

DISSERTATION

PREDATORY AND ENERGETIC RELATIONS OF
WOODPECKERS TO THE ENGELMANN
SPRUCE BEETLE

Submitted by
James Ray Koplin

In partial fulfillment of the requirements
for the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
June, 1967

COLORADO STATE UNIVERSITY

June 1967

IT IS RECOMMENDED THAT THE DISSERTATION PREPARED BY _____

JAMES RAY KOPLIN

ENTITLED PREDATORY AND ENERGETIC RELATIONS OF WOODPECKERS

TO THE ENGELMANN SPRUCE BEETLE

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENT FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Paul H. Baldwin
Major Professor

Harold W. Steinhoff

Noel D. Wygant

David Pettus

W. J. F. ...
Head of Department

Examination Satisfactory

Committee on Final Examination

Noel D. Wygant

W. J. F. ...

David Pettus

Harold W. Steinhoff

Paul H. Baldwin
Chairman

Permission to publish this dissertation or any part of it
must be obtained from the Dean of the Graduate School.

Abstract of Dissertation

PREDATORY AND ENERGETIC RELATIONS OF WOODPECKERS
TO THE ENGELMANN SPRUCE BEETLE

A general theory of the population dynamics of predator-prey systems was developed from a survey of pertinent literature. According to the theory, populations of simplified predator-prey systems fluctuate wildly and periodically. Complicating factors dampen the amplitude of the population fluctuations and thus exert a stabilizing influence on the systems.

The predator-prey system between the Northern Three-toed, Hairy and Downy Woodpeckers, and the Engelmann spruce beetle was chosen for an investigation of the population dynamics of a natural predator-prey system.

The population densities of several species of bark beetles attracted to trees killed and damaged by a fire on the study area in Northern Colorado, increased to levels that attracted the feeding attention of the woodpeckers.

The numerical response of the woodpeckers to prey density was graded, that of the Northern Three-toed Woodpecker was the most pronounced and that of the Downy Woodpecker was the least pronounced.

Spatial and temporal differences were noted in the foraging behavior of the three species of woodpeckers; similar but less apparent differences were also noted in the foraging behavior between the sexes of the Northern Three-toed and Hairy Woodpeckers.

Both the interspecific and intersexual differences in foraging behavior were correlated with morphological and dietary

differences.

The metabolic demands of free-living woodpeckers were estimated by feeding diets of known caloric content to active woodpeckers in cages at several different ambient temperatures. Estimates were also made of the caloric content of Engelmann spruce beetle larvae and the rate at which they are digested by the woodpeckers. Combining these estimates with the estimates of the relative densities of woodpeckers, and the average number of spruce beetle larvae found per woodpecker stomach made it possible to calculate the number of larvae consumed by each species of woodpecker. This method gave results very similar to the usual method whereby the number of larvae surviving in bark protected from woodpeckers is compared with the number surviving in bark exposed to woodpeckers.

Every aspect of the predator-prey system between woodpeckers and the Engelmann spruce beetle, except the number of larvae destroyed, conforms to general theory. The number of prey destroyed in this predator-prey system is higher than that known for any other system between vertebrate predators and invertebrate prey.

James Ray Koplin
Department of Zoology
Colorado State University
June, 1967

ACKNOWLEDGEMENTS

This study was supported in part by cooperative aid from the U. S. Forest Service, through the auspices of Dr. Noel Wygant, principal Entomologist, of the Forest Insect Research Laboratory of the Rocky Mountain Forest and Range Experiment Station. The study was also supported by National Science Foundation Grants, GB-753 and G-2478, awarded to Dr. Paul H. Baldwin.

I wish to thank Dr. Baldwin for his assistance and guidance throughout the study. I am grateful to Drs. O. Wilford Olsen, David Pettus, Noel Wygant, and Harold Steinhoff for their services as committee members and for their many helpful comments and suggestions.

Donald Beaver, Douglas Post, Gerald Lorentzson and James Gibson assisted in the field work and George M. Matthews assisted in the metabolic experiments. I had many helpful discussions of the subject of this dissertation with Douglas Post, Patrick Stallcup and Albert W. Spencer.

A special note of thanks is due Mrs. Bernice M. George for her many acts of assistance during my tenure in the field on the Deadman study area. Finally, I am most grateful to my wife, Phyllis, for her patience and encouragement throughout the study, and for her help in preparing the manuscript.

Most of the field equipment used in this study was supplied by the Forest Insect Research Laboratory, Rocky Mountain Forest and Range Experiment Station.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
Statement of Problem	2
Development of a General Theory	3
The Need for a General Theory	3
Models of Predator-Prey Interactions	5
Field Studies of Interactions Between Vertebrate Predators and Vertebrate Prey	16
Field Studies of Interactions Between Invertebrate Predators and Invertebrate Prey	18
Field Studies of Interactions Between Vertebrate Predators and Invertebrate Prey	20
Efficacy of Predators and Ecological Efficiency	21
Competition and Niche	23
Summary Statement of the General Theory	29
METHODS	31
Study Area	31
Measurement of Forest Composition and Stand Density	31
Temperature Records	34
Techniques for Manipulating the Spruce Beetle Population	34
Spruce Beetle Census Technique	35
Woodpecker Census Techniques	36
Measurement of Realized Niche	38
Metabolic Techniques	40
RESULTS	44
Forest Composition and Stand Density	44
Temperature	49
Wind Thrown Trees	49
Bark-Beetle Populations	54
Woodpecker Populations	59
Foraging Behavior	64
Food Habits	86
Linear Measurements of Morphological Characters	95
Energetics	99

TABLE OF CONTENTS (Continued)

	Page
DISCUSSION	116
Components of Character Displacement	116
Spatial and Temporal Differences	117
Dietary Differences	129
Morphological Differences	136
Components of Predation	145
Spruce Beetle Densities	145
Numerical Response of Woodpeckers to Prey Density . .	151
Functional Response of Woodpeckers to Prey Density . .	155
Spruce Beetle Mortality from Woodpecker Predation . .	156
Factors Regulating the Effectiveness of Predation by	
Woodpeckers	166
Nesting Territoriality	168
Differential Selections of Prey	169
CONCLUSIONS	174
SUMMARY	177
LITERATURE CITED	179

LIST OF TABLES

Table		Page
1	Density and basal area of Engelmann spruce in each two-inch diameter class on the Deadman study area	45
2	Density and basal area of subalpine fir in each two-inch diameter class on the Deadman study area	47
3	Density and basal area of lodgepole pine in each two-inch diameter class on the Deadman study area	48
4	Relative location and year of initial invasion by bark beetles of blowdowns discovered on the Deadman study area	55
5	Number of acres censused and woodpeckers observed per census period on the Deadman study area . .	60
6	Number of acres censused and woodpeckers observed per census period outside the area of the 1962 burn	61
7	Number of acres censused and woodpeckers observed per census period within the area of the 1962 burn	62
8	Comparisons of relative use of tree types and of foraging positions within trees for Northern Three-toed and Hairy Woodpeckers for the period July 16 to October 15, 1962 to 1965	68
9	Comparisons of relative use of tree types and of foraging positions within trees for Northern Three-toed and Hairy Woodpeckers for the period October 16 to May 10, 1962 to 1965	69
10	Comparisons of relative use of tree types and foraging positions within trees for Northern Three-toed and Downy Woodpeckers for the period October 16 to May 10, 1964 to 1965	70

LIST OF TABLES (Continued)

Table		Page
11	Comparisons of relative use of tree types and foraging positions within trees for Hairy and Downy Woodpeckers for the period October 16 to May 10, 1964 to 1965	71
12	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Northern Three-toed and Hairy Woodpeckers for the period July 16 to October 15, 1962 to 1965	73
13	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Northern Three-toed and Hairy Woodpeckers for the period October 16 to May 10, 1962 to 1965	74
14	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Northern Three-toed and Downy Woodpeckers for the period October 16 to May 10, 1964 to 1965	75
15	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Hairy and Downy Woodpeckers during the period October 16 to May 10, 1964 to 1965	76
16	Comparisons of relative use of tree types and foraging positions within trees for female and male Northern Three-toed Woodpeckers for the period July 16 to October 15, 1962 to 1965	78
17	Comparisons of relative use of tree types and foraging positions within trees for female and male Northern Three-toed Woodpeckers for the period October 16 to May 10, 1962 to 1965	79
18	Comparisons of relative use of tree types and of foraging positions within trees for female and male Hairy Woodpeckers for the period July 16 to October 15, 1962 to 1965	80

LIST OF TABLES (Continued)

