, t + \Delta t) \text{ given attack is not in } (0, t))}{\Delta t}$$

The hazard rate  $\lambda(t)$  can be viewed as the conditional proportion dying per unit time in a short period of time after time  $t$ , given survival up to time  $t$ .

When the time of attack is distributed exponentially ( $f(t) = \theta e^{-\theta t}$  or  $F(t) = 1 - e^{-\theta t}$ ) the hazard rate is constant;  $\lambda(t) = \theta$ . When the time of attack is uniformly distributed over an interval  $(a, b)$  the density is  $f(t) = 1/(b-a)$  and the hazard rate is  $\lambda(t) = 1/(b-t)$ , for  $t$  in  $(a, b)$ , which is increasing in  $t$ .

## APPENDIX B

Here we derive the value of  $c$  for the case with two agents and the hazard rates being proportional. Together, Eqs. (7a, b) can be expressed as

$$1 - d_A - d_B = (1 - m_A)^{(d_A + d_B)/d_A} = (1 - m_B)^{(d_A + d_B)/d_B}$$

Taking logs and simplifying yields

$$d_B = d_A \frac{\ln(1 - m_B)}{\ln(1 - m_A)} \quad (A1)$$

Upon substituting (A1) for  $d_B$  in (5b) and then solving (5a) and (5b) in terms of  $c$ , yields  $c$  as given in Eq. (8).

## APPENDIX C

Here we develop the relationship between the proportion dying and marginal attack rates for a predator/parasitoid system, where the predator may discriminate between parasitized and unparasitized hosts.

Let  $\pi_A$  = probability that predator A encounters the host and  $\pi_B$  = probability that parasitoid B encounters the host. Here, the meaning of encounter needs to be clearly defined. We allow for the possibility that the parasitoid can "encounter" the host even after it has been consumed by the predator in the sense that the parasitoid reaches the position where the host was located and if it hadn't been consumed by the predator it would be a potential victim of the parasitoid. The definition of encounter is such that it is reasonable to assume the events "encountered by A" and "encountered by B" are independent. Let

$$q_B = P(\text{parasitoid enters an encountered host})$$

$$q_A = P(\text{predator devours and encountered host given no parasitoid is present}), \text{ and}$$

$$r_A = P(\text{predator devours host given parasitoid is present}).$$

Define  $p = r_A/q_A$  which represents a preference ratio for parasitized hosts by the predator. The marginal attack rates are defined to be the probabilities of being encountered and killed by each of the

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agents in the absence of the others. These become

$$m_A = q_A \bar{\pi}_A \quad \text{and} \quad m_B = q_B \bar{\pi}_B.$$

$$\begin{aligned} \text{Let } d_A &= P(\text{observe death due to } A) \\ &= P(A \text{ encounters, B doesn't encounter and A consumes}) \\ &\quad + P(\text{both A and B encounter but cause of death is A}) \\ &= P(A \text{ encounters, B doesn't encounter and A consumes}) \\ &\quad + P(\text{both A and B encounter, A is first to encounter, cause of death is A}) \\ &\quad + P(\text{both A and B encounter, B is first to encounter, cause of death is A}). \end{aligned}$$

Let  $AB$  denote the event A encounters and then B encounters and let  $BA$  denote the event B encounters and then A encounters Now

$$d_A = q_A \bar{\pi}_A (1 - \bar{\pi}_B) + P(AB)q_A + P(BA)(q_B r_A + (1 - q_B)q_A).$$

For the event  $BA$ ,  $q_B r_A$  represents the probability that B enters host times the probability A consumes given host has been previously parasitized and  $(1 - q_B)q_A$  represents the probability that B does not enter the host and then A consumes the unparasitized host. However  $P(AB) + P(BA) = \pi_A \bar{\pi}_B =$  probability both encounter. Define  $s = P(AB/\pi_A \bar{\pi}_B)$  which is the probability that A encounters first given that both A and B encounter the host and  $1 - s = P(BA)/\pi_A \bar{\pi}_B$ . This leads to

$$d_A = q_A \bar{\pi}_A (1 - \bar{\pi}_B) + s \pi_A \bar{\pi}_B q_A + (1 - s) \bar{\pi}_A \bar{\pi}_B (q_B r_A + (1 - q_B)q_A).$$

Expanding and cancelling terms and recalling  $m_A = q_A \bar{\pi}_A$  and  $m_B = q_B \bar{\pi}_B$  leads to

$$\begin{aligned} d_A &= m_A \bar{\pi}_A \bar{\pi}_B (q_B r_A - q_A q_B - s q_B r_A + s q_A q_B) \\ &= m_A + m_A m_B (c - 1) \end{aligned}$$

(A1)

where  $c = s + p - sp$  and recall  $p = r_A/q_A$ .

For the observed death due to the parasitoid B,

$$\begin{aligned} d_B &= P(\text{death due to B}) = P(\text{B only encounters and death due to B}) \\ &\quad + P(\text{A and B both encounter and death is due to B}). \end{aligned}$$

Using the relationships above and a development similar to that in deriving  $d_A$  leads to

$$= q_B \bar{\pi}_B (1 - \bar{\pi}_A) + P(AB)(1 - q_A)q_B + P(BA)q_B(1 - r_A)$$

which after simplification becomes

$$d_B = q_B \bar{\pi}_B + \bar{\pi}_A \bar{\pi}_B q_A q_B (sp - s - p) = m_B - m_A m_B c.$$

The case  $p = 1$  corresponds to no discrimination and leads to  $c = 1$ . When  $s = 1$  this means that the parasitoid always follows the predator in time and  $c = 1$  here also. When  $s = 0$ , the parasitoid is always first in which case  $c = p$ .

#### APPENDIX D

Here we discuss how  $c$  is obtained in the case where the first agent to attack is the cause of death. In Eq. (5), the quantity  $c$  is the probability that A attacks the host first given that both A and B attack the host. Formally, let  $Y_A$  denote the time at which A would contact and consume host if only A was in system and let  $Y_B$  denote the time at which B would contact and consume host if only B was in system. For each

predator A and B there is some distribution of time to attack. We assume these two times are independent which means that the distribution of  $Y_A$  is the same whether or not B is in the system and vice-versa. If we are observing the system up to time  $t_0$ , then

$$\begin{aligned} c &= P(\text{observed cause is A} \mid Y_A < t_0, Y_B < t_0) \\ &= P(Y_A < Y_B \mid Y_A < t_0, Y_B < t_0) = \frac{P(Y_A < Y_B < t_0)}{P(Y_A < t_0, Y_B < t_0)}. \end{aligned}$$

For specific distributions, one can determine  $c$  by evaluating the above probabilities though it may not always be straightforward. For exponential distributions one obtains  $c$  as in Eq. (8). If the time to deaths are uniformly distributed over  $(0, t_A)$  for cause A and over  $(0, t_B)$  for cause B, then  $m_A = t_0/t_A$  and  $m_B = t_0/t_B$  with the larger marginal attack rate due to the cause over which uniform deaths occur in a shorter amount of time. The hazard rate for A and B are both increasing in  $t$  and are not proportional. Evaluating the earlier expression leads to  $c$  equals 0.5. Essentially what happens is that given the time of death has occurred before  $t_0$ , the actual time of death is uniform over 0 to  $t_0$  and this is true for either cause of death. Hence conditioned on the fact that both times are less than  $t_0$  (i.e., the host is attacked by both causes), the probability that A is first is 0.5.