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Title: SAMPLING AND ESTIMATING POPULATIONS OF INSECT

SEED - PREDATORS IN CONIFEROUS FORESTS

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Ralph E. Berry

Quantitative studies of seed predation require reliable proce-
dures for estimating the principal quantities of interest.   This inves-
tigation specifically addresses itself to the development of probability
sampling methods for estimating populations of conifer cones and
seeds and their associated insect fauna.   Field studies in the
Buckhead Seed Production Area, Lane County, Oregon, focussed
on the estimation of pupal populations of Barbara colfaxiana
(Kearfott), the Douglas fir cone moth, in stands of Pseudotsuga
menziesii (Mirbel) Franco, the Douglas fir tree.   Fieldwork was
conducted during a year of high cone production.   Eighty-nine percent
of the trees on six acres of the study site bore cones.   The estimated
mean populations per tree, on a two-acre plot, were 310 ± 66 pupae
and 4082 ± 966 cones.   The estimated intensity was 0.076 pupae per
cone.   The sample data permit certain inferences regarding the
behaviour of B. colfaxiana females in their search for oviposition
sites on cones.

The sampling strategy is conceptualized as a two-phase (double) sample, in which the first phase estimates the cone population, and the second estimates the parameters of a regression or ratio relationship between insects (or seeds) and cones. The evidence presented in this study suggests that the cones are most efficiently estimated by using a visual index as an auxiliary variable at each stage of a two-stage sample, where trees and branches respectively represent the first and second stage sampling units. The regression relationship between insects (or seeds) and cones is estimated from a sub-sample of the branches employed in cone estimation. The bias that may result from the arbitrary sub-sampling of cones from individual branches is discussed, and the need for strict probability sampling is stressed. It is felt that both the conceptual and methodological aspects have general applicability.

Ecological and coevolutionary aspects of seed predation in temperate coniferous forests are discussed. The possible role of host-specific, insect seed-predators in determining the natural distribution and abundance of conifer trees is considered, and suitable opportunities for field investigations are described. An argument is advanced for the population dynamics of cone and seed insects. The availability of cones is not regarded as being the sole factor limiting population growth, and the role of natural enemies is thought to be significant. It is suggested that a holistic, systems approach would

be appropriate for the study of the interactions of insect and vertebrate seed-predators and their conifer host trees. Topics for further study, including problems of both ecological and economic interest, are outlined.

Sampling and Estimating Populations of
Insect Seed-Predators
in Coniferous Forests

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Chairman of Department of Entomology

Dean of Graduate School

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

SAMPLING AND ESTIMATING POPULATIONS OF INSECT SEED - PREDATORS IN CONIFEROUS FORESTS

INTRODUCTION

A number of herbivorous insect species may feed on flowers

and related plant structures, but there are certain species which

exploit the reproductive structures as their principal source of nutri-

tion. These insects might be expected, therefore, to have a signifi-

cant influence on plant reproduction (Janzen, 1979, 1970; Harper and

White, 1974) and the production of certain crops. Indeed, the litera-

ture of economic entomology, in which insects are often classified

by the symptoms of their damage to plant structures, provides a

ready guide to the range of flower parts that can be affected and to

the economic importance of such insects (Anon., 1968; Pfadt, 1971;

Barcia and Merkel, 1972; Berry, 1976) (Table 1).

It is of interest to consider the ecological and evolutionary

consequences of the interaction of flower-feeding insects and their

plant hosts. The coevolution of the insect-flower relationship, for

instance, with regard to insect pollination in out-breeding genetic

systems, has produced a fascinating and remarkable series of

mutualistic coadaptations. The morphological aspects are conspicu-

ous and well known (Faegri and Van Der Pijl, 1971; Proctor and Yeo,

1973), and were the subject of some of the earliest studies in

Table 1. The range of flower structures exploited as a principal food resource by insects.

Flower structure	Host	Insect		Order
Microsporangiate strobili (male cones)	Pines	Catkin sawflies	_Xyela_ spp.	Hymenoptera
Megasporangiate strobili (female cones)	Douglas fir	Cone moth	_Barbara colfaxiana_ (Kft.)	Lepidoptera
Pollen and nectar	Diverse species	Honey bee	_Apis mellifera_ L.	Hymenoptera
Flower buds	Alfalfa	Lygus bugs	_Lygus_ spp.	Hemiptera
Seeds	Peas, Beans	Weevils	_Bruchus_ spp.	Coleoptera
Indehiscent dry fruits	Corn	Corn earworm	_Heliothis zea_ (Boddie)	Lepidoptera
	Stored grain	Grain weevils	_Sitophilus_ spp.	Coleoptera
Dehiscent dry fruits	Cotton	Boll weevil	_Anthonomus grandis_ Boheman	Coleoptera
Fleshy fruits	Cherry	Fruit flies	_Rhagoletis_ spp.	Diptera
Swollen receptacles (false fruits)	Apple	Codling moth	_Laspeyresia pomonella_ (L.)	Lepidoptera

coevolution (Darwin, 1899). More subtle physiological features have come to light relatively recently (Heinrich, 1975). It may be argued by analogy, therefore, that other aspects of the insect-flower relationship may be equally profound, even if less obvious. Janzen (1969), for instance, has argued that seed predators are responsible for the toxicity of seeds, influence seed size and numbers, and effect seed dispersal. The characteristically wide dispersion and high species diversity of tropical trees have also been attributed to the effects of seed predation (Janzen, 1970). Studies of cone insects in temperate coniferous forests would therefore provide an ecologically interesting counterpart to those of tropical seed-predators. They would also be justified by the economic importance of these insects in the regeneration of forests (Hedlin, 1974; Ebel et al., 1975). However, an implicit feature of almost all such studies is that both the cone and the insect populations should be reliably estimated, but, in practice, this problem is often poorly addressed or even completely ignored. The techniques of sampling and population estimation therefore deserve attention (Koerber, 1960; Schenk et al., 1972).

This investigation is concerned with the development of probability sampling methods for reliably estimating populations of conifer cones and seeds, and their associated insect fauna. Specifically, the research effort was devoted to:

(1) estimating populations of <u>Barbara colfaxiana</u> (Kft.), the

Douglas fir cone moth, and of cones of <u>Pseudotsuga</u> <u>menziesii</u>

(Mirb.) Franco in a given area of forest.

(2) identifying a. the major sources of variation reducing the

precision of the estimates,

b. an appropriate sample unit,

c. an appropriate attribute to measure on the

sample unit,

d. useful supplementary information,

e. useful auxiliary variables for ratio, regression

or variable probability estimation,

f. the optimum allocation in a two-stage sample

design, and

(3) developing a general conceptual approach to the cone-insect

sampling problem.

ECOLOGICAL ASPECTS OF SEED PREDATION

Herbivory and Plant Abundance

Plant communities are characteristically comprised of a few abundant and many rare species (Hough, 1936; Brown and Curtis, 1952; Odum, 1971). Although physical factors and interspecific competition are no doubt important influences, the impact of herbivores on the observed vegetational patterns can also be significant. The biological control of Hypericum perforatum L. (St. Johnswort) in California (Huffaker and Kennett, 1959) and of Opuntia species (Prickly Pear) in Australia (Dodd, 1936; 1940) provide spectacular examples. It is significant that these dramatic changes in plant distribution and abundance are often associated with the introduction of an exotic species (Price, 1975). One must suppose that the indigenous flora and fauna of a region have already arrived at some kind of equilibrium, but that the impact of herbivores on thevegetation may be no less spectacular.

Seed predators have been credited with producing the wide dispersion and high species diversity characteristic of trees in tropical forests (Janzen, 1970). It could also be argued that selective seed predation, by critically altering the reproductive capacity of a plant and so influencing the outcome of inter-specific competition, might influence a tree species' natural distribution. This would apply to

situations where competitive success is probabilistic and dependent on the initial proportions of each species (Neyman et al., 1956), and also to stable equilibria (Wit, 1961; Marshall and Jain, 1969), where presumably seed predation would either alter the equilibrium proportions or cause local extinctions. Seed predation may also permit the coexistence of potentially competing species (Paine, 1966), just as grazing pressure from rabbits maintains the floral diversity of chalk grasslands in England (Harper, 1969).

The characteristics of seed predation which have been suggested as an explanation for the high species diversity of tropical forests (Janzen, 1970) evidently do not apply to the temperate coniferous forests of North America. These forests are remarkable for their unusually low diversity, often being dominated by just one or two species, and it is a feature which has been the subject of considerable comment (Franklin and Dyrness, 1973; Regal, 1977). Consequently, an investigation of seed predation in temperate coniferous forests would be of general interest.

Seed Predation in Temperate Coniferous Forests

Interactions

The agents of predation in coniferous forests are both vertebrate and invertebrate. Mammals and birds derive considerable nourishment from the consumption of tree seeds (Gashwiler, 1967, 1970;

Smith, 1968, 1970; Vanderwall and Balda, 1977), and the diverse

insect fauna may inflict considerable pre-dispersal mortality by feed-

ing on scales, seeds and whole cones (Keen, 1958; Hedlin, 1974;

Ebel et al., 1975).

The selectivity of seed predation is a feature of potential signifi-

cance for host plant dynamics. The vertebrate animals, though rela-

tively unspecialized in their feeding habits, nevertheless combine

strong food preferences (Holling, 1965; Gashwiler, 1967; Smith,

1968; Pank, 1976), search images (Tinbergen, 1960; Croze, 1970)

and profitability (Royama, 1970; Smith, 1974) to effect density-

dependent predation, which can be highly selective, yet flexible

(Southern, 1970; Murdoch, 1969, 1973), in utilizing the available

resources. The insect seed-predators, on the other hand, are more

strictly host-specific, a feature exemplified by the Conopthorus

species of beetles and the Megastigmus species of seed-chalcids

(Keen, 1958), which are generally associated with a single host

species.

It has been argued that one of the host-tree responses to seed

predation is mast-cropping (the synchronous production of large seed

crops at infrequent intervals), which has the effect of satiating seed-

predators and so increasing the survival of seeds (Janzen, 1971, 1974,

1976). There is some evidence that this phenomenon occurs in

temperate coniferous forests, since it has been widely observed

that seed production is irregular both in frequency and amount

(Fowells and Schubert, 1956; Wenger, 1954, 1957; Hedlin, 1964;

Shoulders, 1968; Gashwiler, 1970; Nebeker, 1973; Franklin, 1968;

Franklin et al., 1974). The response of vertebrate predators to the

infrequent occurrence of plentiful food is hoarding and territorial

behaviour (Smith, 1968, 1970; Vanderwall and Balda, 1977). Insects

respond with an extended diapause (Janzen, 1971), and in several

species of cone insects it has been recorded that diapause can extend

the life-cycle, in a proportion of the population, to at least three years

years (Hussey, 1955; Keen, 1958; Hedlin, 1960a, 1960c, 1961; Hedlin

and Johnson, 1963).

Host-specific insect seed-predators would therefore seem to be

capable of dramatic impact on the production of viable conifer seed

and the vertebrate populations which they support. However, neither

prolonged diapause nor mast-seeding appear to be clear-cut phe-

nomena, and so the interactions of insect seed-predators and conifer

seed-production are consequently judged worthy of study. Although it

is generally thought that insects are important influences on seed

production (Kinzer et al., 1972; Hedlin, 1974; Ebel et al., 1975),

reliable data on populations and their impact on seed crops are

difficult to find. Ample opportunities exist, however, for original

observations in both seed orchards and natural situations. Table 2

shows that the climatic gradients associated with altitude on the

Table 2. Distribution and abundance ot conifer tree species on the western slopes of the Cascade Range in Oregon (compiled from information in Franklin and Dyrness, 1973).

Conifer species	Vegetational zones				
	Interior Valley	Tsuga heterophylla	Abies amabilis	Tsuga mertensiana	Timberline
		increasing altitude $\longrightarrow$			
Pinus albicaulis Engelm.				m	M
Tsuga mertensiana (Bong.) Carr.			m	M	M
Abies lasicocarpa (Hook.)Nutt.			m	M	M
Pinus contorta Dougl. ex Loud.			m	M	m
Picea engelmannii Parry ex Engelm.			m	m	
Chamaecyparis nootkatensis (D. Don) Spach			m	m	
Abies procera Rehd.			m	m	
Larix occidentalis Nutt.			m		
Abies amabilis (Dougl.) Forbes		m	M	M	m
Pinus monticola Dougl. ex D. Don		m	m	m	
Tsuga heterophylla (Raf.) Sarg.		M	m	m	
Pseudotsuga menziesii (Mirb.) Franco	M	M	m	m	
Thuja plicata Donn.	m	M	m		
Abies grandis (Dougl.) Lindl.	m	m	m		
Taxus brevifolia Nutt.		m			
Libocedrus decurrens Torr.	m				
Pinus ponderosa Dougl. ex Loud.	m				
Total species (out of 17)	5	7	13	11	5

Key: M = major species, m = minor species

9

western slopes of the Cascade Range in Oregon are reflected in the

changing species composition of the vegetation. It is evident that the

distribution and abundance of 17 conifer species changes markedly

over a short distance. No one species is found throughout the entire

climatic range and the diversity of species in the "Abies amabilis"

zone is twice that of the "Interior Valley" zone. These situations

provide an opportunity to test some of the ideas proposed in this thesis

regarding the potential impact of seed predators on plants. This is a

a feature of considerable importance when, as Janzen (1976) argues,

the hypotheses regarding tropical seed predation are largely untest-

able, because, even if the species themselves are not yet extinct, the

relevant interactions are no longer operating as a result of Man's

interference.