Table		Page
19	Comparisons of relative use of tree types and of foraging positions within trees for female and male Hairy Woodpeckers for the period July 16 to May 10, 1962 to 1965	81
20	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female and male Northern Three-toed Woodpeckers for the period July 16 to October 15, 1962 to 1965	82
21	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female and male Northern Three-toed Woodpeckers for the period October 16 to May 10, 1962 to 1965	83
22	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female and male Hairy Woodpeckers for the period July 16 to October 15, 1962 to 1965	84
23	Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female and male Hairy Woodpeckers for the period July 16 to May 10, 1962 to 1965. .	85
24	Indices of difference in foraging behavior between Northern Three-toed, Hairy, and Downy Woodpeckers	87
25	Indices of difference in foraging behavior between the sexes of the Northern Three-toed and Hairy Woodpeckers	87
26	Stomach content analyses of 24 Northern Three-toed Woodpeckers collected in spruce-fir forests supporting endemic populations of the Engelmann spruce beetle	88
27	Stomach content analyses of 56 Northern Three-toed Woodpeckers collected in spruce-fir forests supporting epidemic populations of the Engelmann spruce beetle	89

LIST OF TABLES (Continued)

Table		Page
28	Stomach content analyses of 32 Northern Three-toed Woodpeckers collected in spruce-fir forests supporting post-epidemic populations of the Engelmann spruce beetle	90
29	Stomach content analyses of 18 Hairy Woodpeckers collected in spruce-fir forests supporting endemic populations of the Engelmann spruce beetle	91
30	Stomach content analyses of 21 Hairy Woodpeckers collected in spruce-fir forests supporting epidemic populations of the Engelmann spruce beetle	92
31	Stomach content analyses of 16 Downy Woodpeckers collected in spruce-fir forests supporting epidemic populations of the Engelmann spruce beetle	93
32	Comparison of the numbers of stomachs of male and female Northern Three-toed Woodpeckers containing scolytids and cerambycids	96
33	Measurements of six linear characters from adult female and male Downy, Northern Three-toed and Hairy Woodpeckers	97
34	Coefficients of difference among culmen lengths and cube roots of weight of female and male Downy, Northern Three-toed and Hairy Woodpeckers	100
35	Ratios of character difference among female and male Downy, Northern Three-toed and Hairy Woodpeckers	101
36	Percentage difference ratios calculated by $(L - S)/L$ among female and male Downy, Northern Three-toed and Hairy Woodpeckers	103
37	Standard metabolic rates in kilocalories per day for female and male Downy and Hairy Woodpeckers	105
38	Weights of woodpeckers and the existence energies calculated from them	108

LIST OF TABLES (Continued)

Table		Page
39	Caloric values of insects and of woodpecker excreta	110
40	Caloric values from the feeding experiments for female and male Downy, Northern Three-toed and Hairy Woodpeckers	111
41	Equations to estimate energetics of cage activity from weight for three temperatures	112
42	Equations to estimate energetics of cage activity from temperature for female and male Downy, Northern Three-toed and Hairy Woodpeckers	112
43	Indices of interspecific difference in spatial and temporal components of character displacement	119
44	Indices of intersexual difference in spatial and temporal components of character displacement	126
45	Indices of interspecific difference in the dietary component of character displacement	130
46	Indices of intersexual difference in the dietary component of character displacement of North American Accipiters, calculated from weight-class differences	132
47	Indices of interspecific difference in mean culmen length of adult male birds	139
48	Indices and ratios of intersexual difference in mean culmen lengths of adult female and male woodpeckers	143
49	Estimated densities of Engelmann spruce beetle brood per acre, calculated from the average number found per square foot of infested bark on prostrate and standing trees	148
50	Seasonal rates of turnover, or rates at which larvae of the Engelmann spruce beetle are digested by woodpeckers for average conditions of temperature in spruce-fir forests	162

LIST OF TABLES (Continued)

Table		Page
51	Estimated number of Engelmann spruce beetle larvae consumed per acre per year as a result of woodpecker predation	164

LIST OF FIGURES

Figure		Page
1	Map of the study area in the vicinity of Deadman Lookout showing the relative positions of the two fixed-width census plots	32
2	Temperatures recorded within the forest on the Deadman study area for the months June through early September	50
3	Temperatures recorded within the forest on the Deadman study area for the months September through December	51
4	Temperatures recorded on the lookout tower on the Deadman study area for the months June through early September	52
5	Temperatures recorded on the lookout tower on the Deadman study area for the months September through early December	53
6	Semilog graph of the densities of Engelmann spruce beetle larvae in trap logs felled on the Deadman study area	56
7	Woodpecker densities on the Deadman study area during the period June 1962 through August 1965	65
8	Woodpecker densities on the Deadman study area outside the 1962 burn	66
9	Woodpecker densities on the Deadman study area within the 1962 burn	67
10	Culmen lengths of female and male Downy, Northern Three-toed and Hairy Woodpeckers plotted as functions of the cube roots of their weights . . .	98
11	Log graph of standard metabolic rate, and existence exercise energies at 32° F and 86° F plotted as functions of the average weights of woodpeckers	107

LIST OF FIGURES (Continued)

Figure		Page
12	Existence energy per gram body weight of female and male Downy, Northern Three-toed and Hairy Woodpeckers plotted as functions of temperature	114
13	Exercise energy per gram body weight of female and male Downy, Northern Three-toed and Hairy Woodpeckers plotted as functions of temperature	115
14	Daily rates of turnover or number of larvae of the Engelmann spruce beetle digested per day per woodpecker throughout the range of temperatures recorded on the Deadman study area	160
15	Functional and numerical responses combined to show percentages of the total number of Engelmann spruce beetle larvae consumed per year by Downy, Northern Three-toed and Hairy Woodpeckers at various larval densities	167

INTRODUCTION

Predator-prey systems are technically very difficult to study in nature because of the problems encountered in obtaining estimates of the population densities of the animals, and because of the problems in obtaining estimates of the number of prey consumed by the predators. Methods for estimating population densities of free-living, mobile animals are so crude that very large changes in density can go completely undetected by the investigator; as a result the disappearance of a large number of prey is necessary before the investigator can definitely say that prey are disappearing. Even then, the investigator has difficulty in determining what percentage of the prey animals that disappeared were killed by predators. He must resort to the indirect method of examining the contents of the stomachs of the predators. As a rule the investigator cannot determine the length of time expended by the predator in obtaining the prey found in the predator's stomach, so he has no idea of how often the predator must obtain a meal equivalent to the one found in the stomach.

Natural populations of woodpeckers (Picidae) and bark beetles (Scolytidae) possess a number of characteristics that make them suited for investigations on the population dynamics of natural predator-prey systems. Woodpeckers and bark beetles are sufficiently numerous that it is possible to obtain reliable estimates of the population densities of both. The number of beetles destroyed by woodpeckers

can readily be estimated by comparing the number of insects surviving in bark protected from woodpeckers with the number surviving in bark exposed to woodpeckers. Finally, woodpeckers can be maintained in captivity in a state of activity comparable to that in nature; the energetics of this activity can be measured and equated with the number of prey required to maintain the level of activity.

Statement of Problem

Previous work in the subalpine forests of Colorado has implicated woodpecker predation as an important factor limiting the densities of epidemic populations of the Engelmann spruce beetle, Dendroctonus obesus (Mannerheim) (= engelmanni Hopkins). Hutchison (1951) determined that this beetle represented about 99 per cent of the winter diet of three species of woodpeckers: the Northern Three-toed, Picoides tridactylus; the Hairy, Dendrocopos villosus; and the Downy, D. pubescens. Massey and Wygant (1954) showed that the beetle composed approximately 65 per cent of the summer diet of these woodpeckers. Baldwin (1960) found differential feeding attention and differential responses of wintering populations of these woodpeckers to the beetle. Amman and Baldwin (1960) have worked out techniques suitable for censusing populations of woodpeckers wintering in beetle-infested forests, and Knight (1958) has developed methods for evaluating the impact of woodpecker predation upon populations of the bark beetle in infested trees.

Very little of this previous work describes woodpecker activity in subalpine forests harboring endemic populations of the Engelmann spruce beetle. One objective of this dissertation is to

provide such a description. In addition, the response of woodpeckers to an increasing food supply is described. In order to assess better the impact of predation by woodpeckers upon populations of the Engelmann spruce beetle, a study to determine the energy requirements of these woodpeckers is reported. Finally, because there exists no formal theory regarding the population dynamics of predator-prey systems, a survey of the literature was conducted in order to develop the theory. It is this latter objective that will be treated first.

Development of a General Theory

The Need for a General Theory

Requisite for any understanding of the population dynamics of predator-prey systems is a consideration of the concepts and principles of disoperative coactions. Disoperations are deleterious interrelationships between individuals or species (Allee, et al 1949); thus parasitism, predation, and competition are considered to be disoperations (Kendeigh, 1961).

The distinction between a predator and a parasite is not always clear. In fact, disoperations, wherein one individual or species is benefited at the expense of another, may be viewed as a spectrum grading from obligate parasitism, in which living hosts are necessary for the welfare of the parasite, to predation, in which a free-living animal locates, captures, kills and devours its prey. It is the latter extreme of the spectrum that is of concern here.

