

## COMPETING RISKS ANALYSIS IN MOUNTAIN PINE BEETLE DYNAMICS

Walter E. COLE

Intermountain Forest and Range Experiment Station, USDA  
Forest Service, Ogden, Utah 84401, U. S. A.

### INTRODUCTION

The mountain pine beetle (*Dendroctonus ponderosae* HOPK.) is an organism indigenous to and exerting numerous and various effects upon the lodgepole pine (*Pinus contorta* DOUGL.) ecosystem. Historically, the mountain pine beetle has infested lodgepole pine forests, periodically depleting them by killing the largest, most vigorous trees. This ever-present beetle pressure and the associated recurring mortality are primary concerns in the management of such stands. Understanding the life processes within the beetle population is basic to providing management with alternative methods of growing lodgepole pine.

Loss of trees to the mountain pine beetle is in part a function of stand structure (diameter distribution) within habitat type and in part a function of food supply (phloem thickness) within trees. Generally, the large-diameter trees in the stand contain thick phloem. This intercorrelation is basic to population dynamics of the mountain pine beetle. The attack density of the mountain pine beetle is related to diameter and provides the basis for brood production. Brood production is the foundation for crowding within the population. Since diameter of trees is related to food supply and attack density is related to diameter, this then relates to crowding and brood survival.

AMMAN (1969) found that brood production in phloem of a given thickness is inversely related to elevation, which in turn is associated with temperature (particularly winter temperatures). Mountain pine beetle brood production is quite low at elevations above 8,000 feet; consequently, survival of lodgepole pine is much higher. Throughout the elevation zones sampled, the complement of the probability of lodgepole pine being attacked by the mountain pine beetle is a linear function of the elevation of the stand. This finding held even in the presence of an ample food supply (thick phloem in trees of large diameter) at high elevations. However, at low elevations where growing conditions are optimal for the beetle, brood production was directly related to food quantity. Thus, the foregoing substantiates food regulation at low elevations and temperature regulation at high elevations.

Crowding can act in either a passive or beneficial role. As crowding increases, food supply decreases; as a result, brood mortality increases. Within a given small food quantity (thin phloem), crowding shortens the developmental period of the

surviving larvae. Conversely, within a given large quantity of food the developmental period lengthens. This in turn affects the sex ratio—more females survive as the developmental period increases; increased crowding decreases reproductive capacity of the female adult beetle; and forthright mortality increases as crowding increases (COLE, 1973).

Temperature also has a direct effect upon larval (brood) survival, particularly during the winter. This effect is tempered by the depth of bark, which is related to tree diameter in the amount of insulation provided the beetle brood. Small-diameter trees usually have thinner bark and thus provide less insulation to the brood and greater brood mortality can occur than within the larger diameter trees.

Discussion has prevailed concerning the value of parasites and predators as regulators and/or controlling factors within most insect populations. The possibility of manipulating these factors of mortality in the sense of biological control in insect populations has been omnipresent. The mountain pine beetle is no exception. The inability to evaluate the effects of parasites and predators upon the mountain pine beetle population has confounded these efforts.

This paper presents an approach used in analyzing life tables by competing risks (factors of mortality) to evaluate the effects of these three known risks—crowding, temperature, and parasites and predators—and one group of unknown risks; and to determine the most effective combinations of risks. Conceivably, this technique could be used to determine (a) the population level of a specific risk or specific combinations of risks that would be needed for reducing the insect population and the level of probability at which it will occur; (b) the probability of death and the extent of population reduction if a particular force of mortality is applied during a specific stage; and (c) a predictive basis for pest control that would make possible both forecasts of outbreaks and prognoses of the effects of changes in forest management practices.

#### DATA SOURCE

Mountain pine beetle populations in lodgepole pine were sampled for 3 years based on the scheme developed by CARLSON and COLE (1965). Four trees were sampled within each of three diameter classes (9, 12, and 15 inches diameter at breast height (d. b. h.)) on one plot for each of the 3 years. A systematic random sampling method was used to select trees. The insect population on each of the two 15.2- by 15.2-cm samples per tree was recorded by individuals surviving, dying, and cause of death within the developmental stage.