Population Dynamics of Host-Specific Insect Seed-Predators

Observations on the effect of fluctuating cone crops on popula-

tions of cone insects are not readily found (Schenk et al., 1972), but

Hedlin's (1964) study suggests that asynchrony may occur to the extent

that temporal heterogeneity in the availability of cones and seeds is

a factor limiting population growth. Since one generation does not

affect the number of cones available for the next, one would expect

the dynamics of cone-insect populations to share features in common

with other insects exploiting resources of low durational stability
(Southwood et al., 1974; Southwood and Comins, 1976). However,
studies of the effects of fertilizing pine trees to increase cone yields
have not reported increased losses to cone-insects (McLemore, 1975).
If it may be inferred, therefore, that the availability of cones is not
directly limiting, then density-dependent predation by vertebrates
and other insects, particularly during the period of extended diapause,
may be acting in a regulatory fashion. There is some evidence to
support this view. Certain species leave the cones to seek over-
wintering sites in the forest litter (Hedlin, 1961; Hedlin and Johnson,
1963), and are presumably then exposed to a density-dependent pre-
dation of the type inflicted by small mammals on sawfly cocoons
(Holling, 1959), or from non-random search by insect parasitoids
(Hassell, 1971; Hassell and Rogers, 1972; Corbet, 1973). Insects
such as lepidopterous larvae, which remain inside the cones to
overwinter, are in no safer a position. Gibb (1958, 1960) has de-
scribed a density-dependent predation by birds (Parus spp.: Paridae)
on eucosmid larvae in pine cones, and they also suffered an incidental
mortality from squirrels destroying the cones in search of seed. It
is probable, therefore, that cone insects have population parameters
intermediate on the 'r-K' continuum (Pianka, 1970; Southwood et al.,
1974), and that natural enemies are important in population regulation
(Southwood and Comins, 1976).

It may be argued that a knowledge and understanding of the population dynamics of insect seed-predators would not only be of interest as an ecological study, but might also provide useful insight to a number of current management practices in seed orchards and seed production areas. Fertilization and tree selection for more frequent cone crops, combined with insecticidal applications (Schenk et al., 1967; Copony, 1972; Stoakley, 1973; Werner, 1974; Dewey et al., 1975) may well be increasing the vulnerability of seed crops to insect attack (Doutt and Smith, 1971; Hedlin, 1974).

A holistic investigation of the potentially complex interactions of conifer reproduction, small mammals, birds and host-specific insects would seem to be both appropriate and necessary in future studies of cone insects. The existence of a conceptual framework (Koestler, 1967; Klir, 1969; Overton, 1972a) combined with the existence of a hierarchical systems model processor (White and Overton, 1974), makes such a project an attractive possibility. However, a fundamental requirement of any such quantitative study is the ability to reliably estimate the populations of interest, and so the techniques of sampling and estimation deserve attention.

THE CONE-INSECT SAMPLING PROBLEM

Much of the published work on cone-insect populations is charac-
terized by a neglect of sampling theory and a poor conceptualization
of the sampling problem, with the inevitable result that the data
collected are of doubtful value. It is illuminating that many papers
make no explicit reference to a sampling universe, frame, unit or
rule,[1] and most provide little inspiration for the development of
probability sampling schemes. A summary is presented here with
a view to providing some clarification of earlier efforts.

The sampling universe, being dependent on the choice of the
sample unit, has very often been "improper" i. e. poorly-defined.
Examples include the selection of trees with "good cone-crops"
(Kaufman and Posey, 1953) or of "average" diameter at breast-
height (D. B. H.) (Smith, 1968), branches from the "mid-crown"
(Radcliffe, 1952), or cones from "branch-tips" (Schenk et al. , 1967).
The natural sample units of cone, branch or tree have commonly
been employed, although a unit area of forest floor has been used
for sampling seeds (Garman, 1951; Fowells and Schubert, 1956;
Wenger, 1957; Gashwiler, 1967, 1970), cones (Gibb, 1958) and
dipterous larvae (Hedlin, 1960b).

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[1]Refer to standard sampling texts (e. g. Cochran, 1963) for an
explanation of these terms.

The sampling rule (the size and method of selection of the sample), though rarely stated explicitly, often has either circumvented the problem of sampling altogether by completely enumerating the cones on a tree (Kaufman and Posey, 1953; Wenger, 1954; Gibb, 1958; Hedlin, 1964; Silen, 1967; Shoulders, 1968; Schenk et al., 1972), or has employed subsampling in such a manner that the sample was unlikely to be free from bias. This may arise from the improper use of stratification (Winjum and Johnson, 1964; Kozak, 1964; Silen, 1967; Schenk et al., 1967; Yates and Ebel, 1972; Ebel and Yates, 1974) or by the arbitrary, rather than strictly random, sampling procedure which usually results when individual cones are taken from the many on a tree (Schenk et al., 1972; Ebel and Yates, 1974).

The estimation of populations, as opposed to the intensity of insects, has rarely been attempted, and when it has, the estimator employed has often not been explicitly stated. Many papers have presented data on the intensity of insects or seeds per cone, when additional observations on cones as an auxiliary variable would have permitted a ratio estimate of the insect population, as in Hedlin's (1964) study. In estimating cone populations, the possibilities of employing auxiliary variables in regression estimation have been explored on several occasions. Smith (1968) used the tree diameter at breast-height, and a common approach has been to use a visual index of the number of cones per tree or per branch (Garman, 1951;

Wenger, 1953, 1954; Fowells and Schubert, 1956; Hoekstra, 1960;

Winjum and Johnson, 1962; Shoulders, 1968; Schenk et al., 1972;

Franklin, 1968, Franklin et al., 1974). Probably the most rigorous

and sophisticated sample design developed for estimating cone popula-

tions is a variable probability, three-stage systematic random sample

using a visual index at each stage as an auxiliary variable (Nebeker,

1973).

The purely logistical problems of sampling cone insects from

conifer trees have no doubt contributed to the relatively poor state

of the art. It is an aspect of sampling which cannot be ignored,

since some conifers may grow to heights of approximately 100

meters and they often occur in areas of difficult access. It is not

surprising that most studies of cone insects have confined themselves

to trees of moderate height (30 meters or less) in seed orchards or

production areas, where cones may be collected with comparative

ease by climbing or with mechanical aids. However, techniques

recently developed to gain access to the canopy of mature conifer

trees (Denison et al., 1972; Denison, 1973) now make cone insect

studies in "old-growth" forests a distinct possibility.

METHODS

The Choice of Organisms

Pseudotsuga menziesii (Mirbel) Franco (Pinaceae), the Douglas

fir tree, and Barbara colfaxiana (Kearfott) (Lepidoptera:Olethreutidae),

the Douglas fir cone moth, were selected to be the primary subjects

of this study, although the sampling methodology subsequently devel-

oped undoubtedly has wider application. The research effort was

designed to complement a concurrent study, on the same site, of the

population dynamics of B. colfaxiana (Nebeker, 1973), whose goal

was the construction of a life-table for the 1971 generation.

P. menziesii is the dominant tree species of much of the na-

tural forest west of the Cascade Range in the Pacific Northwest of

North America, and it is also the preferred species in the regenera-

tion of cut-over land for timber production (Franklin and Dyrness,

1973). In the 1971 season in which this study was conducted, there

was an exceptionally abundant production of cones on the study site,

in sharp contrast to the succeeding year in which cone production was

very poor (Nebeker, 1973).

B. colfaxiana is generally regarded as being one of the major

insect species affecting the seed production of P. menziesii (Keen,

1952, 1958; Clark et al. , 1963; Hedlin, 1960c, 1974), and it was the

principal species causing obvious damage to cones at the study site.

The Field Study Site

Field research was conducted in the Buckhead Seed Production

Area of the Willamette National Forest, Lane County, Oregon, an

area administered by the U.S. Forest Service (Lowell Ranger District).

The general area is at an elevation of approximately 650 meters,

and has been subjected to timber cutting operations in the past. The

regenerated vegetation of the region includes P. menziesii, Abies spp.

and some hardwoods.

The seed production area was subjected to a thinning operation

in 1964, which left only P. menziesii, and subsequently received

application of fertilizer (urea) and a variety of insecticides (Cygon,

Bidrin and Meta-Systox), of which the last, prior to this study, was

in 1970 (Nebeker, 1973). The stand of trees was comprised of indi-

viduals of approximately the same age (20-30 years) and height (15-25

meters), which facilitated the design and execution of the sampling

program.

The Sampling Strategy

The Choice of the Sampling Universe and the Sample Unit

The female cones (megasporangiate strobili) of P. menziesii

are hierarchically organized into groups comprised of the population

of trees, the collection of cone-bearing branches within a tree, and

the clusters of cones on any one branch. These natural groupings

favor the use of a multi-stage sample design. A two-stage sampling

procedure was adopted where:

Stage One sample unit = the cone-bearing tree

Stage Two sample unit = the cone-bearing branch

In this study, the branch was chosen as the basic sampling unit

because it was the only practicable choice for the construction of

a sampling frame. The cones themselves are usually too numerous

and too difficult to uniquely and unambiguously identify. The use of

a two-stage design restricted the sampling frame of branches to just

those trees included in the first stage sample, although a sampling

frame for the trees was then also required. The conceptual aspects

of a two-stage sample are summarized in Appendix 2.

Stratification of the Sampling Universe

Stratification is a common technique for isolating known or

anticipated sources of heterogeneity to increase the precision of

population estimation (Sampford, 1962; Cochran, 1963; Southwood,

1966). It was employed in this study as a precautionary measure at

both stages of sampling.

Schenk and Goyer (1967) observed that stand density and spacing

affected the distribution and abundance of cones and insects, and

since the study site exhibited considerable variation in these features,

three two-acre plots were constructed.

The anticipated uneven dispersion of insects and cones within the tree canopy (Winjum and Johnson, 1964; Southwood, 1966; Debarr et al., 1975) led to the stratification of branches within trees by canopy level, though further stratification by aspect (Winjum and Johnson, 1964; Southwood, 1966) was not considered practicable.

Constructing the Sampling Frame

The sampling universe within a given stratum at the first stage of sampling (U) is represented as:

$$[U] = \{C_1, C_2, \ldots C_h \ldots C_k\}$$

where $[U]$ is the partitioned universe of branches on the set of K trees; a tree, C, represents a cluster of cone-bearing branches; and $h = \{1, 2, \ldots K\}$ is an identification index.

The sampling universe of trees was defined according to the criteria in Table 3, which provided a basis for constructing a sampling frame. In retrospect, these criteria seem unnecessarily restrictive, and the single criterion of accessibility (which included 87% of the cone-bearing trees) is the only one now held to be reasonable. The trees excluded from the sampling universe comprise a population, or stratum, which was ignored in this particular study.

The sampling universe within a given tree at the second stage of sampling (U_c) is represented as:

Table 3. The sampling universe and the construction of a sampling frame. (Data from all three study plots combined.)

	Total	%
Trees with live foliage	270	-.-
Trees bearing cones visible to an observer on the ground (= "cone-bearing trees") :	239	--
(1) Accessible by climbing	209	87
(2) > 15 meters in height	200	84
(3) Canopy separate from other trees	158	66
(4) Not previously sampled (destructively) in concurrent study by Nebeker, 1973	74	31
(5) Destructively sampled no more than once previously by Nebeker, 1973	177	74
Number of trees meeting the following sets of criteria:		
A. 1-3, 5 (this study)	81	34
B. 1-5	25	10
C. 1 only	209	87

$$U_c = \{u_1, u_2, \ldots u_i \ldots u_{N_c}\}$$

where u is a cone-bearing branch, and $i = \{1, 2, \ldots N_c\}$ is an identifi-

cation index. The "cone-bearing branch" is defined as being one

bearing cones visible to an observer within the tree, and it is assumed

that any branches excluded from the sampling universe, because their

cones were overlooked, represented an insignificant fraction of the

total.