Predation is of interest from several points of view: to the student of evolution interested in the adaptive adjustments between prey and predator; to the student of communities interested in

trophic dynamics; and to the student of populations interested in factors limiting population growth (Allee, et al 1949). The emphasis of this dissertation is on the last point of view, but it must be realized that none of these points of view can be studied to the complete exclusion of the others.

Predator control is one of the earliest in a series of controls inaugurated in game management programs (Leopold, 1933). This practice is predicated upon the notion that predators in some way adversely limit the population density of prey, a notion which has agitated more polemic furor than possibly any other biological phenomenon. In general sportsmen and livestock owners, who often favor rigorous predator control in the belief that such control results in higher levels of game abundance and in fewer losses of livestock, are vigorously opposed by 'balance of nature' advocates.

At the opposite extreme, agrarians who often practice the application of insecticides to farm crops because of the actual or assumed ineffectiveness of predation in controlling populations of injurious phytophagous insects, have been severely criticized by students of natural history (Carson, 1962; Egler, 1964a, 1964b; Rudd, 1964) because of the deleterious side effects of the stable organochlorides used as insecticides.

The reasons for these conflicts of opinion center around the debilitating influence of man's activities upon the diversity of natural assemblages of organisms. A decrease in the diversity of species produces a concomitant loss of integrity within a given assemblage which in turn produces instability in the populations of the constituent organisms (Margalef, 1963). It is the instability of

the constituent organisms that attracts the attention of the sportsman, the stockman and the agrarian; each is concerned directly or indirectly with herbivorous populations, and vested interests dictate subsequent courses of action.

Too often the course of action results in unpredictable and irreparable consequences. For example, between the years 1907 and 1923 an estimated 3,805 carnivores (674 cougars, 3,000 coyotes, 11 wolves and 120 bobcats) were removed from the Kaibab Plateau of Arizona (Mann and Locke, 1931, from Russo, 1964). During this same period the mule deer population increased from about 4,000 to an estimated 100,000 animals, thus far exceeding the estimated carrying capacity of 30,000 deer for the plateau. Starvation reduced the herd from 100,000 to 40,000 animals during the winters of 1923-1924 and 1924-1925, and from 40,000 to 10,000 animals between 1925 and 1939 (Leopold, 1943).

The probable solutions, if indeed there are any, to these conflicts of interest lie in research aimed at the development of selective predator control, biological control and less stable pesticides (Leopold, et. al., 1964; Thimann, 1964). Such research, however, has to be based upon an understanding of the basic principles of predator-prey interactions.

Models of Predator-Prey Interactions

Leopold (1933) listed five variables affecting the mortality in a given prey species as a consequence of predation:

- 1) density of the prey population
- 2) density of the predator population

- 3) characteristics of the predator (e.g., its food preferences)
- 4) characteristics of the prey (e.g., its escape mechanisms)
- 5) abundance and quality of alternative prey.

The well known deterministic predator-prey equations of Lotka and Volterra (Andrewartha and Birch, 1954) deal with the first two of Leopold's variables. Animals in the Lotka-Volterra equations must conform to the following assumptions:

- 1) They move about at random to one another.
- 2) Every encounter of a predator with a prey results in the capture and consumption of the prey.
- 3) Isolated populations of either predator or prey manifest sigmoid growth--conform to the logistic theory.

The Lotka-Volterra equations predict that the population densities of such animals fluctuate periodically, the predator population lagging behind the prey population.

A number of laboratory experiments (reviewed by Andrewartha and Birch, 1954) designed to demonstrate empirically the validity of the Lotka-Volterra model have largely failed. In each case an initial increase of the prey population was followed by an increase in the predator population; thereafter, both populations would peak and then decline as predicted by the model. Inevitably, however, the predators would completely exterminate the prey, then starve, the reason being, presumably, that the experimental systems were too simple.

Rosenzweig and MacArthur (1963) propose that the limitation of the population density of predators below the level that would be

imposed by the supply of prey confers stability on predator-prey interactions. That is, when a resource such as space, the number of observation posts, etc., is more limiting than the supply of prey, the population density of the predators can never reach a level sufficient to overexploit the available prey and effect a decrease in prey density. Thus stability ensues if the predator can increase only when the prey are quite abundant, and instability ensues when the predator is as efficient at capturing prey that the predator increases even when prey are scarce. Additional complicating factors such as prey refuges, alternate prey, a predator "ceiling" imposed by territoriality, etc., all dampen the fluctuations in population density of predator-prey interactions.

Gause (1934) studied the predator-prey interactions between Didinium and Paramecium in the laboratory. He complicated the system by periodically adding prey, thereby simulating the immigration of prey from protective refuges. In so doing he induced two complete predator-prey cycles. More recently Huffaker (1958) conducted a set of experiments to demonstrate the effect of complicating the environment of a predator-prey system. He used two species of mites: one was phytophagous and fed on oranges, while the other was predaceous and fed on the phytophagous mite. In experiments in which both predator and prey were allowed to wander freely from orange to orange, the predator located and exterminated the prey and then died out. In experiments in which the movements of the prey, which had the ability to disperse from high places on strands of silk, were speeded relative to the movements of the predators, which are unable to move on strands of silk, the predator was unable to exterminate

the prey, and three complete predator-prey oscillations resulted. The prey were evidently able to colonize previously unoccupied oranges and build up local populations from which emigrants could move and colonize other oranges at a slightly faster rate than the predators could locate and exterminate the concentrations of local prey.

Thus, the Lotka-Volterra equations seemingly predict the outcome of two-species predator-prey systems under environmental conditions sufficiently complex to reduce predator efficiency to the point of allowing the escape of enough prey to establish new concentrations while the predators are in the process of exterminating the older concentrations. The clumping manifested by Huffaker's system, however, is not in accord with assumption (1) of the Lotka-Volterra equations, and to this extent the system is not an empirical demonstration of the Lotka-Volterra model.

The periodic fluctuations in population densities of certain arctic microtines, lagomorphs and tetraonids, and of their mammalian and avian predators were once thought to be manifestations of the Lotka-Volterra equations. There is abundant evidence, however, suggesting that populations of herbivores at high latitudes fluctuate more or less independently of the influence of their predators (Elton, 1942; Chitty, 1950; Pitelka, et al., 1955). In general, microtine and lagomorph populations continue to decline, even after their predators have dispersed or starved. Lack (1954a) postulated a relationship between the fluctuations of populations of lagomorphs or microtines and of grouse. He suggested that as lagomorphs or microtines decline in numbers, because of an overutilization of their

food supply, predators ordinarily feeding on the mammals begin feeding on grouse. The grouse cannot long sustain this predation, so their numbers soon begin to decline. Implicit in Lack's theory is that the decline of the grouse population always follows that of the lagomorph or rodent population; Hoffmann (1958) refuted the theory by citing eight cases in which local grouse populations declined ahead of lagomorph or rodent populations in the same area.

General disagreement exists among students of populations as to the nature of the factor or factors, causing the periodic fluctuations of populations of herbivores at high latitudes. While a review of the theories proposed to account for these fluctuations is beyond the scope of this dissertation, there are, broadly speaking, two types of explanations offered: extrinsic theories (Andrewartha and Birch, 1954) and intrinsic theories (Chitty, 1960), or a combination of both (Cole, 1954). In any event, the periodic fluctuations of prey populations at high latitudes are not caused by predation. If anything, predation exerts a dampening effect on microtine oscillations at high latitudes. Koplin (1963) live-trapped simultaneously two separate but comparable microtine populations during a period in the fall when the numbers of the microtines were increasing. Animals in one population were removed, simulating predation, while animals in the other population were marked and released. Trapping during the subsequent spring revealed that the population which had been experimentally "preyed" upon still persisted, while the other population had crashed sometime during the previous winter. Regardless of the factors responsible for periodic fluctuations of herbivore populations at high latitudes, little doubt

exists that their oscillations are responsible for those of predator populations (MacLulich, 1937; Pitelka, et al., 1955).

Nicholson and Bailey (1935) raised three major objections to the Lotka-Volterra model:

- 1) The model fails to allow for any period of delay between the time of predator-prey contact and a later manifestation of the contact. Such delays are known for insect parasitoids where the result of an encounter may be delayed for as much as one generation of the predator.
- 2) The model does not consider differences in age-specific interactions during the life-cycles of either predator or prey.
- 3) The model is based upon two simultaneous differential equations which do not take into account the discontinuities in variation of the various developmental stages during the life-cycles of either predator or prey.

To rectify these shortcomings, Nicholson and Bailey developed a model dealing mainly with the first two of Leopold's variables; animals in their model are assumed to have the following characteristics (from Andrewartha and Birch, 1954):

- 1) The predators are actually parasitoids which deposit their eggs in or on the bodies of their prey.
- 2) The prey are uniformly distributed within a homogeneous environment.
- 3) The predators search for prey at random with respect to other predators.
- 4) The predators have an inexhaustible supply of eggs.