Based on previous life table work, five observations are adequate to detect causes of change during the generation year of the beetle :

1. Early fall      Sample fixed the base population (=egg population).
2. Late fall        Sample determined the number of larvae (2nd and 3rd instar)

- entering the winter.
3. Spring            Sample established the number of larvae (3rd and 4th instar) that survived the winter.
  4. Summer         Sample established larvae and pupae population.
  5. Emerging adults    Sample established the emerging adult population.

### COMPETING RISKS

CHIANG (1968) has defined risk (of dying) as each mortality factor present in a population prior to the death of an individual within that population and after death, that mortality factor (risk) becoming the cause of death. CHIANG uses three types of probabilities of death from specific causes in his work with human populations. The reader is referred to CHIANG for a mathematical discussion of the relations between the following definitions :

1. *The crude probability*—The probability of death from a specific cause in the presence of all other risks acting in a population, or

$Q_{i\delta} = Pr$  {an individual alive at time,  $x_i$ , will die in the interval  $(x_i, x_{i+1})$  from cause,  $R_\delta$ , in the presence of all other risks in the population},

and its estimator is

$$\hat{Q}_{i\delta} = \frac{d_{i\delta}}{l_i}, \quad i=1, 2, \dots, u; \delta=1, 2, \dots, r,$$

where  $d_{i\delta}$  and  $l_i$  are the number of deaths from  $R_\delta$  during the interval and the number of survivors at the beginning of the interval, respectively.

2. *The net probability*—The probability of death if a specific risk is the only risk in effect in the population, or

$q_{i\delta} = Pr$  {an individual alive at  $x_i$  will die in the interval  $(x_i, x_{i+1})$  if  $R_\delta$  is the only risk acting on the population};

or, conversely, the probability of death if a specific risk is eliminated from the population, or

$q_{i,\delta} = Pr$  {an individual alive at  $x_i$  will die in the interval  $(x_i, x_{i+1})$  if  $R_\delta$  is eliminated as a risk of death},

and the estimators are

$$\hat{q}_{i\delta} = 1 - \left( \frac{l_{i+1}}{l_i} \right)^{d_{i\delta}/d_i}$$

and

$$\hat{q}_{i,\delta} = 1 - \left( \frac{l_{i+1}}{l_i} \right)^{(d_i - d_{i\delta})/d_i}, \quad i=1, 2, \dots, u; \delta=1, 2, \dots, r.$$

3. *The partial crude probability*—The probability of death from a specific cause when another risk is eliminated from the population or

$Q_{i\delta,1} = Pr$  {an individual alive at  $x_i$  will die in the interval  $(x_i, x_{i+1})$  from  $R_\delta$  if  $R_1$  is eliminated as risk of death}; or

the probability of death from a specific cause when other risks are eliminated from the population, or

$Q_{i\delta,12} = Pr$  {an individual alive at  $x_i$  will die in the interval  $(x_i, x_{i+1})$  from  $R_\delta$  if  $R_1$  and  $R_2$  are eliminated as risks of death}; and the estimators are

$$\hat{Q}_{i\delta,1} = \frac{d_{i\delta}}{d_i - d_{i1}} \left[ 1 - \left( \frac{l_{i+1}}{l_i} \right)^{(d_i - d_{i1})/d_i} \right]$$

and

$$\hat{Q}_{i\delta,12} = \frac{d_{i\delta}}{d_i - d_{i1} - d_{i2}} \left[ 1 - \left( \frac{l_{i+1}}{l_i} \right)^{(d_i - d_{i1} - d_{i2})/d_i} \right]$$

$$, i=1, 2, \dots, u; \delta=3, 4, \dots, r.$$

When the cause of death is not specified, we have the probabilities,

$p_i = Pr$  {an individual alive at  $x_i$  will survive the interval  $(x_i, x_{i+1})$ }

and

$q_i = Pr$  {an individual alive at  $x_i$  will die in the interval  $(x_i, x_{i+1})$ }

with  $p_i + q_i = 1$ .