The Sampling Rule

Stage 1: Systematic Random Sample (Sy· RS), on the set ordered

by a visual index (x) of the cones per tree, where:

$$x = \{1, 2, \ldots 10\}$$

Sample size: k = 6 trees

An index of one was assigned to a tree with very few visible cones,

and an index of ten to those with a large number of cones. A sys-

tematic sample was chosen in order to investigate the regression

relationship between insect intensity and the number of cones per

tree. A sample of size six was considered adequate to provide a

minimum number of data points.

Stage 2: Systematic Random Sample (Sy· RS) on the set ordered

by a visual index (x_c) of the number of cones per branch, where:

$$x_c = \{1, 2, \ldots 17\}$$

Sample size: n_c = 6 branches

x_c was based on a quick, rough count of the visible cones, and rounded downwards to the nearest unit of ten (17 was the highest value observed). A systematic sample was chosen to investigate the relationship between insect intensity and the number of cones per branch. Subsequent stratification by canopy level (lower, middle and upper) reduced the within-stratum sample size to two.

The Attributes Chosen for Measurement

In general, $y(u_i)$ represents the specified attribute to be observed on every element u in the sample. The following observations were made on the cone-bearing branches (u) with a view to determining the most appropriate attribute to measure:

1. Total of live cones,

2. Total of cone-clusters, and

3. Total of B. colfaxiana pupae.

The Collection of Cones and their Associated Insects

The timing of cone collections for estimating pupal populations of B. colfaxiana is not crucial, since the larvae pupate and overwinter in the cones (Hedlin, 1960c). However, sampling was scheduled for late August and prior to the commencement of the fall rains because (1) squirrels may destroy and remove the cones in the fall (Smith, 1968), and (2) the fall rains stimulate midge larvae (Contarinia spp.)

to leave the cones (Hedlin, 1961; Hedlin and Johnson, 1963), and it was hoped to extend observations to these other insects at little extra cost. An unexpected aspect of timing was revealed by the observation that _Glypta evetriae_ Cush. (Ichneumonidae:Hymenoptera), the principal parasite of _B. colfaxiana_ (Hedlin, 1960), may emerge in the fall as well as in the spring. If this reflects a partial second generation for the parasite, the apparent intensity of parasitization may vary with the timing of sampling.

In order to collect all the cones associated with the sampled branches, and to record the appropriate information on cluster sizes, it was necessary to remove the branches from the trees. The sawn-off branches were gently lowered to the forest floor where the cones were transferred to paper bags on which the relevant information was recorded. The bags were then chilled until the cones could be trans-ferred to muslin-covered, wide-mouthed "rearing" containers. The cones were sprayed with benzoic acid to inhibit the growth of molds and were stored through the winter in an unheated, well-ventilated building in Corvallis, Benton County, Oregon (elevation: 70 meters). In May, those insects which had emerged from the cones and collected in the debris at the bottom of the containers (principally _Contarinia_ spp,) were sorted and counted. The pupae of _B. colfaxiana_ were collected by splitting each cone by hand. The live pupae so obtained were reared to adulthood to determine whether or not they were

parasitized. Empty pupal cases were attributed to the earlier

emergence of a parasite, and in most instances the parasite con-

cerned could be located. Cones showing the characteristic symp-

toms of damage by B. colfaxiana, but containing no pupae, were

assumed to have contained larvae subject to mortality and were

recorded as "damaged cones."

RESULTS AND DISCUSSION

Estimates of the Pupal Population of B. colfaxiana

A comparison was made between three estimates of the B. colfaxiana population in plot 2 (Table 4), using the sample data obtained by a two-stage, stratified systematic random sample (Appendix 1, Table 2). The three estimators employed (Appendix 3) are summarized here as:

1. SRS/SRS   (SRS = Simple Random Sample)

2. Sy. RS/SRS   (Sy. RS = Systematic Random Sample)

3. RATIO/RATIO   (auxiliary variable : visual index of cones)

The stratification of branches within each tree by canopy level reduced the within-stratum sample size to two and consequently made calculation of the sample variance difficult. As a matter of expediency, therefore, the stratification and Sy. RS rule at the second stage have been ignored and a SRS estimator with n_c = 6 has been employed. The inflation of variance and the possible bias that may result is acknowledged. The use of a SRS estimator at the first stage for Sy. RS data will result in an inflated variance in 1 above, but it provides a useful comparison for the ratio estimate.

It is apparent that the estimator Sy. RS/SRS is the most efficient. However, the focus of interest lies with the larger variance of the ratio estimate. The technique of using a rapidly-assigned,

visual index as an auxiliary variable in regression or ratio estima-

tion has many attractive features, and so it will be of interest to

examine the causes of its apparent inefficiency in this instance.

Table 4. Summary and comparison of population estimates of B. colfaxiana pupae (Plot 2, Buckhead S. P. A. , 1971; sample data in Appendix 1, Table 2).

Stage 1	Stage 2	$\hat{T}y$	$S(\hat{T}y)$ or $\sqrt{MSE(\hat{T}y)}$	Coefficient of Variation	Relative Efficiency
SRS	SRS	4334	931	0. 21	99
Sy. RS	SRS	4334	924	0. 21	100
RATIO	RATIO	3899	1118	0. 30	61

(Estimated mean total of pupae per tree (Sy. RS/SRS estimator) = 310± 66)

An Evaluation of the Benefits of Stratified Sampling

Stage 1

Deviations from the specified sampling rule in plots one and

three mean that the ratio estimator, being independent of the samp-

ling rule, provides the only valid estimates of the pupal population of

B. colfaxiana in all three study plots (Table 5). A comparison of

absolute population levels (t-tests) and intensities (Anova) (Tables 5

and 6) reveal no significant differences, from which it is concluded

that, in this instance, nothing was gained by stratification. Support

Table 5. Two-stage ratio estimates of B. colfaxiana pupae in three study plots on the Buckhead S. P. A., 1971 (sample data in Appendix 1, Tables 1, 2 and 3).

Plot	$\hat{T}y$	$\sqrt{MSE\,(\hat{T}y)}$	Coefficient of variation
1	6928	3482	0.50
2	3899	1188	0.30
3	1584	722	0.46
Total	12,411	3749	0.30

$T_{y_1} - T_{y_3} = 5344$; $t = 1.50$, 6 d.f. $P > 0.1$

$T_{y_2} - T_{y_3} = 2315$; $t = 1.67$, 8 d.f. $P > 0.1$

Table 6. Comparison of intensity of B. colfaxiana pupae (per cone) between plots (Buckhead S.P.A., 1971) (sample data in Appendix 1, Table 5: Ratio estimates).

Source	S.S.	D.F.	M.S.	V.R.
Between Plots	0.1031	2	0.0516	2.5647[a]
Within Plots	0.2817	14	0.0201	
Total	0.3848	16		

[a]Not significant at $P < 0.05$

for this conclusion is derived from the concurrent studies on the same site by Nebeker (1973) (Table 7), in which no significant differences between plots were observed in the intensity of B. colfaxiana eggs per cone. The plots described in this thesis are a subset of those studied by Nebeker (1973).

Table 7. A comparison of the intensity of B. colfaxiana eggs (per 60 cones) between plots. (Buckhead S. P. A., 1971; data from Nebeker's (1973) Tables 8 and 10).

Source	S. S.	D. F.	M. S.	V. R.
Between Plots	552.4	9	61.38	1.49[a]
Within Plots	2057.3	50	41.15	
Total	1609.7	59		

[a] Not significant at $P < 0.05$

Stage 2

A comparison over the sampled trees of variation in the intensity of B. colfaxiana pupae per cone, between canopy levels and by "aspect," revealed no significant differences (sample data in Appendix 1, Tables 1-4):

1. Canopy Levels (Paired t-tests):

$\overline{D}$ = level 2 - level 3 = 0.06 - 0.11 = -0.05

$t = 1.13$, with 16 d. f. $P > 0.20$

$\overline{D}$ = level 1 - level 3 = 0. 14 - 0. 13 = 0. 01

$$t = 0.90, \text{ with 5 d. f. } P > 0.50$$

2. North (W. N. W. to E. N. E.) and South (S. W. S. to E. S. E.) facing

branches (t-test):

$\overline{D}$ "North" - "South" = 0. 083 - 0. 051 = 0. 032

$$t = 1.09, \text{ with 61 d. f. } P > 0.20$$

These findings are similar to those of Hedlin (1960c) and

Winjum and Johnson (1964), although Debarr et al. (1975) observed

significant differences in insect intensity per cone between levels

and quadrants. The stratification of branches within trees appears

to have been an unnecessary complication of the sample design in

this instance.

<div align="center">

An Appraisal of the Ratio Estimate of
B. colfaxiana Populations

</div>

General Considerations

The auxiliary variable used in the ratio estimate was a visual

index assigned to each member of the sampling universe and based

on the number of observed cones. Its usefulness, therefore, will be

limited by its ability to accurately represent the number of cones

and also by the degree of correlation between the number of cones

and the number of insects. The relative inefficiency of the ratio

estimate in this instance (Table 4) is shown to arise from the

relatively low precision at the first stage of sampling (Table 8). Its

contribution to the overall mean square error is so great that it

masks the greater efficiency of the ratio estimate at the second

stage.

Appraising the Ratio Estimate at Stage Two

1. Regression Relationship of Pupae and the Visual Index.

In the absence of significant differences between plots (Table 6),

data points were taken from trees sampled in all three plots. The

non-significant relationship (Figure 1) between pupae and the visual

index of cones per branch apparently contradicts the evidence in

Table 8. The explanation may lie in the poor correlation of either

the numbers of pupae or the visual index with the number of cones

per branch. Both possibilities will be examined.

2. Regression Relationship of B. colfaxiana Pupae and Cones

per Branch. The regression of pupae on cones per branch (Figure 2)

is not significant, but it is possible that heterogeneity of insect inten-

sity among trees (observed by Prebble, 1943; Stark, 1952; Morris

and Reeks, 1954; Morris, 1955, Howse and Dimond, 1965) may be

masking a significant relationship operating separately within each

tree. The existence of such heterogeneity is confirmed (Table 9).