- 5) The predators each have a constant area of search during their lifetime.
- 6) The predators each find a constant proportion of the prey population.

According to the Nicholson-Bailey model, the degree of mortality experienced by the prey as a result of predation is a function of the density of the predator.

Andrewartha and Birch (1954) cite two studies designed specifically to test the Nicholson-Bailey model. One of these was a laboratory experiment involving pupal house flies as the prey and a hymenopteran as the predator. The generation time of both predator and prey and the reproductive rate of the prey were artificially controlled to render the study feasible. In seven generations the system underwent fluctuations in density that approximated very closely the fluctuations predicted by the Nicholson-Bailey equations. One cannot help but question, however, to what extent the artificial manipulations influenced the fit of the observed and the expected data.

The second study involved natural populations of the knapweed gallfly (Urophora jaceana) as the prey and the hymenopterous Eurytoma sp. as the predator. It was assumed from the outset that density-dependent mortality from predation by Eurytoma was the only important factor regulating the gallfly population, even though non-specific mortality factors--those not discriminating between predator or prey--accounted for more than 90 per cent of the annual mortality of the prey. Observed values compared favorably with those predicted by the model. Andrewartha and Birch (1954), however, raise three objections

to this study as an empirical demonstration of the Nicholson-Bailey model:

- 1) The study was conducted in the field, a heterogeneous environment; thus violating premise (2).
- 2) There were two major errors of logic in the calculation and interpretation of the results:
 - a) A value was arbitrarily assigned for nonspecific mortality to make it agree with the remainder of the data collected.
 - b) The "steady density" was calculated from data gathered for only two generations; whereas the estimated reproductive rate of the prey required a minimum of four generations to assure that any two consecutive generations would fall on either side of the "steady density".
- 3) Variability of the samples was large and some of it, skewed; thus, fiducial limits calculated for some of the parameters estimated from the sample were too small.

The Lotka-Volterra and Nicholson-Bailey models have stimulated much research and in this respect have filled for ecologists the role that the theoretical models developed by Fisher and Wright have for population geneticists. The ecological models, however, have not enjoyed the degree of predictive success of the genetical models. Part of the difficulty is that the ecological models were developed from the point of view of classical physics, whereas, the organismal constituents of populations are behaviorally much more complex than the particulate constituents of physical phenomena (Slobodkin, 1965).

Therefore, the predators and prey in the Lotka-Volterra and Nicholson-Bailey models behave more like molecules than like animals.

In a series of recent papers, Holling (1959a, 1959b, 1961, 1963, 1964, 1965, 1966) has set out to develop a model of predator-prey systems that incorporates the qualities of completeness, realism, precision, and generality lacking in the Lotka-Volterra and Nicholson-Bailey models. Holling hopes eventually to analyze all five of Leopold's variables as renamed to correspond with the nomenclature proposed by Solomon (1949). The variables are characterized by their basic components (always present) and subsidiary components (present in some situations and not in others). The variables are the functional response to prey density, the functional response to predator density, the numerical response, and the quality and abundance of alternative prey.

The functional response to prey density is defined as the total number of prey destroyed per predator as a function of prey density. The basic components of the variable are searching rate of the predator, exposure of prey to the predator, and the time spent by the predator handling prey. The basic components produce a response curve, representing the number of prey killed per predator plotted as a function of prey density, that rises with a continually decreasing slope to a plateau. The subsidiary component of hunger, which is subsidiary because some predators continue to kill even when satiated, does not affect the shape of the basic response curve. Two other subsidiary components, learning (the searching image of Tinbergen, 1960) and prey inhibition, as caused by unpalatability of the prey, do modify the response curve. A search image produces an

S-shaped response curve, and an unpalatable prey produces a dome-shaped response curve. A causal relationship between prey density and the reinforcement threshold of learning behavior (equivalent to the threshold of prey security proposed by Errington, 1946 and 1963) is apparently involved in both modifications of the basic response curve. Palatable prey at densities below the threshold of learning are destroyed to a lesser extent than those above the threshold, and unpalatable prey at densities above and below the threshold are destroyed to a lesser extent than those near the threshold. Learning behavior is much more characteristic of vertebrates than of invertebrates, so it is not surprising that the modifications of the basic response curve are known only for vertebrates.

The functional response to predator density is defined as the total number of prey destroyed per predator as a function of predator density. The basic components of this variable are exploitation and interference; both components produce a response curve, representing the number of prey killed per predator plotted as a function of predator density, that declines with a continuously decreasing slope. The component of exploitation originates because of a decreasing prey population. As predator density increases, the chance of locating prey decreases. Interference between predators increases as prey density decreases and predator density increases. One subsidiary component, group stimulation, known as the Allee affect, produces a response curve that initially arises and then declines. No other subsidiary components of this variable have been identified.

The two functional responses can affect the number of predators present, so that a numerical response may arise in addition to the

functional ones. The numerical response, when present, is correlated either directly or inversely with prey density. The total number of prey destroyed is a combination of the functional and numerical responses: the product of the number of prey killed per predator and the number of predators present. The total response is the proportion of the total prey population destroyed by predation plotted as a function of prey density. A direct numerical response produces a curve which increases with a decreasing slope to a peak and then declines with a continually decreasing slope; no numerical response produces either a curve which increases slightly to a peak and then declines, or a curve that simply declines; and an inverse numerical response produces either a curve that increases very slightly to a peak and then declines, or a curve that simply declines.

As of this date, Holling (1966) has presented experimental solutions to the parameters of 77 equations employed in his analysis of the components of the functional response of invertebrate predators to the density of prey. Thus, in order to achieve the desired elements of completeness, realism, precision and generality lacking in the Lotka-Volterra and Nicholson-Bailey models, one also apparently must sacrifice the relative simplicity of the Lotka-Volterra and Nicholson-Bailey models. From the point of view of the field biologist, the utility of mathematical models stems from their ability to predict the outcome of events when parameters derived from field estimates are fed into the formulae underlying the models. Although all three models predict that predators exert a depressing influence on high densities of prey, the Lotka-Volterra and Nicholson-Bailey models cannot be trusted to predict the effectiveness of a given predator in

controlling the density of a given prey; thus one is left with the hope that, even though complex, Holling's approach will provide the field worker with the analytical tools for obtaining more sophisticated answers than previously possible. The final test of Holling's approach will have to wait until he has completed the experimental analyses of the components of the remaining variables, i.e., the functional response of vertebrate predators to prey density, the functional response to predator density, and the numerical response. In the meantime, there are a multitude of field studies dealing with the effectiveness of predators in controlling the density of prey.

Field Studies of Interactions Between Vertebrate Predators and Vertebrate Prey

One of the most convincing situations on record was the previously mentioned increase in the Kaibab deer herd following the slaughter of their canid and felid predators (Russo, 1964).

From a comprehensive review of literature on vertebrate predation Errington (1946) concluded:

- 1) Except in the case of some cervids, the numbers of mammals and birds are much less likely to be influenced by predation than are the numbers of fishes, amphibians and reptiles.
- 2) Canids are the most skillful predators; other mammals and birds are less so; and fishes, amphibians and reptiles are least so.

Behavior is an important characteristic of prey which limits the effectiveness of predation; thus, numbers of territorial species are

influenced less by predators than are numbers of non-or weakly territorial species. The behavior of predators, too, influences the effectiveness of predation. As mentioned earlier, the recognition of prey can lower the threshold of the functional response of predators to the density of prey so that a predator with a learned search image is expected to destroy more individuals of a given prey at low densities than would a predator with more stereotyped searching behavior.

Errington felt that when predation is important, the number of prey exceeds the carrying capacity of the prey's habitat and predators are merely removing the excess prey. Furthermore, he viewed predation as simply one of a number of possible "intercompensatory" mortality factors. That is, prey in excess of the carrying capacity are doomed, regardless of whether they are killed by predation or by one of many other possible factors.

Errington's concept of intercompensatory mortality thus de-emphasizes the importance of predation as a factor controlling prey density. Most of the literature reviewed by Errington dealt with the effects of one species of predator on one species of prey, or the effects of a number of species of predators on a given species of prey, or the effects of a given species of predator on a number of prey species. The Craigheads (Craighead and Craighead, 1956) studied the effects of a number of species of predators on a number of species of prey. They concluded that pressure exerted by the combined action of all the predators in a given area is an important source of mortality for certain species of prey but less so for others. They worked out an index of vulnerability, ranging from 1 for

the most vulnerable prey to 7 for the least vulnerable prey. The index was based upon two major components: "prey density and prey risk." Prey density is the basic component; and prey risk, including the behavioral characteristics of both predator and prey, is the subsidiary component. Prey risk operates with prey density to render a given species of prey more or less vulnerable to predation. The most vulnerable prey were meadow voles (Microtus pennsylvanicus) and the least vulnerable were fox squirrels (Sciurus niger), with Peromyscus, small birds, game birds and rabbits being intermediate in vulnerability. Predators reduced the numbers of the more vulnerable prey in two ways:

- 1) By killing prey during the spring months, predators reduced the breeding stock and thus lowered the number of young prey produced.
- 2) Predators killed prey throughout the year, and the maximal amount of mortality from predators occurred when prey were most numerous; predation thus provided an automatic check on increases in prey density.