and the estimators are

$$\hat{p}_i = \frac{l_{i+1}}{l_i}$$

and

$$\hat{q}_i = \frac{d_i}{l_i} \text{ or } 1 - \hat{p}_i = \hat{q}_i, \quad i=1, 2, \dots, u.$$

#### ANALYSIS OF AN EXAMPLE

The abridged cohort life table, in which a generation of beetles is sampled at particular points in time, was used in our study of the mountain pine beetle. The abridged cohort life table was not followed in its strictest sense because of destructive sampling. Death of the last individual was not recorded; instead, the emergence of the adult beetle was equated with the end of life for that particular cohort.

Throughout the example, we assume that all individuals within the sample were subject to the same forces of mortality and that the survival of one individual is independent of the survival of any other in the group. By making this assumption, we avoid unnecessary complications (Based on CHIANG 1968). Table 1 shows an expanded life table for these data to include the fraction of the last age interval of life ( $a_i$ ), observed life expectation ( $\hat{e}_i$ ) and its variance ( $V\hat{e}_i$ ), proportion of survival ( $p_i$ ) and death ( $q_i$ ) during the intervals. When the cause of death is not specified, the probabilities of survival and death ( $p_i, q_i$ ) and their variances can be determined at this point.

All life table studies focus centrally on life expectation and survival rates. By comparing these, we can evaluate the intensity of risks measured during the stages of population growth. The rate of survival (or conversely, mortality) can more or

Table 1. An example of abridged cohort life table for mountain pine beetle populations<sup>1</sup>  
(9 inches d. b. h.)

Interval (i)	Interval length (days) ( $x_i$ to $x_{i+1}$ ) (1)	Number living at start of $x_i$ ( $l_i$ ) (2)	Number dying during $x_i$ to $x_{i+1}$ ( $d_i$ ) (3)	Proportion of individuals		
				Surviving $x_i$ to $x_{i+1}$ ( $p_i$ ) (4)	Dead $x_i$ to $x_{i+1}$ ( $q_i$ ) (5)	Variance ( $Vp_i = Vq_i$ ) (6)
1	30	3,079	325	0.8944	0.1056	0.000031
2	180	2,754	958	.6521	.3479	.000082
3	60	1,796	676	.6236	.3764	.000131
4	30	1,120	403	.6402	.3598	.000206
5	60	717	717	.0000	1.0000	—

Fraction of last age interval of life ( $a_i$ ) (7)	Life expectation		
	Observed at age $x_i$ ( $e_i$ ) (8)	Variance ( $Ve_i$ ) (9)	Standard error ( $SEe_i$ ) (10)
0.50	212.748	2.10379	1.450
.50	206.084	.99393	.997
.50	88.004	.81996	.906
.50	65.013	.75280	.868
—	60.000	—	—

<sup>1</sup> Equations for calculating column values are found in CHIANG (1968).

less govern life expectation. For the mountain pine beetle, the total life interval from egg to adult is approximately 360 days. High mortality rates could lessen life expectation, whereas low mortality rates would bring it closer to actuality. Such interaction and mortality forces could then influence the timing of flight, pupation, and other biological events during the generation life (about 1 year) of the beetle.

Expectation of life ( $e_x$ ), the average number of time intervals yet to be lived by an individual now at age  $x$ , is considered most important in human life-table analysis. However, ecologists, particularly entomologists dealing with insects that have discrete generations, as in this case, and populations that are not stationary do not usually attach the same importance to  $e_x$ . The same can be considered for the use of  $a_i$ , the fraction of last age interval of life. This statistic depends upon the trend of mortality within the growth interval stage and may be considered a constant if the mortality trend within the interval varies little. In this example, we will consider both  $e_x$  and  $a_i$  (assumed to be 0.50 for lack of data on mortality trend within interval) for discussion purposes because some interpretation can be made of the values of  $e_x$  based on *a priori* biological knowledge of the beetle. The increased expectation of life during the 2nd and 3rd life stages (=observations) for trees 12 and 15 inches d. b. h. (Table 2) is probably associated with the increased attack density of the beetle by diameter. Prior studies (COLE, 1973) have shown that crowding tends to increase stadal duration due to the food-per-capita supply decrease, and that crowding is influenced by attack density.