A 49-fold difference between the highest (0. 264 pupae per cone) and

the lowest (0. 005 pupae per cone) intensity was observed. This
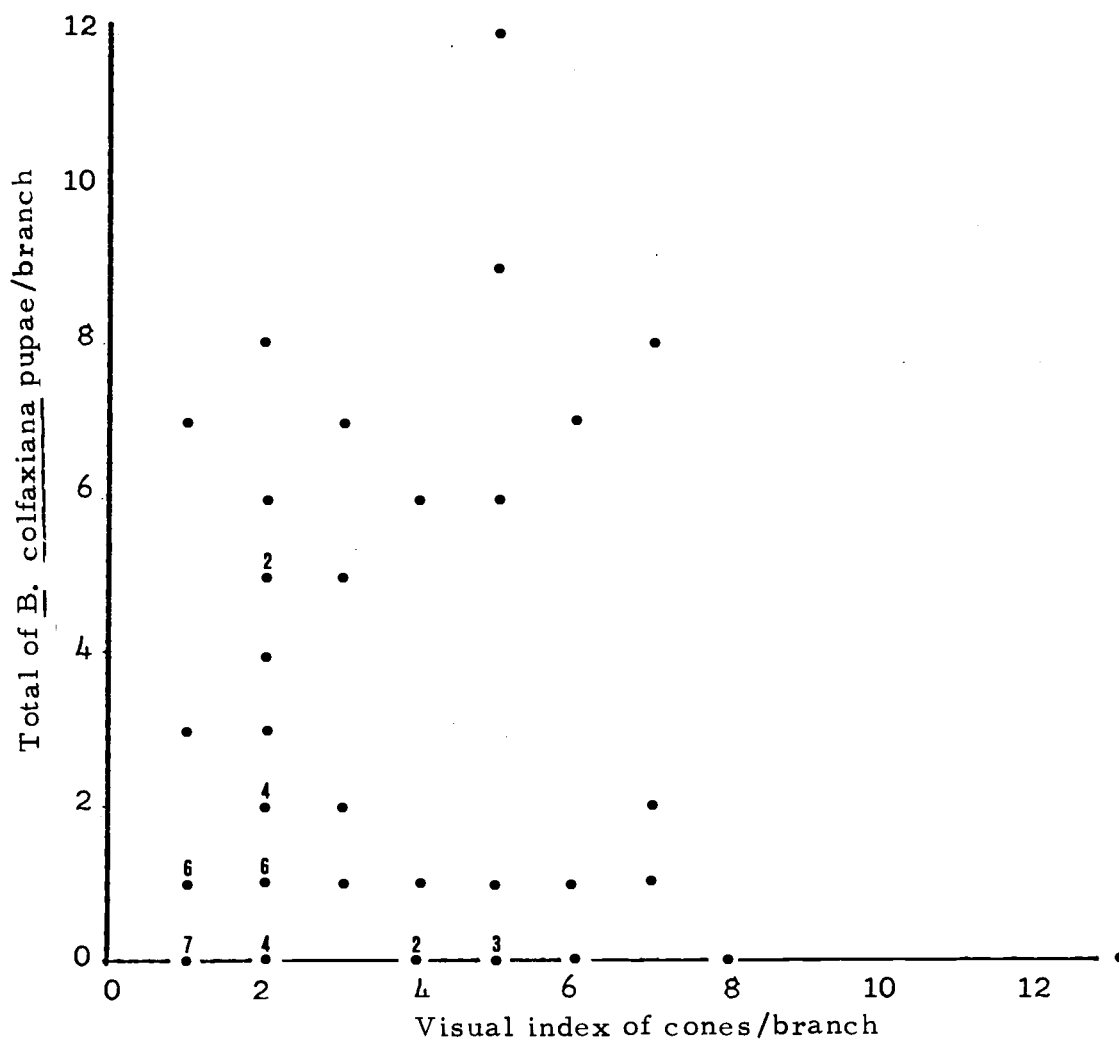
Figure 1. Sample regression of the total of B. colfaxiana pupae per branch on the visual index of the total of cones per branch (data from arbitrarily and intensively sampled trees excluded).
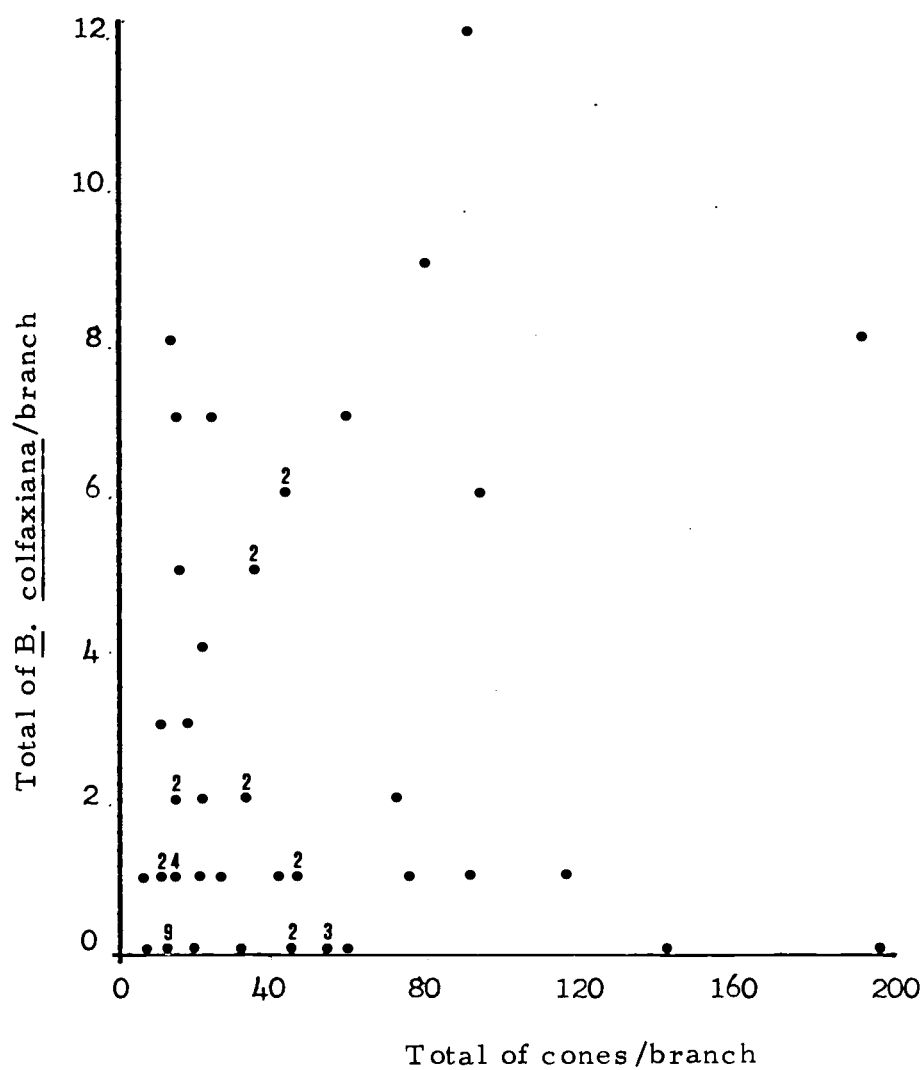
Figure 2. Sample regression of the total of B. colfaxiana pupae
per branch on the total of cones per branch (data from
arbitrarily and intensively sampled trees excluded).

Table 8. A detailed comparison of SRS and RATIO estimators of B. colfaxiana pupae (Buckhead S. P. A., 1971; Plot 2).

Estimator:	SRS/SRS	RATIO/RATIO
Quantity	$\hat{V}(\hat{T}y)$	MSE ($\hat{T}y$)
Contribution at:		
Stage 1	712, 791	1, 308, 875
Stage 2	154, 370	102, 010
Total	867, 161	1, 410, 885

Table 9. A comparison of the intensity of B. colfaxiana pupae per cone between trees (Buckhead S. P. A., 1971; sample data in Appendix 1, Tables 1-4).

Source	S. S.	D. F.	M. S.	V. R.
Between Trees	0. 3984	14	0. 0285	3. 0932**
Within Trees	0. 5077	55	0. 0092	
Total	0. 9061	69		

**Significant at P < 0.01

variation between trees in their apparent susceptibility or resistance to attack may be ascribed to intrinsic, genetic factors or to extrinsic, environmental factors. Possible genetic factors would include kairomones (Whittaker and Feeny, 1971) or chemical and physical protections. Environmental factors might include the proximity of other trees, the degree of insolation or shading affecting moth activity and other site-specific phenomena. Evidently the number of cones on a tree is not an important stimulus affecting oviposition behaviour (Figure 5), at least in a year like 1971 when cone production was very high on most trees.

The existence of heterogeneity between trees may be adduced as further justification for using a two-stage sampling design, since the M. S. Between Trees is three times larger than the M. S. Within Trees (Table 9).

The existence of a relationship operating separately within each tree, between the numbers of pupae and cones per branch, may be tested by comparing the branches sampled systematically within each stratum of each tree, between which a consistent difference in the numbers of cones would be expected. The appropriate data is summarized in Appendix Tables 1-4 by branches "1" and "2" at each level of the tree. A paired t-test establishes a significant difference in the numbers of pupae per branch: Mean per Branch 1 (many cones) - Mean per Branch 2 (few cones) = $\overline{D}$

$\overline{D} = 2.62 - 1.21 = 1.41$ $t = 2.61$ with 33 d. f., $P < 0.05$.

A comparison of the mean intensities of pupae per cone falls just short of statistical significance:

$\overline{D} = 0.058 - 0.098 = -0.04$ $t = 1.91$ with 33 d. f., $P > 0.05$

However, there remains the possibility that there is an inverse relationship between the numbers of pupae and cones per branch. This would imply that the egg-laying behaviour of B. colfaxiana females is such that they do not respond positively to the aggregations of cones on branches. In their search for oviposition sites within a tree it would seem that they are searching through a volume of space rather than being attracted to some stimulus provided by the cones. This inference is supported by the observation that female moths settle on the foliage, rather than directly on the cones, and proceed to walk about, feeling continually with the ovipositor, until a cone is encountered (Hedlin, 1960c).

3. Regression Relationship of the Visual Index and Number of Cones per Branch. The ability of the visual index to represent the number of cones per branch is regarded as satisfactory (Figure 3: $r^2 = 0.78$; $b \neq 0$, $P < 0.01$).

It is concluded from the foregoing observations that the heterogeneity between trees of the insect intensity requires that a separate, rather than a combined, ratio estimate (Cochran, 1963) be used in each tree.

Figure 3.   Sample regression of the visual index of the total of
            cones per branch on the total of cones per branch
            (data from arbitrarily and intensively sampled trees
            excluded).

Appraising the Ratio Estimate at Stage One

The lack of correlation between the estimated total of <u>B.</u>

<u>colfaxiana</u> pupae and the visual index assigned to each tree (Figure 4)

is responsible for the poor performance of the ratio estimate (Table 8).

The explanation lies in the lack of correlation between pupae and cones

per tree (Figure 5), since the correlation of the visual index and the

cones per tree is significant, even if unimpressive (Figure 6; r^2 =

0.52; b ≠ 0, P < 0.01; a ≠ 0 is not significant at P < 0.05).

Estimates of the Cone Population of Pseudotsuga menziesii

The estimation of the cone population in a given area of forested

land is as important as estimating the cone-insect populations them-

selves. Data on proportions of cones damaged by insects are of little

value when the absolute numbers of both cones and insects may fluctu-

ate. Furthermore, the cone population becomes an integral part of

insect population estimation when "two-phase" ratio estimation is

employed.