The Craigheads calculated that predation by raptors killed 5 per cent of the least vulnerable prey, 4 to 47 per cent of the moderately vulnerable prey, and 22 to 26 per cent of the most vulnerable prey; a given source of mortality annually removing 22 to 47 per cent of the individuals from a population can hardly be thought of as ineffective.

Field Studies of Interactions Between

Invertebrate Predators and Invertebrate Prey

In predator-prey systems among invertebrate animals, especially

involving insects, the limiting influence of predation is more apparent. The evidence, mainly from studies of biological control, is usually fairly straightforward. Typically, an herbivorous insect is accidentally introduced into a new area, where it increases enormously to become an agricultural pest. Sometime later, natural predators of the pest are located and also introduced; the predators then increase and bring about a decrease of the pest, and subsequently both prey and predator continue to exist in much reduced numbers. A classic example involved the control of the mealybug which was accidentally brought from Australia into California, where, following an increase in numbers, the insect became a serious pest in the citrus groves; later a ladybird beetle was also introduced and the predator, after a spectacular increase in numbers, brought the mealybug under control (Nicholson, 1947).

A second, more complicated example involves the control of predators by "hyperpredators". The early stages of an introduction of a braconid predator into New Zealand to control the cabbage riddler moth nearly failed because of the accidental introduction of a pteromalid hyperpredator along with the braconid. New introductions of the braconid accompanied by proper rearing techniques subsequently established the parasite, and it is now considered an important predator of the cabbage riddler (Andrewartha and Birch, 1954).

A number of similar attempts at biological control have also been quite successful, although it has sometimes been necessary to introduce several species of predators to effect a control. Other attempts, however, for one reason or another, have not produced the desired effect. Andrewartha and Birch (1954) cite several examples

where the differential effects of climatic factors on the reproductive and developmental rates of prey and predator may slow the length of time required to complete the life-cycle of the predator relative to that of the prey to such an extent that the predator, which is quite effective in controlling prey in certain areas, becomes ineffective in controlling the same prey in other areas. Other characteristics of the predator may change in relation to equivalent characteristics of the prey to render an otherwise effective predator essentially useless in controlling the insect pest. For example, the speed of dispersal of a ladybird beetle relative to that of its mealybug prey was shown to be so low that the predator was unable to control the prey. However, when reared in insectories and artificially dispersed throughout orchards, the beetle was able to control the mealybug (Clausen, 1951).

Field Studies of Interactions Between Vertebrate Predators and Invertebrate Prey

Buckner (1966), in a review of the field and laboratory studies concerning the influence of vertebrate predators in limiting the numbers of forest insects, presents the following major points:

- 1) All classes of vertebrates have been shown to prey upon forest insects; the higher metabolic demands of homoiothermous vertebrates bestow upon them a much greater potential for the consumption of prey than that possessed by the poikilothermous vertebrates with their lower metabolic demands.
- 2) Birds characteristically exhibit more pronounced

numerical responses to density of their prey than do mammals because of the much greater mobility of birds. Thus, birds destroy more prey than do mammals, even though both predators may show equal functional responses.

- 3) Much of the disagreement among theorists concerning the effectiveness of predation in limiting the numbers of their prey is due to a lack of necessary data: three measurements--prey density, predator density, and the number of prey destroyed by the predators--needed for even the most elementary evaluation are available in only a few predator-prey studies; the reason being that estimates of the measurements are technically difficult to obtain.
- 4) A highly variable mortality factor can have an important limiting influence on populations (Morris, 1957); the predatory actions of birds on spruce budworms have been shown to be quite variable.
- 5) A limited number of studies have suggested that the numerical response of avian predators is sufficiently great to limit significantly pest populations of only low to moderate densities; the numbers of prey in epidemic populations apparently overwhelm the limiting influence of birds.

Efficacy of Predators and Ecological Efficiency

Critics of the effectiveness of predation as a limiting factor

are quick to point out that predators never completely control, i.e. annihilate, a given prey; and advocates, while quick to retort with evidence showing the depressing influence of predators upon prey populations, are ultimately forced to agree. Explanations of this fact usually involve the inability of predators to find the last surviving prey, the effect of alternate prey in diverting the attention of predators from the primary prey, etc. These explanations, although logically appealing and based upon evidence, still beg the question of why the seemingly selfish process of natural selection does not lead to adaptations in predators for harvesting the additional prey that appear to exist in superabundance, despite the predation.

Slobodkin (1959, 1960) and coworkers (Richman, 1958; Armstrong, 1960) have provided experimental evidence suggesting that predator-prey systems maintain an overall ecological efficiency--defined as the ratio of calories of prey eaten by predators per unit time to the calories of food eaten by prey per unit time--of approximately 10 per cent. That is, prey convert about 10 per cent of the food they eat into surplus prey population which can be harvested by predators without harming the future production of prey. Ecological efficiencies calculated from field data, although much less precise than those from laboratory data, range from 5.5 to 13.3 per cent, values well within the experimentally derived value of 10 per cent. Thus it appears as if natural selection, instead of leading to adaptations for harvesting of prey which would result in overexploitation of prey followed by reduction in yield, as might be expected, rather leads to adaptations for harvesting prey that maintain the highest yield of prey possible.

Competition and Niche

Surprisingly few population ecologists have considered the competitive disoperations implied in studies on the limiting influence of predators on prey populations. More than two decades ago Lack (1945, 1946) suggested that when the diets of two congeneric predators include common prey in excess of 5 per cent, the predators must be exploiting the commonly utilized prey in fundamentally different ways. Lack's postulate has been substantiated by the recent recognition of the phenomenon of character displacement (Brown and Wilson, 1956) and the subsequent elaboration of the principle of competitive exclusion (Hardin, 1960). Investigators studying the combined effects of two or more closely related predators on a single species of prey are obligated to consider the inevitable question of how the predators are able to share the same resource in apparent violation of the principle of competitive exclusion.

Much difference in opinion exists over the meaning of the term 'competition' (Andrewartha and Birch, 1954; Birch, 1957). According to Park (1962), "It is often held that competition is mediated by two component, but different, processes. The first is called 'exploitation'; the second, 'interference'. Exploitation operates when the organisms draw upon a particular resource (food, say) which is present in limited supply. The more limited this resource, and the larger the population draining it, the greater is the intensity of competition. Interference operates when interactions between organisms affect their reproduction or survival. For example, imagine two populations one of which is small and the other crowded. Assume further that more food is available for both

populations than can be used . . . The small group obtains adequate nourishment but the crowded group does not, for the reason that its members so disturb each other that the opportunity to feed is restricted. If this causes a decrease in birth rate, or an increase in death rate, interference can be said to be functioning." So defined, the terms exploitation and interference are identical to the same terms used by Holling (1961) to denote the basic components of the functional response to predator density; and to this extent the concepts of competition and of functional response to predator density are equivalent.

It has been possible to demonstrate competition only in laboratory situations, and then only by inference. Many studies on competition (Gause, 1934; Gause and Witt, 1935; Crombie, 1945, 1947; Frank, 1952; Istock, 1966) have set out to determine under equivalent physical and chemical conditions of environment how the attributes of populations of two species such as reproductive rate, age composition, and sex ratio differ when the two species are cultured separately as compared to when the two species are cultured together. Typically, in combined culture, one species 'competes' the other into extinction; the winning species then achieves a population level comparable to that when cultured in isolation.

As with predator-prey systems, there are deterministic mathematical models which ostensibly predict the outcome of competitive systems; and of these the simultaneously differential equations of Lotka and Volterra are the best known (see Gause, 1934). Under certain environmental conditions, however, it is not always predictable which species will win (Park, 1948), but in such situations one

species always has a higher probability of winning than the other (Park, 1954a, 1954b; Neyman, et al., 1958). Thus, there is an indeterminant element in competitive systems not predicted by the deterministic models. Andrewartha and Birch (1954), in addition to giving the previously mentioned criticisms of the predator-prey equations of Lotka and Volterra, have also criticised the competitive equations of Lotka and Volterra. They question the validity of assigning biological meaning to the proportionality constants unique to each equation; they also point out the irrationality of giving different meanings to dependent variables common to the equations; finally, they suggest that by ignoring the limitations of the equations, experimenters have erroneously confirmed results predicted by the models. Taken literally, therefore, the models may be more misleading than helpful in predicting the outcome of interspecific interactions. Nevertheless, as was shown to be the case for Holling's equations, the designing of models to account for all conceivable variables results in extremely complex mathematical analyses, and the need for some kind of basis from which to work would seem to justify use of the deterministic models so long as they are not applied beyond the scope set by the limitations of the models (Odum, 1959).