Table 2. Observed expectation of life in days ( $\hat{e}_x$ ) and the sample variance of  $\hat{e}_x$  of the mountain pine beetle within trees of 9, 12, and 15 inches d. b. h.

Observation period	Tree diameter class (d. b. h.)					
	9 inches		12 inches		15 inches	
	$\hat{e}_x$	$V\hat{e}_x$	$\hat{e}_x$	$V\hat{e}_x$	$\hat{e}_x$	$V\hat{e}_x$
1	212.748	2.10379	187.937	2.59026	184.363	3.25332
2	206.084	.99393	198.845	1.11988	204.440	1.23188
3	88.004	.81996	91.816	.98969	88.718	1.03133
4	63.013	.75280	68.635	.74268	64.144	.91364
5	60.000	—	60.000	—	60.000	—

The basic life tables for the mountain pine beetle, stratified by tree diameters 9, 12, and 15 inches d. b. h. are shown in Fig. 1. In each case, the sample error was equal to or less than 5% of the proportion of individuals dying within the interval. The probability of death when the cause was not specified, ( $q_i$ ), was calculated for the mountain pine beetle within each tree-diameter stratum (Fig. 2). It is interesting

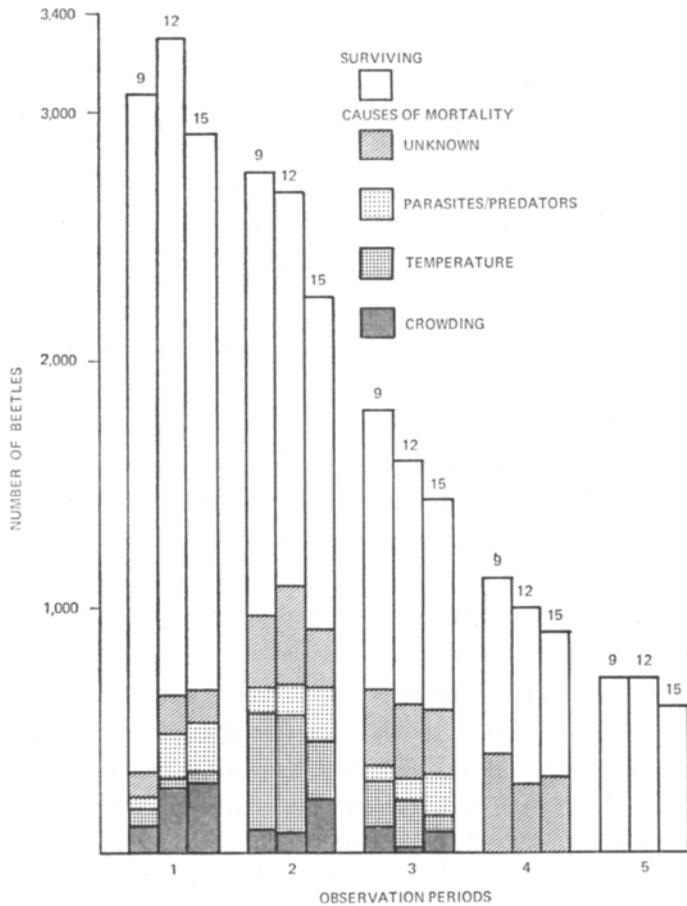


Fig. 1. Graphic representation of the basic life table for the mountain pine beetle in host trees of three d. b. h. classes (9, 12, and 15 inches).