The sample design and anlaysis for cone estimation is the same

as that employed in insect estimation. The estimates are summarized

in Table 10. An interesting result is that the RATIO/RATIO estimate

is here more efficient than Sy· RS/SRS, in contrast to the estimation

of pupal populations (Table 4). It will be of interest to examine the
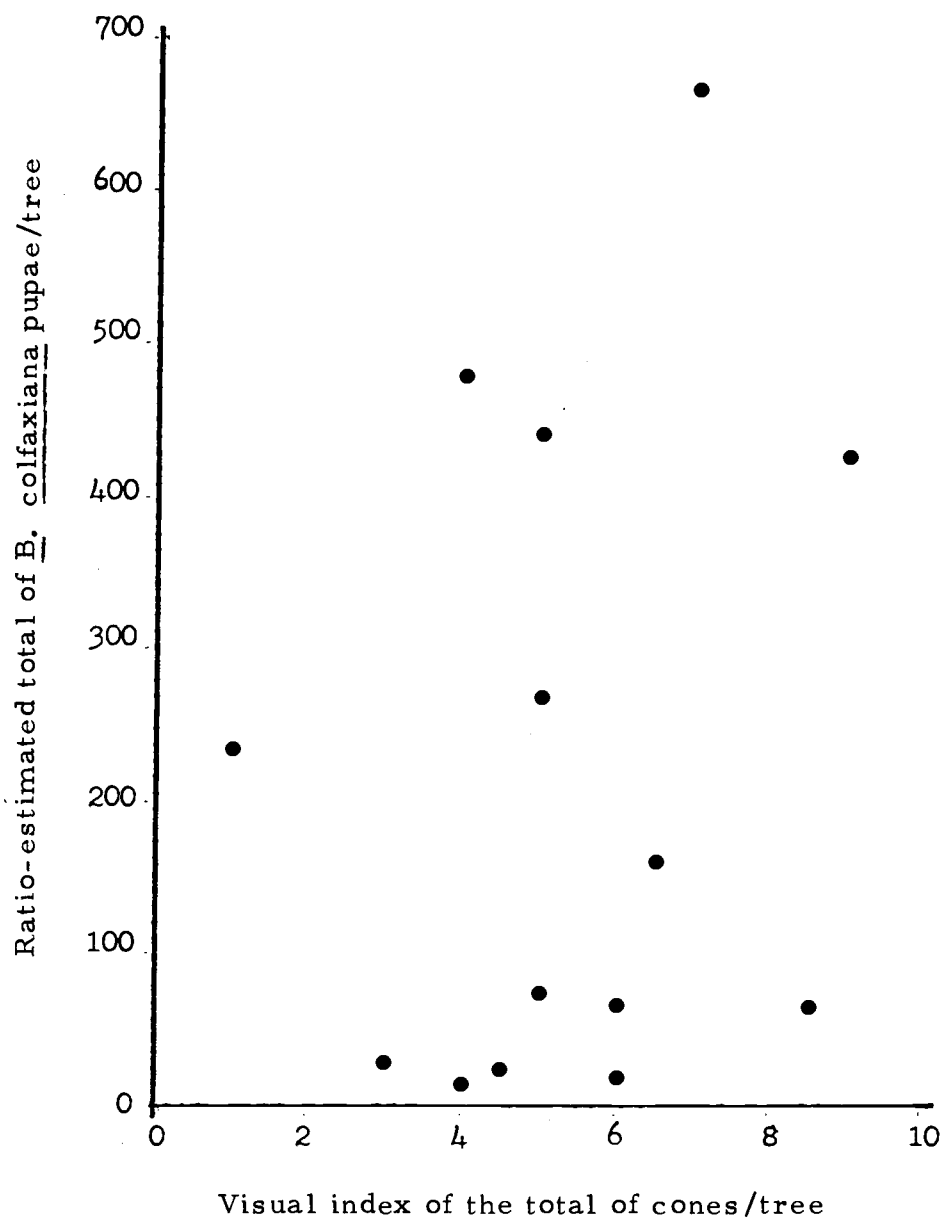
Figure 4. Sample regression of the ratio-estimated total of B. colfaxiana pupae per tree on the visual index of the total of cones per tree.
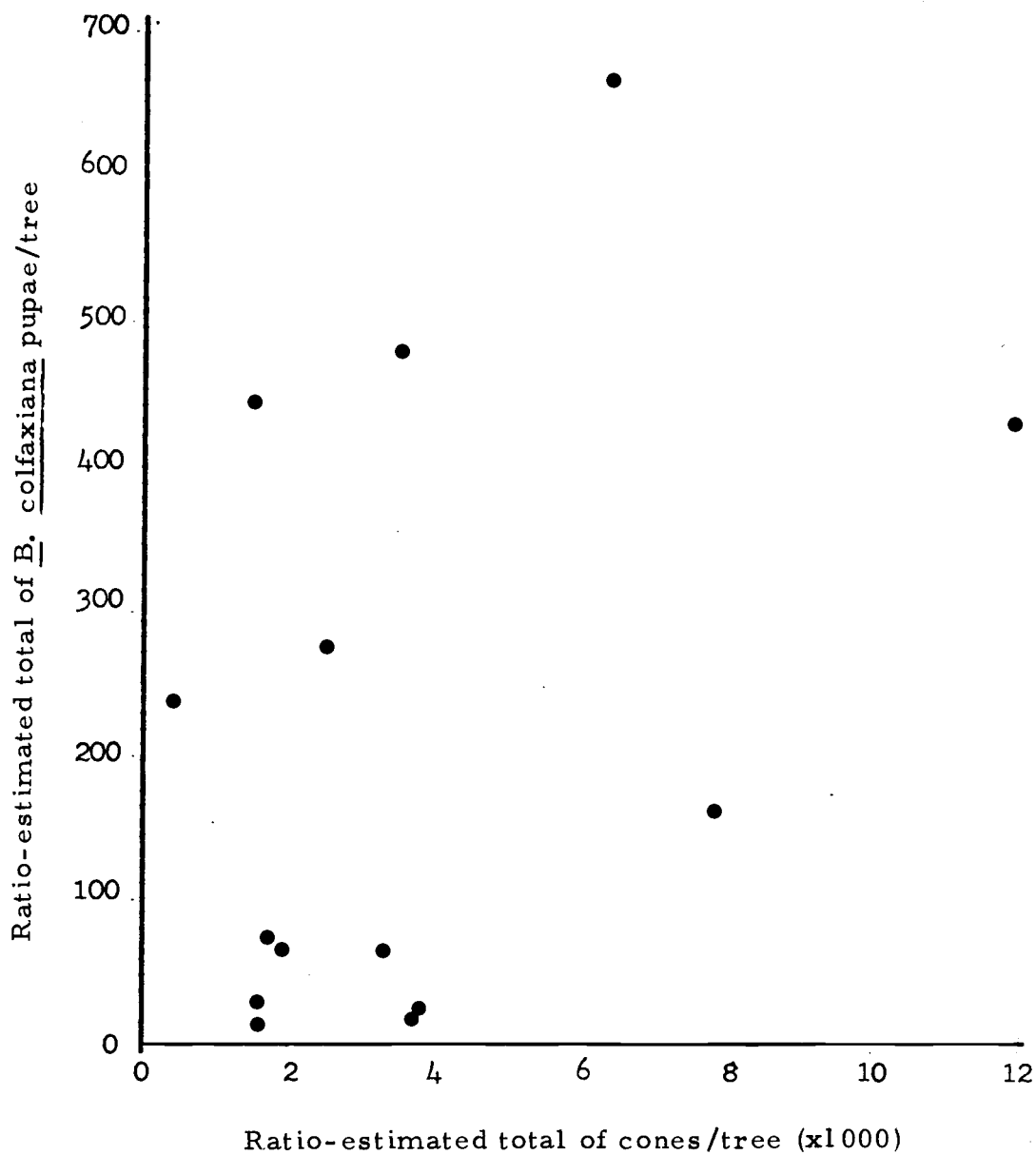
Figure 5. Sample regression of the ratio-estimated total of
B. colfaxiana pupae per tree on the ratio-estimated
total of cones per tree.
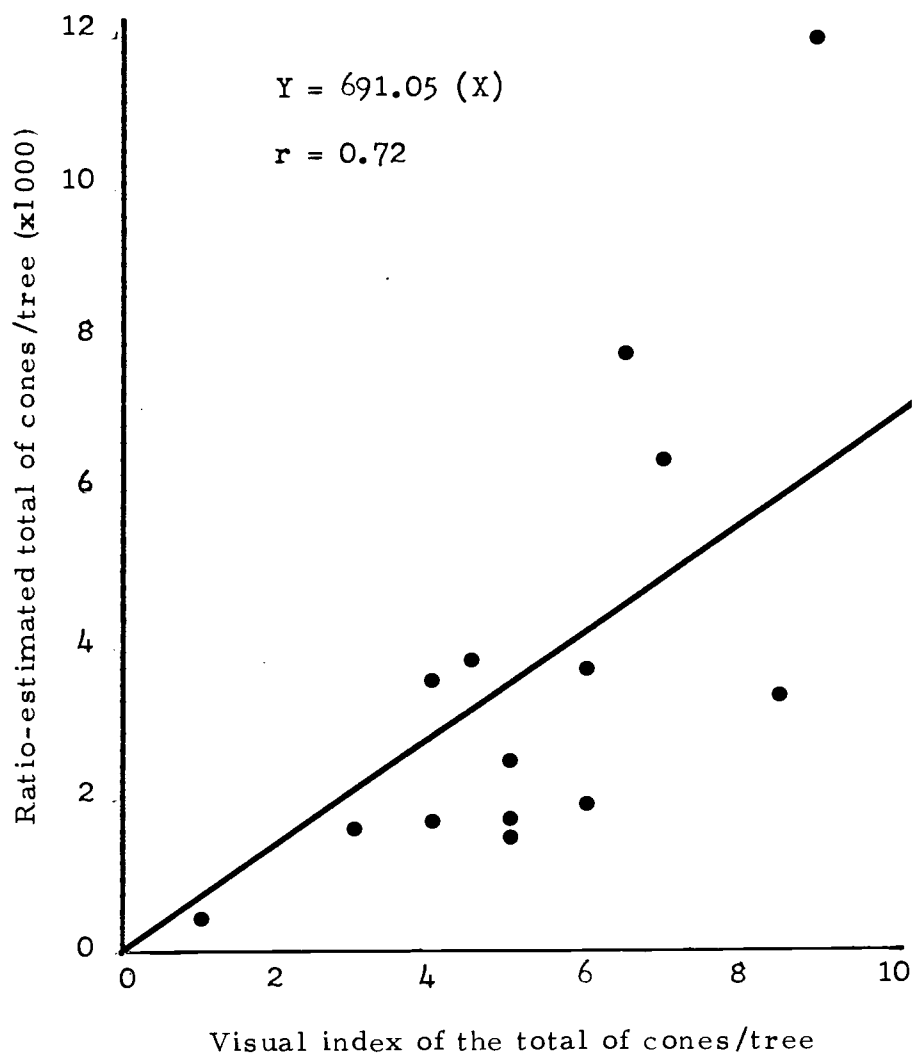
Figure 6.   Sample regression of the ratio-estimated total of cones per tree on the visual index of the total of cones per tree.

Table 10. Summary and comparison of population estimates of the cones of P. menziesii (Plot 2, Buckhead S. P. A. , 1971; sample data in Appendix 1, Table 2).

Estimator: Stage 1	Stage 2	$\hat{T}y$	$S(\hat{T}y)$ or $\sqrt{MSE(\hat{T}y)}$	Coefficient of Variation	Relative Efficiency
SRS	SRS	57, 154	17, 390	0. 30	60
Sy· RS	SRS	57, 154	13, 530	0. 24	100
RATIO	RATIO	47, 471	10, 396	0. 22	169

(Estimated mean total of cones per tree (Sy· RS/SRS estimator) = 4082 ±966)

Table 11. A detailed comparison of the SRS and RATIO estimates of the cone population of P. menziesii (Plot 2, Buckhead S. P. A. , 1971).

Estimator:	SRS/SRS	RATIO/RATIO
Quantity	$\hat{V}(\hat{T}y)$	$MSE(\hat{T}y)$
Contribution at:		
Stage 1	285, 429, 477	105, 347, 462
Stage 2	16, 969, 953	2, 719, 375
Total	302, 399, 430	108, 066, 837

basis of its efficiency in this instance, with a view to using observations on cones as an auxiliary variable in two-phase ratio estimates of cone-insects.

An Appraisal of the Ratio Estimate of the Cone Population

A detailed comparison of the two-stage estimates of the cone population, using SRS and RATIO estimators (Table 11), reveals that the ratio estimate is the more efficient at both stages. As with the pupal estimates, it is the efficiency at Stage One which has the most significant influence on the overall estimate.

Appraising the Ratio Estimate at Stage Two

It has been previously shown that the visual index is likely to be a useful auxiliary variable in cone estimation (Figure 3), and Cochran's (1963) test confirms the superiority of the ratio estimate relative to that of SRS:

$$b = 0.05 > \tfrac{1}{2} \cdot \hat{R} = 0.04$$

where b = the sample regression coefficient of y on x, and

R = the sample estimate t_y/t_x of the population ratio T_y/T_x.

Appraising the Ratio Estimate at Stage One

The regression of the estimated total of cones per tree on the visual index of cones is significant (Figure 6; $b \neq 0$, $P < 0.01$), and

while the correlation is not impressive (r^2 = 0.52), the ratio estimate

is nevertheless more efficient than that of SRS (Table 11; Cochran's

test: b = 1058 $> \frac{1}{2}R$ = 346). If the indexing procedure itself could be

improved, which is a distinct possibility, still greater precision might

be achieved with the use of these visual indices.

Sub-sampling the Chosen Sample Unit

There will be instances when the ability to sub-sample the cones

from a branch is desirable. These situations will arise when the

Stage Two sampling costs are high, as in estimating viable seed or

insect damage in the field (Asher, 1964; Kozak, 1964), or when esti-

mating potentially very large populations like seeds, seed-infesting

insects (Hussey, 1955) and cone midges (Hedlin, 1961; Hedlin and

Johnson, 1963). In so extending the sampling to three stages, the

manner of sub-sampling should be carefully considered.

The common practice of arbitrarily sub-sampling cones from

trees is likely to result in considerable bias. As an example, the

predilection of samplers to collect the more easily accessible cones

from the tips of branches may result in an over-estimate, since

observations on a single tree showed that the intensity of B. colifaxiana

pupae in cones at the tips of branches was twice that over the rest of

the branch (Appendix 1, Table 6; Paired t-test: t = 2.28 with 26 d.f.,

P < 0.05). This is no doubt a reflection of the fact that the female

moths hover around the extremities of branches before alighting on

the foliage to search for cones on which to lay eggs (Hedlin, 1960c).

A strict probability sample will remove the possibility of bias in the

estimate of the population total and its variance.

The Choice of Attributes for Measurement

A number of studies on the searching behavior of insects for

oviposition sites show that it is non-random (Whittaker and Feeny,

1971; Hassell and Rogers, 1972; Corbet, 1973) and is affected by the

degree of host aggregation (Hassell, 1971; Cheke, 1974). Therefore,

the clustering of cones into groups of varying sizes (a range of 1 to 8

was observed), and their frequency distribution on branches, is of

potential significance in cone-insect population estimation, since the

insect intensity (of eggs, larvae, etc.) may vary between cone clusters

of different sizes. The nature of the specific insect species' response

to this clustering would determine whether most precision is obtained

by recording the following for each branch: (1) insects per cone,

(2) insects per cone-cluster, or (3) insects per cone within strata

defined by size of cone-cluster. A complex, non-linear relationship

between intensity and cone cluster size would require a stratified

sample design of the last type.

In one tree, for which the appropriate information is available,

the intensity of B. colfaxiana pupae did not vary significantly between

cluster sizes (Table 12) and there was a significantly smaller vari-

ance for the intensity based on cones rather than on clusters (F = 2.70

with 28, 28 d. f., P < 0.01).

Table 12. Comparison of intensity of $\underline{B}$. colfaxiana pupae per cone in cone-clusters of different sizes from an individual tree (Plot 2, Buckhead S. P. A., 1971; sample data in Appendix 1, Table 7).

Source	S. S.	D. F.	M. S.	V. R.
Between Cone Clusters	0.0535	4	0.0134	1.1921[a]
Within Cone Clusters	1.2590	112	0.0112	
Total	1.3125	116		

[a]Not significant at P < 0.05

The Optimum Allocation of Sampling Effort

The Components of Variance

The components of the variance of y_{i_c}, the measurement on the ith branch of a tree C, are (from Table 13):

$$\hat{\sigma}_1^2 = 30.81$$

$$\hat{\sigma}_2^2 = 8.67$$

Table 13. Anova of the mean intensity of __B. colfaxiana__ pupae per branch in a two-stage sample: Sy· RS/SRS (Plot 2, Buckhead S. P. A., 1971).