The demonstration of interspecific competition in natural populations is a much more difficult proposition. The evidence in support of competitive exclusion, however, strongly suggests the previous existence of competition. There are six main sources of evidence (Orians and Collier, 1963):

- 1) Careful study of closely related sympatric species has

usually revealed important ecological differences.

- 2) Closely related species are morphologically and ecologically more different in areas of sympatry than in areas of allopatry.
- 3) Animals on faunally impoverished mountains and islands nearly always occupy a wider range of habitats than their continental counterparts, which must partition the available resources with a full faunal complement.
- 4) A limited number of studies suggest that there are fewer closely related species cohabiting communities than would be expected if species were distributed at random.
- 5) There is a rather consistent logarithmic relationship among the relative abundances of breeding birds; this distribution is expected if niches are essentially contiguous and nonoverlapping.
- 6) Agonistic interactions between species under natural conditions probably evolved in response to selective pressures from competitive interactions.

Fundamental to an understanding of competition is an understanding of the concept of niche. One of the earliest ideas about the relationship between competition and niche is discussed by Darwin (1859). In a carefully defined application of the Malthusian term 'struggle for existence,' Darwin distinguished intraspecific from interspecific relations by referring to the differential degree of severity between the two. He concluded that intraspecific interactions are more intense because conspecific individuals ". . . frequent the same districts, require the same food, and are exposed to the same

dangers." He also recognized that competition between congeneric species would be more severe than competition between more distantly related species because of the greater similarity in habits, constitution and structure in the former than in the latter.

Grinnell (1917, 1924) coined the term 'ecological niche' and initially conceived of an animal's niche as its spatial and temporal limitations within a particular set of physical environmental factors; later, Grinnell (1928) extended his concept of niche to include food and enemies as well. Elton (1927) felt that an animal's functional position in the biotic community--its relation to food and enemies--defined the niche of the animal. Niche is currently viewed as an elaboration of these basic premises; the niche of a particular species is dependent upon both physical and biotic factors, as well as structural, physiological and behavioral adaptations (Kendeigh, 1961; Lindsdale, 1957).

In a recent formalization of niche, Hutchison (1957) stated that the upper and lower limits of the set of physical and biological variables relevant to the life of a given species, plotted on a multivariate coordinate system, produces an n-dimensional hypervolume. Every point in the hypervolume corresponds to a set of values of the variables permitting the species to exist. If no competitors are present, the hypervolume defines the fundamental niche of the species. If a number of closely related species are living together, the hypervolumes of each species will generally be smaller than the hypervolumes delimiting their fundamental niches because, by the principle of competitive exclusion, no point in one hypervolume is also in another. The smaller hypervolume thus defines the realized niche of

a given species. Several practical difficulties are associated with Hutchison's model of the niche: the probability of maintenance of a steady state of existence must be considered at each point in the hypervolume rather than the all-or-none existence implied; also, linear ordering of every variable delimiting the hypervolume is impossible. However, these difficulties are minor compared to the utility of the model for it permits unequivocal statement of the fact that the actual set of variables determining the existence of a local population is a subregion of the more broadly defined fundamental niche peculiar to the species (Slobodkin, 1961). Thus, the realized niche of a local population of a broadly adaptable species with a 'large' fundamental niche would be expected to be much smaller when compared to the fundamental niche of the species than would the realized niche of a local population of a highly adapted species with a 'small' fundamental niche. Also it is not necessary to order every variable to define the niche of a given species; in fact, linearly ordering as few as two variables permits an operational definition of niche. For example, Miller (1964) studied the influence of soil depth and soil texture on the distribution of four closely related species of pocket gophers. The optimal conditions for all four species are provided by deep, light textured soils; when in competition the gophers can be arranged in a series of decreasing competitive ability: Geomys bursarius, Cratogeomys castanops, Thyomomys bottae and T. talpoides, the first species tending to displace all the others and the last none, in favorable habitats. The last species is the most adaptable, as it can live throughout the complete range of soil depths and soil textures, and it has the widest fundamental

niche; whereas, the first is the most adapted, as it can live only in the optimal habitat, and it has the narrowest fundamental niche.

Summary Statement of the General Theory

The foregoing considerations suggest that populations of two species predator-prey systems cannot persist in the absence of complicating factors. In these simple systems, the predators locate and exterminate every individual of the prey and then starve.

The addition of prey refuges results in persistence of the system, but the populations fluctuate wildly and periodically. The addition of another complicating factor, such as alternative prey, additional species of predators, ceilings to the population density of predators, etc., depresses the amplitude of the fluctuations. The addition of a third complicating factor depresses even further the amplitude of the fluctuations; in fact, each complicating factor that is added exerts a dampening influence on the amplitude of the fluctuations.

Many field studies have shown that predators usually kill less than 50 per cent of the animals in a given population of prey. Predators don't utilize larger percentages of their seemingly superabundant prey because maximum yield of prey results when approximately 10 per cent of the food energy consumed by the prey is utilized by the predators in the form of prey animals.

Many field studies have implied that a given species of prey was being utilized by more than one species of predator. By the principle of competitive exclusion, when the prey is limited in supply, the different species of predators must be utilizing the

common prey in fundamentally different ways.

With the previously developed concepts and principles in mind, it is now practicable to describe this study on the predatory relationships between populations of the Northern Three-toed, Hairy and Downy Woodpeckers and an endemic population of the Engelmann spruce beetle.

METHODS

Study Area

The field portion of this study was conducted in the vicinity of Deadman Lookout in the Red Feather District of the Roosevelt National Forest. The study area is located nine airline miles west-northwest of Red Feather Lakes, Larimer County, Colorado at an elevation of from 10,000 to 10,800 feet. The majority of observations were made in sections 13, 14, 23 and 24 of Township 10 North, Range 75 West; and sections 18 and 19 of Township 10 North, Range 74 West. The forest, situated on a rather flattened north-south oriented ridge draining the headwaters of the North Fork of the Cache la Poudre River to the east and the headwaters of Deadman Creek to the west, is a subalpine stand. Engelmann spruce, Picea engelmanni, subalpine fir, Abies lasiocarpa and lodgepole pine, Pinus contorta, are the most important trees in the area. A few wind-blown specimens of limber pine, Pinus flexilis, grow out of the rocky soil near the tower and about the perimeter of the large natural clearing south of the tower. Several small isolated patches of stunted quaking aspen, Populus tremuloides, grow from crevices in the rocks east of the tower. Within the last 20 years portions of the area have been logged by clear cutting (see Fig. 1); previous to that it had been selectively logged.