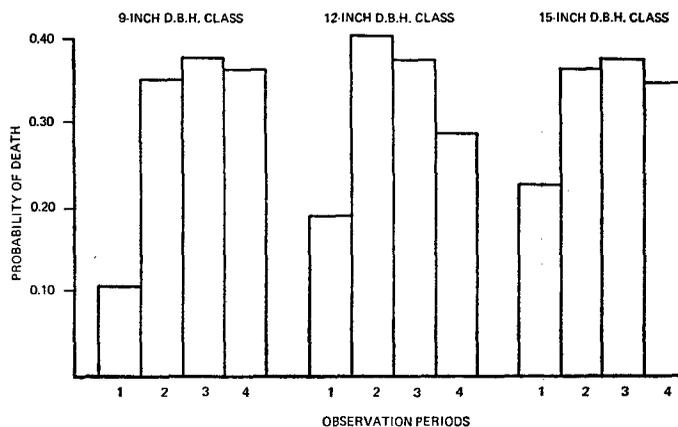


Fig. 2. Probability of death for individual mountain pine beetles in host trees when the cause of death is not specified.

to note here that the probability of dying in the first interval was greatest in the largest trees. Again, this observation probably reflects the influence of crowding upon the lengths of early larval stadia in relation to attack density. The probability of an individual surviving the entire growth period, 1st instar larvae to adult, was 0.01539, or a little over 1.5% chance for any individual to survive all developmental stages. One might interpret this finding to mean that if the probability of survival increases to greater than 1.5%, an increasing trend toward epidemic levels is likely; if such a probability decreases or remains the same, an endemic or static situation is possible.

Within the crude probabilities, two or three trends are interesting (Fig. 3). The probability of death due to crowding in the presence of the other risks during the first observation interval is greatest within the 15-inch (d. b. h. class) trees, again reflecting the influence of attack density. Temperature appears to exert a greater influence within smaller trees during the winter interval (second observation)—possibly because of thinner bark and less insulation. The parasite-predator group exerts the least influence of the risks presented here, except within trees of large diameter which contain the largest beetle populations. These findings *might* indicate density dependence by this risk group. However, the parasite-predator group population is usually so small that if there is a density-dependent change in the population level, it is not noticeable to any extent of population reduction.

Necessarily, unknown risks exert not only an increasing influence over intervals but are the only risks accounted for during the last interval. The fourth interval ends with the fifth observation (the collecting and counting of emerged adults from the cages attached to the tree). No mortality was assessed during this sampling observation period; so all causes of death during this interval were classified as unknown causes. Of the risks measured, crowding and temperature generally

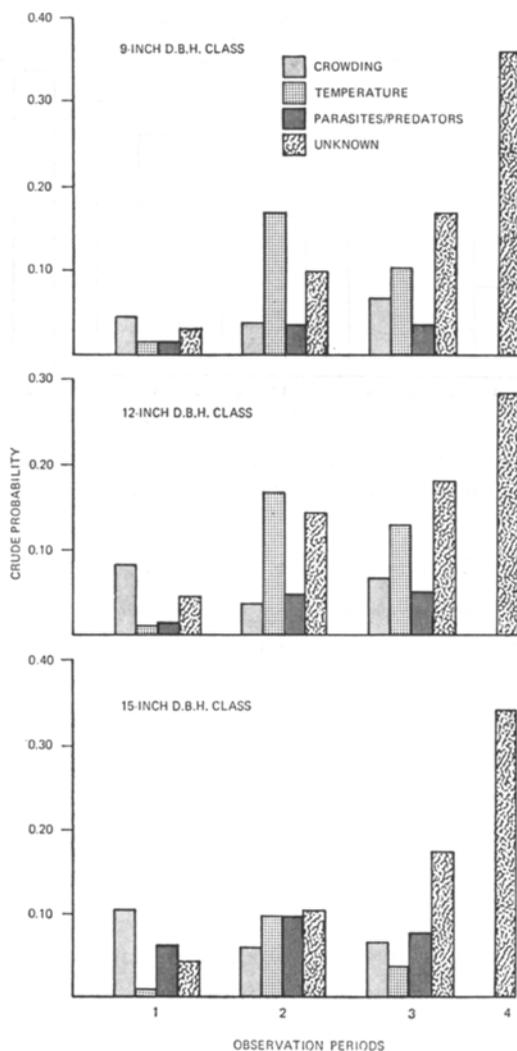


Fig. 3. Crude probabilities of death from specific causes in presence of all other risks for individual mountain pine beetles in host trees of three d. b. h. classes (9, 12, and 15 inches).

appeared to most influence population mortality within the 9- and 12-inch (d. b. h. class) trees, while these risks plus parasites and predators are rather evenly effective, but inconsequential, risks within the 15-inch (d. b. h. class) trees.