Source	S. S.	D. F.	M. S.	V. R.	Parameters Estimated
Between Trees	-	5	347. 60	40. 11	$\sigma_2^2 + 11\sigma_1^2$
Within Trees	-	627	8. 67[a]		σ_2^2
Total	-	632	356. 27[a]		

[a]See Appendix 4

The Costs of Sampling

The traveling time spent in moving between trees in the small area of the study plots is regarded as unimportant, and so an appropriate cost function for a two-stage sample is:

$$\text{Total Cost, } C = c_1 k + c_2 k \bar{n}_c$$

where c_1 α number of trees in the sample (k)

c_2 α total number of branches in the sample $(k\bar{n}_c)$

The relative costs of sampling in this study are summarized in Table 14, from which an approximate value of $c_1/c_2 = 2$ is obtained. Precise values are not critical (Cochran, 1963).

Optimum Allocation of Sampling Effort

1. Calculation of the optimum sample size, $\bar{n}_c$ (opt.), at Stage 2.

$$\bar{n}_c \text{ (opt.)} = \sqrt{\frac{c_1}{c_2}} \cdot \sqrt{\frac{s_2^2}{s_1^2}} \qquad \text{(from Cochran, 1963).}$$

Using the values derived for the components of variance (Table 13) and costs of sampling (Table 14), $\overline{n}_c$ (opt.) = 0.75 ~ 1.0.

It would appear that the optimum sample size at Stage 2 is generally going to be one, since if the relative values of the variance components are not greatly altered, $\overline{n}_c$ (opt.) = 2 would require a ratio of costs $c_1/c_2 \approx 16$. This thought to be unlikely.

Table 14.   The components of the sampling costs in a two-stage sample of cone-bearing branches

	Approximate Time in Minutes
Components of c_1	
1. Construction of the sampling frame of branches in each tree	45
2. Collection of supplementary information on auxiliary variables	15
Total	60
Components of c_2	
1. Locating the branch specified by the sampling rule	5
2. Removing the branch and/or cones	15
3. Processing the sampled unit in the field (bagging cones, labelling)	5
Total	25

Approximate value of c_1/c_2 = 60/25 $\doteq$ 2

2. Calculation of the optimum sample size, k (opt.), at Stage 1.

In the absence of direct observations on C (the total cost of sampling), the cost equation is used to provide a value of C = 39 and then the value of k (opt.) is calculated as:

$$k \text{ (opt.)} = \frac{C}{c_1 + \bar{n}_c c_2}$$

$$= 26$$

Table 15 compares the optimum allocation with that actually employed.

Table 15. Comparison of actual and optimum allocation of effort in a two-stage sample (Plot 2, Buckhead S. P. A., 1971).

Allocation	Sample Size at:		Total of Branches
	Stage 1 (k)	Stage 2 ($\bar{n}_c$)	Sampled ($k\bar{n}_c$)
Actual	6	11	66
Optimum	26	1	26

Relative Variances and Precisions
for Different Values of $\bar{n}_c$

Cochran (1963) derives an expression for the "Relative Variance" in a two-stage sample, which, using the previously obtained values for the components of variance and sampling costs, yields:

$$\text{Relative variance } (\bar{\bar{y}}) = (1 + \frac{1}{\bar{n}_c} \cdot \frac{s_2^2}{s_1^2}) (\frac{c_1}{c_2} + \bar{n}_c) = (1 + \frac{0.2811}{\bar{n}_c}) (2 + \bar{n}_c)$$

A range of values for $\bar{n}_c$, with a maximum of $\bar{n}_c = 11$ corres-
ponding to the value used in practice, provides data summarized in
Table 16 and Figure 7. It is evident that the sampling effort was
seriously mis-allocated and grossly inefficient relative to the opti-
mum. Furthermore, even slight deviations from the optimum are
shown to result in a significant loss of precision. The allocation of
effort, between the first and second stages of sampling, is therefore
an important consideration.

Table 16. Relative variances and precisions for different values of $\bar{n}_c$ (variance for $\bar{n}_c$ (opt.) = 1, the minimum, used as a standard).

$\bar{n}_c$	1	2	3	4	5	6	7	8	9	10	11
Relative Variance	3.84	4.56	5.47	6.42	7.39	8.37	9.36	10.35	11.34	12.34	13.32
Relative Precision	1.00	.84	.70	.60	.52	.46	.41	.37	.34	.31	.29
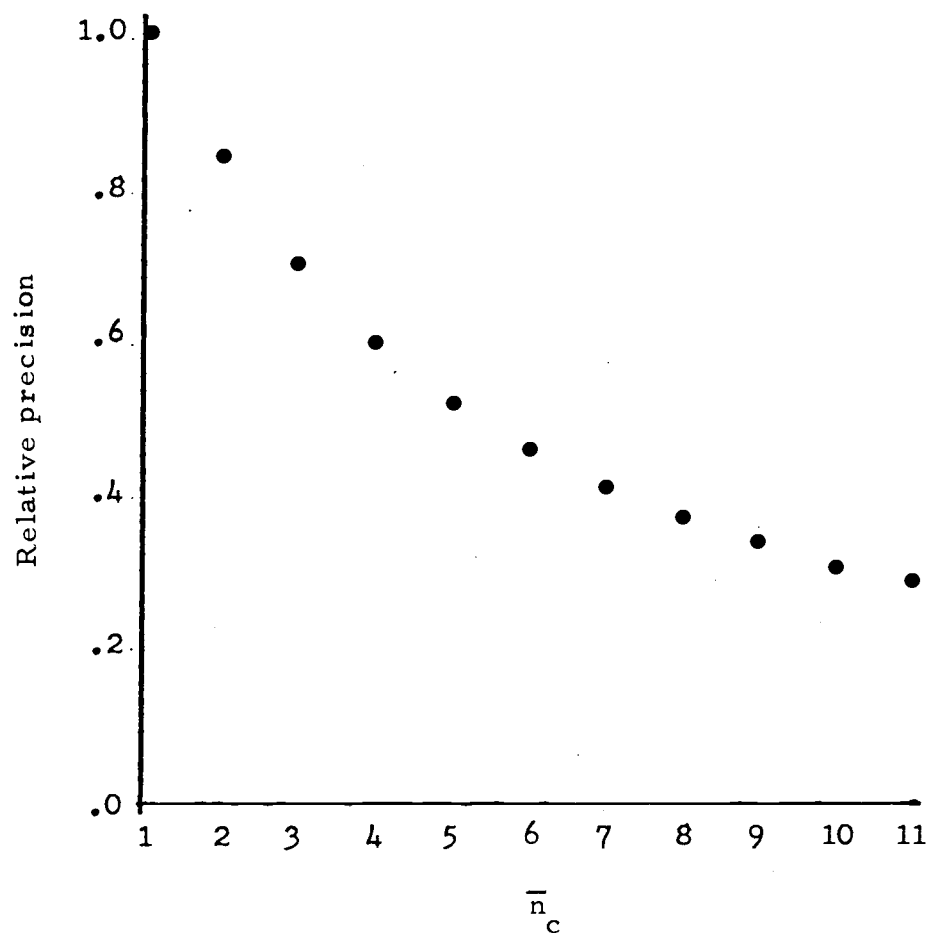
Figure 7. The influence of non-optimum allocation of effort in
a two-stage sample on the relative precision of the
estimate.

SUMMARY AND CONCLUSIONS

Practical considerations in developing a sampling frame oblige

one to use the natural groupings of cones, on branches and trees, as

the basis for a multi-stage design for sampling and estimating cone-

insect or seed populations. The basic sample unit must be the

branch, since the two alternatives are both unsatisfactory: a total

census of cones on a tree is in general inefficient, and a sampling

frame for the individual cones on a tree is impracticable because the

cones are usually too numerous and too difficult to uniquely and un-

ambiguously identify. Therefore a two-stage design, with trees and

branches as the sample units, is most appropriate.

The clustering of cones and their discrete groupings on

branches, combined with the non-random search by insects for

oviposition sites (Hassell and Rogers, 1972), raises the question

of whether to record insect intensity in terms of the cone or the

cluster of cones, or perhaps even to stratify the cones by cluster

size. The evidence suggests that the clustering of cones is not an

important consideration (Table 12). Accordingly, the attributes to

be measured on each of the sampled branches are the totals of in-

sects (or seeds) and cones, from which the intensity of insects (or

seeds) per cone can be derived.

The supplementary information obtained to determine important

sources of heterogeneity, with a view to improving the precision of

the estimates, permits the following observations. The stratification of the tree population by plots, based on observed differences in stand density, was apparently not necessary. It would, however, be a precaution to adopt in general (Southwood, 1966; Schenk and Goyer, 1967). Variation in the intensity of insects per cone between trees is the greatest source of heterogeneity in the samples (Table 9), and this provides additional support for a two-stage sample design in which the populations of each sampled tree are estimated independently. The stratification of branches within each tree, according to their level in the canopy or by aspect, is considered to be an unnecessary complication of the sample design, at least in stands uniformly 15-25 meters in height. No significant differences between such strata were observed. Furthermore, even if differences were detected, any reduction in the variance that might be obtained by such stratification is likely to be small in comparison to the total variance, which is principally due to variation between trees (Tables 8 and 11).

The use of cheaply-obtained, visual indices of cones per branch and per tree, as auxiliary variables in two-stage population estimation, holds much promise. These indices were used as an ordering index in a systematic sample, and also to provide a ratio estimate of cone and cone-insect populations. When estimating cone populations, the ratio estimate achieved greater precision than that of SRS at both the first and the second stages of sampling (Table 11).

The RATIO/RATIO estimate was more efficient than both the SRS/SRS and Sy· RS/SRS estimates (Table 10). When estimating pupal populations of B. colfaxiana, the ratio estimate was more efficient than that of SRS at the second stage only (Table 8). The Sv· RS/SRS estimate was barely more efficient than the SRS/SRS estimate, but was markedly superior to the RATIO/RATIO estimate (Table 4).

Analysis of variance to determine the components of variance, combined with information on the sampling costs, indicate that the optimum allocation of sampling effort in a two-stage sample, when estimating pupae of B. colfaxiana, is one branch in each tree (Table 16, Figure 7). This is likely to apply under a range of conditions, since the marked variation between trees in the intensity of insects per cone is probably a common phenomenon.

In summary, the cone-insect sampling problem is best conceptualized as a two-phase (double) sample, in which the first phase estimates the cone population, and the second estimates the parameters of a regression or ratio relationship between insects (or seeds) and cones. The evidence presented in this study suggests that the cones are most efficiently estimated by using a visual index as an auxiliary variable at each stage of a two-stage sample involving trees and branches. The visual index may be used as an ordering index, as in this study, but it is likely to achieve greatest precision when used to provide the selection probabilities in a variable-probability,

systematic random sample of the type described by Nebeker (1973).

Although the gain in precision through the use of a visual index at the

second stage is relatively minor, the real advantage lies in concen-

trating the sampling effort on branches with the most cones, a feature

of significance in the second phase of sampling when these branches

are sub-sampled for insects or seeds. More complex designs for

sampling branches from trees, like stratification or the interpolation

of the whorls of branches as an additional sampling stage (Nebeker,

1973), are regarded as unnecessary.

The second phase of sampling, that concerned with estimating

the regression or ratio relationship of insects (or seeds) to cones,

in general requires that the total of insects (or seeds) per branch be

observed on a sub-sample of branches, with the sub-sampling of

individual branches as an alternative if appropriate. Sub-sampling

should be strictly randomized in order to obtain a probability sample,

which then permits an unbiased estimate of the population total and

its variance. The practice of casually selecting cones from the tips

of branches is likely to be biased because, apart from the non-random

selection, there is the possibility that the intensity of insects is

higher in the cones at the branch tips.

It is thought that this conceptualization of the sampling problem

and the outline of a sampling strategy, for estimating populations of

cones, seeds and their associated insect fauna, is likely to have

general applicability. However, some modification of the details may be appropriate under certain circumstances. The 1971 cone crop was generally regarded as large, and the regression relationships between insects, cones and visual indices of cones may be different in years of low cone production. Specifically, it is possible that a correlation between the numbers of B. colfaxiana pupae and the numbers of cones per tree and per branch might be observed. The visual index of cones could then be used directly as the auxiliary variable in a single-phase ratio estimate of pupae. A similar possibility also exists for studies on different sites or with different species of insect.

The sample data permit certain inferences regarding the behaviour of B. colfaxiana females in their search for oviposition sites. The apparent decline in intensity of pupae per cone with increasing numbers of cones per branch (page 31) implies that the moths search a volume of space within a given tree, rather than orienting to some stimulus provided by the aggregations of cones. This is confirmed by observations in the field (Hedlin, 1960c). The marked differences in the intensity of attack between trees suggests that the moths strongly discriminate between individuals of the tree population. The possible reasons for this are diverse, and may include factors extrinsic and intrinsic to the trees.