Measurement of Forest Composition and Stand Density

In order to obtain a quantitative description of the coniferous

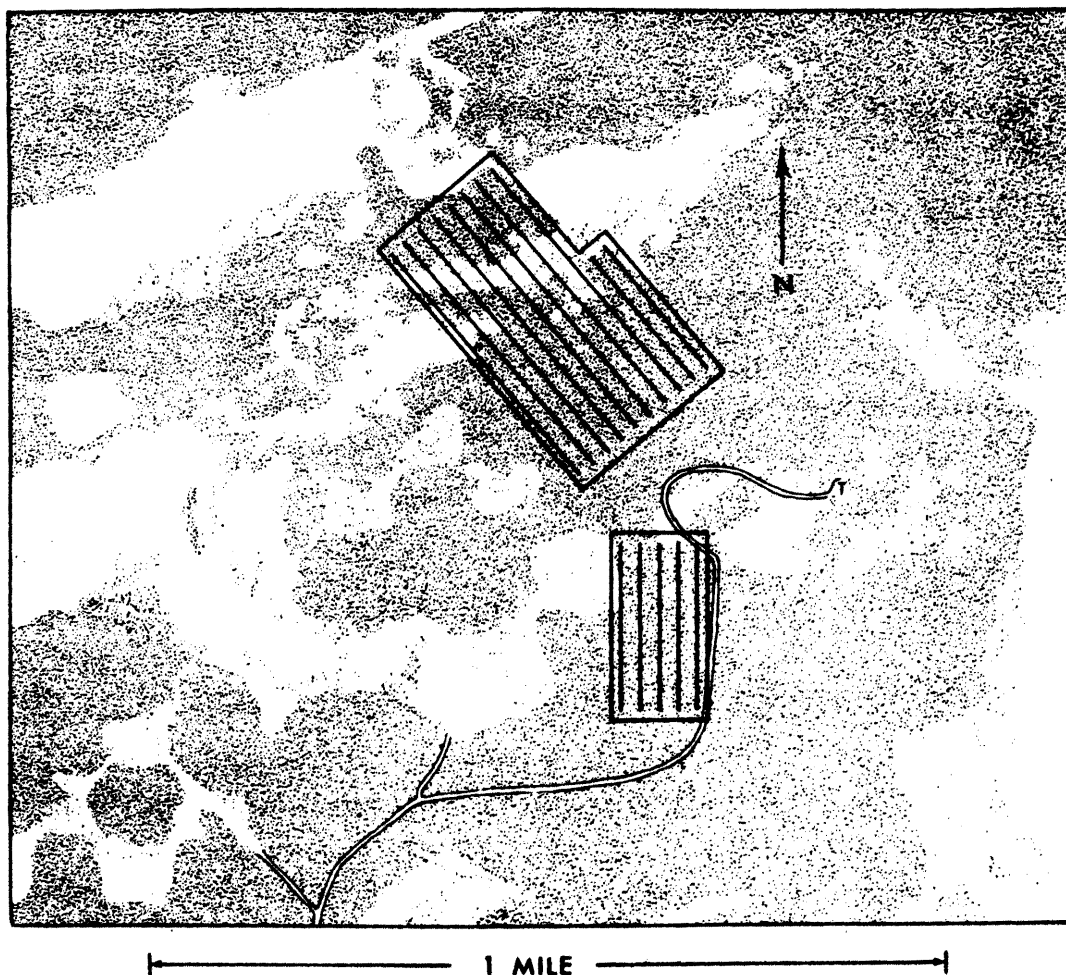


Figure 1. Map of the study area in the vicinity of Deadman Lookout (T), showing the relative positions of the two fixed-width census plots. Stippling represents forested areas.

vegetation on the study plot, a phytosociological study was conducted by means of the quarter method. Of four distance methods compared for describing forest vegetation, Cottam and Curtis (1956) found the quarter method to be the best in most respects. To describe a stand of forest vegetation by means of the quarter method, a minimum of 25 points separated from each other by at least 50 feet are chosen along a predetermined compass line. At each point the space around the point is divided into four quarters, with the compass line of traverse as one bisect and another line perpendicular to this and through the point as the other. Within each quarter, the tree nearest to the point is chosen, its distance in feet from the point, its basal area and its species determined. For absolute density per acre, all of the individual distances are summed and divided by four times the number of points used. This gives an average distance which is equal to the square root of the mean area occupied by all the trees under consideration. The value of the average distance squared, therefore, when divided into the number of square feet per acre (43,560) gives the total number of individuals per acre. This total density when multiplied by the relative density of each species gives the absolute density of that species. The relative density of each species is the number of individuals of one species as a percentage of the total number of individuals of all species.

For this study, 120 points were chosen, 55 oriented in a north-south direction on the woodpecker census plot southwest of the tower; the remainder oriented north 40° west, on the census plot northwest of the tower (see Fig. 1). The interval between points varied from 56 feet on the southwestern plot to 66 feet on the

northwestern plot. Only trees, living or dead, having a diameter at breast height (DBH) of six or more inches were recorded. Trees less than six inches DBH and more than four feet tall were considered saplings, and their density was estimated by measuring the distance from the point to the nearest sapling, regardless of the quarter in which it fell and determining the average point-to-sapling distance for all 120 points. This average distance was squared and then divided into the number of square feet per acre to give the density of saplings per acre. Trees less than four feet tall were called seedlings, and their density was determined by counting the number occurring in quadrats, one yard-square, centered on each point.

Records of wind thrown trees were kept for the two previously mentioned woodpecker census plots. From these it was possible to calculate the rate of wind throw.

Temperature Records

A maximum-minimum thermometer was placed on the study area inside the forest on December 15, 1962; a second was installed on the tower on July 31, 1963. These instruments were read whenever practicable.

Techniques for Manipulating the Spruce Beetle Population

An initial phase of this investigation was the felling of 22 Engelmann spruce trees in October 1961. This was done in my absence by Drs. N. D. Wygant and P. H. Baldwin, and Mr. W. H. MacCambridge. In addition, 20 spruce were felled in October, 1962 and 15 in September, 1964. These logs served to attract Engelmann spruce beetles emerging as adults during the spring and summer months after

the trees had been felled. Since trees felled in the autumn of 1961 were invaded by beetles emerging in June and July of 1962, these logs were then referred to as 1962 trap logs. Spruce trees felled in October 1962, were referred to as 1963 trap logs, etc. Similarly, wind thrown trees were dated according to the year in which they were initially invaded by bark beetles. For example, a tree wind thrown between the months of July 1961, and June 1962 was called a 1962 blowdown, since it would have been initially invaded by bark beetles emerging during the spring of 1962. No 1964 trap logs were felled since it was desired to force Engelmann spruce beetles emerging then to invade standing spruce trees on the study area.

Bolts of spruce, brought to the study area from Wolf Creek Pass and containing the brood of spruce beetles due to emerge in the spring of 1964, were lashed to four standing spruce trees and enclosed in aluminum insect screen to imprison the emerging beetles. It was expected that these beetles would penetrate the bark of the living trees and thus set up sites of attraction for spruce beetles emerging from the 1962 trap logs and blowdowns on the study area. This method had been used successfully by W. H. MacCambridge (pers. comm.) to direct the pattern of attack of the Black Hills beetle, Dendroctonus ponderosae Hopk.

Spruce Beetle Census Technique

Engelmann spruce beetle populations were sampled by making late fall and early spring counts of the larvae, pupae, and adults surviving under six-inch square blocks of bark in a number of trap logs.

The effect of woodpecker predation on the beetle population was estimated by comparing the number of beetles surviving under bark exposed to woodpecker predation with the number surviving under bark protected from woodpecker predation. This method was adopted by Hutchison (1951) in his analysis of woodpecker predation upon epidemic populations of the Engelmann spruce beetle. Sections of bark were screened with one-quarter inch hardware cloth raised an inch or slightly more above the surface of the bark by wooden blocks to safeguard the beetles underneath from woodpecker activity. Four of the 1962 and five of the 1963 trap logs were screened in this manner. Two pairs of six-inch square samples of bark were removed from these logs during the spring. One sample from each pair was taken from bark protected by the hardware cloth, and the other from adjacent bark outside of the hardware cloth.

Woodpecker Census Techniques

Two permanent woodpecker census plots were established on the study area. One, hereafter referred to as the small census plot, was placed southwest of the tower between the road on the east and a clearcut on the west (Fig. 1). The plot was laid out in a manner similar to that recommended by Amman (1958) as the best method for sampling low-density woodpecker populations. The area was divided into five parallel lines, oriented in a north-south direction, 112 feet apart, and each with 21 stations 56 feet apart. The lines were laid out using a hand compass for direction and a 56-foot piece of clothesline rope for length. Each tree nearest successive 56-foot intervals along each transect was marked with blue exterior house

paint. The paint was thinned 50 per cent with turpentine and applied with a household fly sprayer.

The second census plot, northwest of the tower (Fig. 1), was laid out in a similar manner and is hereafter referred to as the large census plot. The ten lines in this plot ran north 40° west, were separated by a distance of 132 feet, and had a station interval of 66 feet. The two easternmost lines had only 19 stations each, since a natural clearing to the northeast precluded further extension of these lines in that direction. The remaining eight lines had 37 stations each.

Amman (1958) stated that under good conditions an active woodpecker can be detected for a distance of one chain--about 66 feet. Therefore, in order to estimate the total area censused, a strip one chain wide was added to the north and south ends of both plots. At the corners of the census plots, however, the scanning process was assumed to encompass a quarter circle, so the area of a quarter circle with a radius of 66 feet was added to each corner. Similarly, the effective census width of the east and west perimeters of the small census plot was 66, rather than 56 feet. Thus, the effective census area of the small census plot was estimated to be 16.6 acres and that of the large census plot, 65.2 acres. The natural clearing in the latter plot was 10.5 acres; therefore, only 54.7 acres of coniferous forest (woodpecker habitat) was censused. The value of 54.7 acres was used in subsequent considerations of this census plot.

In conducting a census on either of the two permanent plots, the length of every line was slowly walked and brief stops were made

at each station where the surrounding vegetation was scrutinized for the presence of woodpeckers. When a bird was detected its approximate position and the time detected were recorded on a mimeographed map of the plot.

Strip censuses were also conducted, during which a rather arbitrary route was followed through both forested and open terrain. The route was marked on maps traced from aerial photos of known scale. A map recorder was later traced over the route and its reading proportionally compared to the scale to estimate the actual distance travelled. The distance to a woodpecker, when first perceived, was paced or visually estimated to the nearest one-quarter chain and then doubled to give the effective census width, which, when multiplied by the length of the route travelled, gave the total area censused. When two or more woodpeckers of the same species were observed during a given census the average census width was used.

Measurement of Realized Niche

Spatial, temporal, dietary and morphological differences are manifestations of niche segregation (Lack, 1945, 1946, 1947; Brown and Wilson, 1956; MacArthur, 1958; Hutchinson, 1959, 1965; MacArthur and Levins, 1964; Schoener, 1965; Selander, 1966).