However, the interpretation of these probabilities is that none of these risks (particularly the parasite-predator risk) acting in the presence of other risks offers much regulating influence upon a mountain pine beetle population. Since all other risks were grouped in the 'unknown group' of risks, and the total unknown risks exceeded any one known risk in only one or two instances, it is reasonable to believe that if this class was separated into individual known risks, none would be

of noteworthy influence upon the population. Thus, if no single risk, or combination of these risks, offers much help, then the contention that mountain pine beetle populations are food-regulated is strengthened (COLE and AMMAN, 1969).

In actuality, net probabilities are not practically useful in either definition, nor can either definition be fully evaluated. Under field conditions, no risk of death can be completely eliminated, nor can all risks be measured; partial crude probabilities cannot be evaluated either. However, this type of information might be useful for possible manipulation of a beetle population. For example, what change in probability of death would occur if it were possible to combine an increase in a parasite's population with removing a definitive portion of the food structure? On the other hand, given other factors at a known level, the probability of death from a specific cause or factor would appear to be more useful for both simulation and manipulation.

No attempt has been made to interpret either net or partial crude probabilities. However, crude probabilities can be estimated directly, but net and partial crude probabilities can only be estimated through their relations with the crude probability. This does not necessarily negate the original objective of this paper, but illustrates the incompleteness of utilizing net and partial crude probabilities at this time.

#### SUMMARY

This paper presents an application and evaluation of competing risks analysis (CHIANG, 1968) of mountain pine beetle life tables. Three known and one group of unknown risks are used. Interpretation of the results imply that only the crude probability of death from a specific cause is applicable to this situation; net and partial crude probabilities are yet incomplete. None of the risks (factors of mortality) exerted sufficient influence upon the population to be considered factors of regulation or reduction. Evidence remains that the mountain pine beetle is food-regulated at optimum temperature conditions and temperature-regulated at optimum food conditions.

#### REFERENCES

- AMMAN, G. D. (1969) Mountain pine beetle emergence in relation to depth of lodgepole pine bark. *USDA For. Serv. Res. Note* INT-96, 8p., illus.
- CARLSON, R. W. and W. E. COLE (1965) A technique for sampling populations of the mountain pine beetle. *U. S. For. Serv. Res. Pap.* INT-20, 13p., illus.
- CHIANG, C. L. (1968) *Introduction to stochastic processes in biostatistics*. 313 p. John Wiley & Sons, Inc., New York.
- COLE, W. E. (1973) Crowding effects among single-age larvae of the mountain pine beetle, *Dendroctonus ponderosae* HOPKINS (Coleoptera: Scolytidae). *J. Envir. Entomol.* 2 (2): 285-293.
- COLE, W. E. and G. D. AMMAN (1969) Mountain pine beetle infestations in relation to lodgepole pine diameters. *USDA For. Serv. Res. Note* INT-95, 7p., illus.

キクイムシの1種 *Dendroctonus ponderosae* の個体群動態  
解析に対する “competing risks analysis” の適用

W. E. COLE

Lodgepole pine の害虫 *Dendroctonus ponderosae* の生命表解析に “competing risks analysis” (CHIANG 1968) の手法を適用した。こみあい, 気温, 天敵という3種の risk (死亡要因) と未知の一群の risk について解析を行なったところ, どの risk の影響も単独では個体群の制御要因とみなしうるほど強くはなかった。このキクイムシの場合, 温度条件が好適な時には食物によって, また食物条件が好適な時には温度によって個体数が制御されていると考えられる。