In 1971, a year with a large cone crop, 89% of the trees on

six acres bore cones. On a two-acre study plot; an estimated

4082 ± 966 cones per tree were produced (Table 10). The estimated

mean number of B. colfaxiana per tree was 310 ± 66 (Table 4), re-

sulting in an intensity of 0.076 pupae per cone, or approximately

eight pupae per hundred cones. The destruction of seed is likely to

have been much less than eight percent, since the seed of an infested

cone is not usually totally destroyed (Hedlin, 1960c). Although no

direct observations on viable seed production were made, seed

destruction would probably have been of the order of five percent.

This can be compared to observations by Kulhavy et al. (1976), in

a year of low cone production, that the greatest seed loss attributable

to a single species was 12%, and that the total seed loss to insects

was 29%. Although the loss of conifer seed to insects may vary

greatly, from almost nothing to 100% (Keen, 1958; Hedlin, 1960c;

Kinzer et al., 1972; Ebel et al., 1975), it would seem that the

dynamics of seed and cone insects is not governed solely by the

availability of cones. McLemore's (1975) study on the effects of

fertilizing pine trees for increased cone crops confirms this view.

It is likely that seed and cone insects have population parameters

intermediate on the 'r-K' continuum (Pianka, 1970; Southwood et al.,

1974), and that natural enemies are important in effecting population

regulation (Southwood and Comins, 1976). If this indeed be the case,

the adaptive significance of mast-seeding in conifers requires closer

examination. If masting truly represents an evolutionary strategy to satiate seed predators and so increase the probability of seed survival (Janzen, 1971), then the relevant seed predators would be the vertebrates: birds like jays and finches, and small mammals like squirrels, chipmunks, mice and shrews. This point of view would seem to be confirmed by the heavy mortality they inflict on seeds and the important influence they are thought to have on forest regeneration (Gashwiler, 1968, 1970; Schmidt and Shearer, 1971; Hooven, 1975; Pank, 1976).

The obligate specificity of insect seed-predators for their plant hosts makes a study of their population dynamics, and their ecological role in temperate coniferous forests, of special interest. This thesis has attempted to elucidate some of the sampling problems involved in providing reliable data for such studies. Future investigations might include: the role of extended diapause, cone availability, and predation in cone insect dynamics; the effects of management practices in seed production areas and orchards on cone insect populations; and the influence of cone insects on the reproduction and consequent distribution and abundance of conifer trees.

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APPENDICES

APPENDIX 1

Table 1. Plot 1, Buckhead S. P. A., 1971

Tree (in order of selection) C_h	Canopy level	Branch (in order of selection) u_c	Visual index of cones x_c	Pupae of B. colfaxiana y_c	Live cones y'_c	Clusters of live cones	Aspect
1	--	--	--	--	--	--	--
2	2. middle	1	5	0	53	39	N
		2	2	0	14	8	NNE
	3. upper	1	5	0	45	31	NNE
		2	2	1	15	13	N
		$n_c = 4$	$t_{x_c} = 14$	$t_{y_c} = 1$	$t_{y'_c} = 127$		
		$N_c = 108$	$T_{x_c} = 182$				
3	1. lower	1	3	5	35	28	NNW
		2	1	0	11	7	WSW
	2. middle	1	6	7	58	45	W
		2	1	0	9	6	S
	3. upper	1	4	6	41	32	ENE
		2	2	0	12	7	ENE
		$n_c = 6$	$t_{x_c} = 17$	$t_{y_c} = 18$	$t_{y'_c} = 166$		
		$N_c = 111$	$T_{x_c} = 253$				
4	1. lower	1	2	2	32	26	E
		2	1	3	10	8	N
	2. middle	1	5	6	92	66	NNW
		2	2	5	33	18	ENE
	3. upper	1	2	6	42	25	NE
		2	1	1	13	10	S
		$n_c = 6$	$t_{x_c} = 13$	$t_{y_c} = 23$	$t_{y'_c} = 222$		
		$N_c = 129$	$T_{x_c} = 373$				
5	2. middle	1	3	1	74	28	S
		2	1	1	10	5	SE
	3. upper	1	6	0	58	20	SE
		2	2	1	14	7	NE
		$n_c = 4$	$t_{x_c} = 12$	$t_{y_c} = 3$	$t_{y'_c} = 156$		
		$N_c = 136$	$T_{x_c} = 254$				
6	--	--	--	--	--	--	--

k = 6
K = 30

APPENDIX 1 (Continued)

Table 2. Plot 2, Buckhead S. P. A., 1971

Tree (in order of selection) C_h	Canopy level	Branch (in order of selection) u_c	Visual index of cones x_c	Pupae of B. colfaxiana y_c	Live cones y'_c	Clusters of live cones	Aspect
1	2. middle	1	1	0	1	1	N
		2	1	0	1	3	E
		3	1	5	10	21	N
		4	1	0	6	5	NE
		5	1	0	2	7	E
	3. upper	1	1	1	1	2	E
		2	1	0	1	4	N
		3	1	3	3	4	SE
		4	1	1	2	3	N
		5	1	3	4	5	NE
		6	1	0	1	2	E
		7	1	6	4	6	N
		8	1	0	1	4	NNW
		9	1	0	1	1	NW
		10	1	6	2	5	NNW

$n_c = 15$ $t_{x_c} = 15$ $t_{y_c} = 25$ $t_{y'_c} = 40$

$N_c = 68$ $T_{x_c} = 141$

Tree C_h	Canopy level	Branch u_c	x_c	y_c	y'_c	Clusters of live cones	Aspect
2	1. lower	1	1	1	14	12	NNE
		2	1	7	14	12	S
	2. middle	1	5	9	78	53	N
		2	2	1	26	19	NE
	3. upper	1	5	12	89	56	N
		2	1	1	5	3	S

$n_c = 6$ $t_{x_c} = 15$ $t_{y_c} = 31$ $t_{y'_c} = 226$

$N_c = 96$ $T_{x_c} = 230$

Tree C_h	Canopy level	Branch u_c	x_c	y_c	y'_c	Clusters of live cones	Aspect
3	1. lower	1	2	2	14	11	W
		2	1	0	6	6	WSW
	2. middle	1	2	4	21	19	E
		2	2	5	15	14	W
	3. upper	1	3	7	23	22	SE
		2	2	8	13	12	N

$n_c = 6$ $t_{x_c} = 12$ $t_{y_c} = 26$ $t_{y'_c} = 92$

$N_c = 120$ $T_{x_c} = 202$

APPENDIX 1 (Continued)

Table 2. (Continued)

Tree (in order of selection) C_h	Canopy level	Branch (in order of selection) u_c	Visual index of cones x_c	Pupae of B. colfaxiana y_c	Live cones y'_c	Clusters of live cones	Aspect
4	1. lower	1	3	2	33	21	NW
		2	2	3	17	12	N
	2. middle	1	7	2	71	51	NE
		2	2	2	21	14	NE
	3. upper	1	4	0	53	39	SSW
		2	2	0	13	9	N

$n_c = 6$ $t_{x_c} = 20$ $t_{y_c} = 9$ $t_{y_c} = 208$
$N_c = 118$ $T_{x_c} = 159$

5	2. middle	1	4	1	41	30	NE
		2	2	2	14	11	N
	3. upper	1	5	0	47	27	S
		2	2	1	14	9	N

$n_c = 4$ $t_{x_c} = 13$ $t_{y_c} = 4$ $t_{y_c}' = 116$
$N_c = 112$ $T_{x_c} = 211$

6	1. lower	1	1	1	8	6	W
		2	1	0	2	2	NW
		3	3	6	23	15	NW
		4	3	0	34	21	SW
		5	4	5	39	28	WSW
		6	4	3	42	29	S
		7	6	12	68	50	NW
		8	8	15	107	55	W
		9	9	11	76	50	SW
	2. middle	1	1	0	12	7	N
		2	1	0	7	4	E
		3	2	4	72	44	NW
		4	2	6	30	17	NW
		5	2	4	86	47	E
		6	4	2	169	100	SE
		7	4	4	67	36	WNW
		8	5	7	193	113	S
		9	5	5	150	98	SE
		10	5	3	127	76	W

APPENDIX 1 (Continued)

Table 2. (Continued)

Tree (in order of selection) C_h	Canopy level	Branch (in order of selection) u_c	Visual index of cones x_c	Pupae of $\underline{B.\ colfaxiana}$ y_c	Live cones y_c	Clusters of live cones	Aspect
	3. upper	1	1	0	26	11	NNE
		2	2	1	29	19	S
		3	3	1	39	30	S
		4	4	1	46	29	SSE
		5	5	1	201	108	SSW
		6	6	1	216	134	S
		7	7	2	88	45	E
		8	9	3	184	101	NE
		9	9	5	263	142	S
		10	17	4	403	189	N

$$n_c = 29 \qquad t_{x_c} = 133 \qquad t_{y_c} = 107 \qquad t'_{y_c} = 2807$$

$$N_c = 119 \qquad T_{x_c} = 562$$

$k = 6$

$K = 14$

APPENDIX 1 (Continued)

Table 3. Plot 3, Buckhead S. P. A., 1971

Tree (in order of selection) C_h	Canopy level	Branch (in order of selection) u_c	Visual index of cones x_c	Pupae B. colfaxiana y_c	Live cones y'_c	Clusters of live cones	Aspect
1	--	--	--	--	--	--	--
2	2. middle	1	5	1	46	30	N
		2	2	1	13	9	N
	3. upper	1	4	0	42	29	S
		2	2	0	12	9	N

$n_c = 4$ $t_{x_c} = 13$ $t_{y_c} = 2$ $t_{y'_c} = 113$
$N_c = 100$ $T_{x_c} = 187$

3	2. middle	1	7	1	90	59	SW
		2	1	0	11	9	NNE
	3. upper	1	13	0	197	80	S
		2	1	1	20	15	NW

$n_c = 4$ $t_{x_c} = 22$ $t_{y_c} = 2$ $t_{y'_c} = 318$
$N_c = 144$ $T_{x_c} = 264$

4	2. middle	1	8	0	141	59	S
		2	1	0	12	9	W
	3. upper	1	2	1	46	35	N
		2	1	0	19	14	S

$n_c = 4$ $t_{x_c} = 12$ $t_{y_c} = 1$ $t_{y'_c} = 218$
$N_c = 97$ $T_{x_c} = 203$

5	2. middle	1	7	8	192	110	ENE
		2	1	1	10	7	ENE
	3. upper	1	6	1	115	61	SW
		2	1	0	31	19	NNW

$n_c = 4$ $t_{x_c} = 15$ $t_{y_c} = 10$ $t_{y'_c} = 348$
$N_c = 126$ $T_{x_c} = 335$

| 6 | -- | -- | -- | -- | -- | -- | -- |

k = 6
K = 37

APPENDIX 1 (Continued)

Table 4. Arbitrarily selected trees: Plot 1, Buckhead S. P. A. , 1971

Tree (in order of selection) C_h	Canopy level	Branch (in order of selection) u_c	Visual index of cones x_c	Pupae B. colfaxiana y_c	Live cones y'_c	Clusters of live cones	Aspect
X	2. middle	1	4	1	40	33	SE
		2	1	1	12	9	E
	3. upper	1	4	2	42	26	SSW
		2	2	0	15	9	SSW

$$n_c = 4 \quad t_{x_c} = 11 \quad t_{y_c} = 4 \quad t_{y'_c} = 109$$
$$N_c = 102 \quad T_{x_c} = 157$$

Y	2. middle	1	7	1	70	53	SSW
		2	2	0	15	12	S
	3. upper	1	5	1	55	42	SW
		2	2	0	21	17	SW

$$n_c = 4 \quad t_{x_c} = 16 \quad t_{y_c} = 2 \quad t_{y'_c} = 161$$
$$N_c = 84 \quad T_{x_c} = 293$$

Z	2. middle	1	2	0	23	22	WNW
		2	2	0	14	13	NNW
	3. upper	1	8	0	80	54	SSE
		2	2	2	14	11	NW

$$n_c = 4 \quad t_{x_c} = 14 \quad t_{y_c} = 2 \quad t_{y'_c} = 131$$
$$N_c = 80 \quad T_{x_c} = 153$$

APPENDIX 1 (Continued)

Table 5. (1) Visual indices of cones per tree (x), and (2) estimates ($\hat{T}_{y_c}$)of cones and B. <u>colfaxiana</u> pupae per tree

Plot	Tree	Visual index (x)	$\hat{T}_{yc}$ (Cones)		$\hat{T}_{yc}$ (Pupae)	
			SRS	RATIO	SRS	RATIO
1	x	8.5	2780	1556	102	57
	y	9	3381	2948	42	37
	z	5	2620	1432	40	22
1	2	4	3429	1651	27	13
	3	5	3071	2469	333	268
	4	7	4773	6370	494	660
	5	8.5	5304	3302	102	64

$t_x = 24.5$

$T_x = 169$

Plot	Tree	Visual index (x)	SRS	RATIO	SRS	RATIO
2	1	1	181	376	113	235
	2	4	3616	3466	496	475
	3	5	1840	1549	520	438
	4	5	4091	1654	177	72
	5	6	3248	1883	112	65
	6	9	11518	11863	439	423

$t_x = 30$

$T_x = 68.5$

Plot	Tree	Visual index (x)	SRS	RATIO	SRS	RATIO
3	2	3	2825	1625	50	29
	3	4.5	11448	3815	72	24
	4	6	5286	3688	24	17
	5	6.5	10962	7772	315	157

$t_x = 20$

$T_x = 140$

APPENDIX 1 (Continued)

Table 6. Intensity of _B. colfaxiana_ pupae in cones from the tips and remaining portions of branches (Tree no. 6, Plot 2, Buckhead S. P. A., 1971)

Canopy level	Branch	Branch-Tip			Remainder of Branch		
		Pupae	Cones	Intensity	Pupae	Cones	Intensity
1	1	0	3	0.00	0	5	0.00
	2	-	-	-	-	-	-
	3	2	7	0.29	4	16	0.25
	4	0	10	0.00	0	24	0.00
	5	4	15	0.27	1	24	0.04
	6	1	18	0.06	2	24	0.08
	7	6	12	0.50	6	56	0.11
	8	8	26	0.31	7	81	0.09
	9	2	13	0.15	9	63	0.14
2	1	0	2	0.00	0	10	0.00
	2	0	5	0.00	0	2	0.00
	3	-	-	-	-	-	-
	4	3	9	0.33	3	121	0.02
	5	3	17	0.18	1	69	0.01
	6	1	13	0.08	1	156	0.01
	7	0	11	0.00	4	56	0.07
	8	1	13	0.08	6	180	0.03
	9	1	10	0.10	4	140	0.03
	10	0	7	0.00	3	120	0.03
3	1	0	18	0.00	0	8	0.00
	2	0	11	0.00	1	18	0.06
	3	0	5	0.00	1	34	0.03
	4	0	17	0.00	1	29	0.03
	5	0	12	0.00	1	189	0.01
	6	0	29	0.00	1	187	0.01
	7	1	16	0.06	1	72	0.01
	8	1	17	0.06	2	167	0.01
	9	0	16	0.00	5	247	0.02
	10	0	29	0.00	4	374	0.01
		Σ		2.45	Σ		1.10
		Mean		0.09	Mean		0.04

APPENDIX 1 (Continued)

Table 7. Intensity of B. colfaxiana pupae per cone in cone clusters of different sizes (Tree no. 6, Buckhead S. P. A., 1971)

Canopy level	Branch	Number of cones per cluster				
		1	2	3	4	5
1	1	0.250	0.0	--	--	--
	2	0.0	--	--	--	--
	3	0.500	0.250	0.0	--	--
	4	0.0	0.0	0.0	0.0	--
	5	0.063	0.286	0.0	--	--
	6	0.0	0.188	0.0	0.0	0.0
	7	0.133	0.118	0.167	0.750	--
	8	0.063	0.083	0.222	0.188	0.100
	9	0.103	0.125	0.167	0.250	--
2	1	0.0	0.0	0.0	--	--
	2	0.0	0.0	--	--	--
	3	0.046	0.033	0.0	0.250	--
	4	0.143	0.250	0.111	--	0.200
	5	0.0	0.100	0.000	0.083	0.0
	6	0.0	0.015	0.024	0.0	0.0
	7	0.0	0.063	0.111	0.0	--
	8	0.032	0.060	0.048	0.0	--
	9	0.026	0.028	0.020	0.050	0.0
	10	0.0	0.030	0.030	0.0	--
3	1	0.0	0.0	0.0	--	--
	2	0.0	0.063	0.0	0.0	--
	3	0.0	0.056	0.0	--	0.0
	4	0.0	0.0	0.0	0.250	0.0
	5	0.0	0.0	0.015	0.0	0.0
	6	0.0	0.0	0.0	0.021	0.0
	7	0.0	0.050	0.0	0.0	0.067
	8	0.020	0.0	0.0	0.046	0.0
	9	0.0	0.027	0.012	0.0	0.025
	10	0.032	0.0	0.012	0.0	0.020
	n_i	29	28	26	20	14
	Total	1.409	1.824	0.937	1.887	0.412
	Mean	0.049	0.065	0.036	0.094	0.029

APPENDIX 2

Conceptual Aspects of a Two-Stage Sample (from Overton, 1977b)

Each primary unit is regarded as a cluster, C, of elements, u, in the sampling universe U, such that:

$$[U] = \{c_1, c_2, \cdots c_K\}$$

$$c = \{u_1, u_2, \cdots u_N\}$$

The Stage 1 sample, S^I, represents a cluster sample from U, such that:

$$S^I \subset [U]$$

The Stage 2 sample, S^{II}, represents a stratified sample from S^I, such that:

$$S_c^{II} \subset C \text{ for every } C \, \varepsilon \, S^I$$

$$\text{and} \quad S^{II} = \{S_c^{II}\}$$

APPENDIX 3

The Estimators

The notation presented here, and used throughout this thesis, has been developed by Overton (1977b) around the sample total of the attribute, y(u), observed on each element, u, in the sample.

Stratified Sampling

$$\hat{T}_y = \sum_{h=1}^{K} \hat{T}y_h$$

$$\hat{V}(\hat{T}y) = \sum_{h=1}^{K} \hat{V}(\hat{T}y_h)$$

$$\sum_{h=1}$$

where $\hat{T}y_h$ = estimate of the population total in stratum h

$\hat{V}(\hat{T}y_h)$ = estimate of the variance of the population estimate

in stratum h

K = total of strata

Two-Stage Sampling: SRS/SRS

Estimator of Population Total:

$$\hat{T}_y = (K/k)\sum_{SI} (N_c/n_c) \cdot t_{y_c}$$

where $\qquad t_{y_C}$ = sample total of y(u) in the cluster C

N_c = total number of elements in cluster C

n_c = number of elements sampled from cluster C

K = total number of clusters in $[U]$

k = number of clusters sampled from $[U]$

Variance:

$$\hat{V}(\hat{Ty}) = K(\frac{K-k}{k})s^2 \hat{Ty}_C + \frac{K}{k} \sum_{S^I} N_c (\frac{N_c - n_c}{n_c}) s^2_{y_C}$$

where $\qquad s^2_{y_C}$ = sample variance in cluster C

$$s^2 \hat{Ty}_C = \frac{1}{k-1} \sum_{S^I} (\hat{Ty}_C - \frac{\sum \hat{Ty}_C}{k})^2$$

Two-Stage Sampling: SyRS/SRS

Estimator of Population Total:

Regarding SyRS as a CLUSTER sample, C', of clusters C, of size k' = 1,

$$\hat{Ty} = \frac{K'}{k'} \sum_{S^I} \hat{Ty}_{C'} = k' \hat{Ty}_{C'}$$

where $\qquad K' = \frac{K}{k}$

and $\qquad \hat{Ty}_{C'} = \sum_{S^{II}} \hat{Ty}_C$

with SRS at Stage-2,

$$\hat{T}y = K' \sum_{S^{II}} \frac{N_c}{n_c} \cdot t_{y_c}$$

Variance (by analogy with that of SRS/SRS):

$$\hat{V}(\hat{T}y) = kK'(K'-1)\,\delta^2_{\hat{T}y_c} + K' \sum_{S^{II}} N_c \left(\frac{N_c - n_c}{n_c}\right) \hat{V}y_c$$

where
$$\hat{V}y_c = s^2_{y_c}$$

and
$$\delta^2 = \text{the Mean Square Successive Difference}$$

where
$$\delta^2_{\hat{T}y_c} = \frac{1}{2} \cdot \frac{1}{k-1} \sum_{i \epsilon S} (\hat{T}y_c(i) - \hat{T}y_c(i+k'))^2$$

where i is an order index.

Single Stage RATIO Estimation

In the ratio modey $y = Rx + \epsilon$,

$$\hat{y} = \hat{R}x$$

and $\hat{T}y = ty + \hat{R}(Tx-tx)$

where x is an auxiliary variable.

Assuming $E(\epsilon^2) = x\,\sigma^2$ for every element $U \epsilon u$,

$$\hat{R} = t_y/t_x \qquad \text{(the ''Ratio of Means'' estimator)}$$

and $\text{MSE}(\hat{T}y \mid s) = T_x \left(\frac{T_x - t_x}{t_x}\right) \sigma^2$

$$\text{where } \hat{\sigma}^2 = s^2_{y \cdot x} = \frac{1}{n-1}\{\sum_S \frac{y^2}{x} - \hat{R}t_y\}$$

Note: the sampling rule is NOT specified.

Two-Stage Sampling: RATIO{RATIO Estimation

Estimator of Population Total:

$$\hat{T}y = \sum_{SI} \hat{T}y_c + \hat{R}\ (T_x - t_x)$$

$$\text{where } \hat{R} = \frac{\sum_{SI} \hat{T}y_c}{t_x}$$

$$\text{Since } \hat{T}y_c = ty_c + \hat{R}_c\ (T_{x_c} - t_{x_c})$$

$$\hat{T}y = \sum_{SI} \{t_{y_c} + \hat{R}_c\ (T_{x_c} - t_{x_c})\} + \hat{R}\ (T_x - t_x)$$

Mean Square Error (by analogy with the variance of the SRS/SRS estimator):

$$MSE\ (\hat{T}_y) = T_x\ (\frac{T_x - t_x}{t_x})\ s^2_{\hat{T}y_c} \cdot T_{x_c} + \frac{K}{k} \sum_{SI} MSE\ (\hat{T}y_c)$$

Contribution to MSE
from sampling at: Stage 1   Stage 2

APPENDIX 4

Calculating the Components of Variance

The calculation of the components of variance in a two-stage sample (Snedecor and Cochran, 1967) assumes a sampling rule of SRS. In this particular study the estimates of the population total and its variance were provided by an alternative rule. Application of the components of variance technique in these circumstances is not strictly legitimate, but can still yield useful insight to the allocation problem.

Anova Table

Source of Variation	D. F.	M. S.	V. R.	Parameters Estimated
Between Units	$k - 1$	s_B^2		$\sigma_2^2 + \bar{n}_c \, \sigma_1^2$
Within Units	$\Sigma N_c - k$	s_2^2		σ_2^2
Total	$\Sigma N_c - 1$	s^2		

Total Mean Square

For the sample of k primary units from the total K in U,

$$\hat{T}_y = N \hat{\bar{y}}$$

$$\hat{V}(\hat{T}_y) = \bar{N}^2 \, \hat{V}(\hat{\bar{y}}) = \bar{N}^2 \, \frac{s^2}{\Sigma N_c}$$

$$\therefore \quad s^2 = \hat{V}(\hat{\bar{T}}y)\frac{\Sigma N_c}{\bar{N}^2} = \hat{V}(\hat{\bar{T}}y)\,\Sigma N_c \cdot \frac{k^2}{(\Sigma N_c)^2}$$

$$= \hat{V}(\hat{\bar{T}}y)\,\frac{k^2}{\Sigma N_c}$$

Since $\hat{V}(\hat{\bar{T}}y) = s^2_{\hat{\bar{T}}_{yc}} \cdot \frac{1}{k},$

$$s^2 = s^2_{\hat{\bar{T}}_{y_c}} \cdot \frac{k}{\Sigma N_c}$$

Notation: $\hat{\bar{T}}_y$ = estimated mean primary unit total

$\hat{\bar{y}}$ = estimated element mean over all k primary units

Other symbols are consistent with those in Appendix 3.

Within-Units Mean Square

1. In a given primary unit, C:

$$\hat{T}_{y_c} = N_c \bar{y}_c$$

$$\hat{V}(\hat{T}_{y_c}) = N_c^2\,\hat{V}(y_c) = N_c^2\,\frac{s_{2_c}^2}{n_c}$$

$$\therefore \quad s_{2_c}^2 = \hat{V}(\hat{T}_{y_c})\,\frac{n_c}{N_c^2}$$

and the sum of squares, S. S. $_{2_c}$ is given by:

$$S.S._{2_c} = \hat{V}(\hat{T}_{y_c})\,\frac{n_c}{N_c^2}\,(n_c - 1)$$

2. The variance within units, between elements, σ_2^2, is

estimated by:

$$s_2^2 = \frac{\text{Pooled S. S.}_2}{\text{Total D. F.}} = \frac{\sum\limits^k \text{S. S.}_{2_c}}{\sum\limits^k n_c - 1}$$