In order to estimate spatial and temporal differences, every effort was made to determine the species, sex, and age of each woodpecker contacted. The species of tree or snag the bird was observed upon was recorded; finally, the woodpecker's position and length of time observed in that position on the tree or snag was also noted. Snags and prostrate trees were classified according to whether they

had bark or not; if they had bark whether it was peeling or not, because the relative length of time a snag or log has been dead is reflected in the stage of decomposition of its bark. For example, the bark on the 1962 trap logs was very loose and beginning to peel away from the underlying sapwood by the summer of 1964; by the summer of 1965 much of it had peeled completely away from the logs. It is expected that logs will decompose at a faster rate than snags since logs are more exposed to precipitation and moisture, fungi, etc. from the ground.

Through the courtesy of Dr. Paul H. Baldwin, who kindly permitted the inclusion of his unpublished data on the food contents of 215 woodpecker stomachs, it was possible to estimate dietary differences. The data were segregated by species of woodpecker and by sex for the Northern Three-toed Woodpecker. The data were further stratified as to whether the stomach contents came from birds shot in spruce-fir forests with endemic, epidemic, or post epidemic populations of the spruce beetle. Woodpeckers collected in forests supporting endemic populations of the spruce beetle came from a number of localities throughout the spruce-fir forests of Colorado and western Montana; woodpeckers collected in forests with epidemic populations of the spruce beetle came from Wolf Creek Pass, Mineral County, Colorado; and woodpeckers collected in forests with post epidemic populations of the spruce beetle came from Owl Mountain, Jackson County, Colorado.

Morphological--bill length--differences were estimated from measurements of the culmen lengths (measured from the anterior edge of the nostril to the tip of the culmen) of 200 adult museum specimens

of the three species of woodpeckers. All woodpeckers measured were collected in the Rocky Mountain regions of Colorado and Western Montana, and are in the bird skin collections of Colorado State University, the University of Colorado, the Denver Museum of Natural History, and the University of Montana.

Metabolic Techniques

Standard metabolic rate--the amount of heat produced per unit time from an animal in a healthy, resting, thermoneutral, post-absorptive condition (King and Farner, 1961)--was estimated for each species of woodpecker by measuring the oxygen consumption of each animal and converting this oxygen utilization to heat production. The measurements were made at night, on woodpeckers starved for at least five hours.

Oxygen was fed to the woodpeckers inside a darkened bell jar. The oxygen was metered into the jar from a syringe through a rubber stopper in the lid of the jar. A manometer, partially filled with kerosene and also fitted into the rubber stopper, was used to assure a constant flow of oxygen by manipulating the plunger of the syringe so as to keep the two limbs of kerosene in the manometer constantly level. Activated soda lime was placed in the bottom of the bell jar to absorb carbon dioxide. The temperature inside the bell jar was determined from a thermometer projecting into the jar through the afore-mentioned stopper. The syringe and the thermometer were read every two minutes for a period of ten minutes. At least three such measurements were conducted for each animal. The readings from the last six minutes of all three observations were averaged; the averages

were then adjusted to conditions of standard pressure and temperature, expressed as liters of oxygen consumed per hour and multiplied by 4.825--the number of kilocalories of heat liberated per liter of oxygen consumed--to give the metabolic rate in terms of kilocalories per hour. The bird was weighed so that the metabolic rate could be related to weight.

Later, use was made of the formula given by King and Farner (1961): $M = 74.3(W^{0.074}).744$,

where:

M = metabolic rate in kilocalories per day

W = the body weight in kilograms

to compute standard metabolic rate.

The energy required for a closely restricted captive animal to maintain a constant weight under conditions of constant temperature and photoperiod is called its existence energy (Kendeigh, 1949, 1963). Each measurement of existence energy is conducted for at least three days, during which time the animal is continually exposed to food, the wet as well as the dry weight and caloric content of which is known. The weight of the food remaining at the end of each run is subtracted from the weight of the food provided, the difference being the weight of the food consumed. The caloric content of this amount is the gross energy. The fecal and urinary material is weighed, and its caloric content, called excrement energy, is determined. The difference between the gross and excrement energy is existence energy.

Kendeigh's technique for determining existence energy was adopted to determine the energetics of a higher level of activity, hereafter called exercise energy. The determination of exercise

energy differs procedurally from the determination of existence energy in that not only are movement and activity within the cage permitted, but actually encouraged. Exercise energy was determined for individuals of each of the three species of woodpeckers at several different temperatures and a ten hour photoperiod.

The birds were separately housed in cages, 28 inches high x 12.5 inches wide x 25 inches long (inside deminsions: 24 x 11.5 x 23), constructed of one-quarter inch hardware cloth stapled to wooden frames. A heavy guage wire fence material with a one-half inch to three-quarter inch mesh was placed above the floor of each cage; the fiberboard floor was covered with aluminum foil, to catch the excrement of each run. A spruce bolt, three to four inches in diameter, was placed in each cage for the birds to peck on. The cages were placed inside walk-in refrigerators for each three-day observation period, although one run was made outside the refrigerators in a basement. Each day the lights were turned on at 0700 and off at 1700, Mountain Standard Time.

The woodpeckers were fed living mealworm larvae (Tenebrio sp.) throughout all observations. The wet weight of each feeding was measured in grams to the fourth place, and the dry weight was calculated by multiplying the wet weight by the percent dry weight. The percent dry weight was determined by first measuring the wet weight of a group of larvae and then reweighing them after they had been oven dried at 75° to 100° C for 18 to 24 hours.

Only the dry weight of the excrement could be measured since it always became intermixed with, and had to be separated from chips of wood which the birds continually chiseled off the spruce bolts and

cage frames. The best method was to scrape the excrement from the wood after drying in the oven.

Caloric values of the oven-dried larvae of Tenebrio sp., Dendroctonus obesus and Ips pilifrons Swaine; adults of D. obesus and I. pilifrons; and woodpecker excrement were obtained by measuring their heat of combustion in a Parr oxygen bomb calorimeter (model 13051).

The body weight of each woodpecker was recorded before and after each three day run in order to express the different energetic variables in terms of heat production per unit body weight per unit time.

RESULTS

Forest Composition and Stand Density

A total of 41 conifer seedlings was counted in the 120 quadrats: 22 spruce, 9 fir and 10 unidentifiable, resulting in a calculated density of 1657 seedlings per acre: 888 spruce, 364 fir and 405 unidentifiable. While no lodgepole pine seedlings were tallied in any of the quadrats, they were, nevertheless, observed fairly often.

Sapling densities based upon the point method are: 690 spruce, 598 subalpine firs and 206 lodgepole pines per acre.

The results of the tree study, summarized in Tables 1-3, are presented according to the estimated number and basal area of each species of tree per acre in each two-inch diameter class. The density estimates were obtained by multiplying the total number of each species of tree per acre by its observed frequency in each diameter class. The basal area per acre in each diameter class was calculated by multiplying the estimated number of trees per acre in each diameter class by the average basal area of the respective diameter class.

The densities of the trees were estimated to be: 149 spruce, 46 subalpine fir, and 91 lodgepole pines per acre. The basal areas were estimated to be: 16.7 square feet of spruce, 23.9 square feet of subalpine fir, and 68.3 square feet of lodgepole pine per acre. These estimates, with the exception of those for the lodgepole pine,

TABLE 1. Density and basal area of Engelmann spruce in each two-inch diameter class on the Deadman study area

Diameter class (inches DBH)	6.0-8	8.1-10	10.1-12	12.1-14	14.1-16	16.1-18	18.1-20
Trees/acre	32.4	16.4	24.5	15.8	18.3	15.3	10.4
ESB mort./acre ^a				0.4		1.4	0.4
Total dead/acre	0.8	1.2	1.6	1.8	1.5	1.4	0.4
Total live/acre	31.6	15.2	22.9	14.0	16.8	13.9	10.0
Basal area/acre ^b	8.6	7.2	16.2	14.6	22.4	24.1	20.5
Basal area of ESB mort./acre				0.4		2.2	0.8
Basal area of all mort./acre	0.1	0.5	1.1	1.7	1.9	2.2	0.8
Basal area of live/acre	8.5	6.7	15.1	12.9	20.5	21.9	19.7

^aESB mort. = Trees killed by Engelmann spruce beetles.

^bbasal area in square feet

TABLE 1.--Continued

Diameter class (inches DBH)	20.1-22	22.1-24	24.1-26	26.1-28	28.1-30	30.1-32	32.1-34 ⁺
Trees/acre	6.1	2.6	2.0	1.0	2.0	1.0	1.0
ESB mort./acre ^a						0.4	
Total dead/acre	0.8	0.4				0.4	
Total live/acre	5.3	2.2	2.0	1.0	2.0	0.6	1.0
Basal area/acre ^b	14.7	7.5	6.4	4.0	9.2	5.2	6.9
Basal area of ESB mort./acre						2.2	
Basal area of all mort./acre	1.9	1.2				2.2	
Basal area of live/acre	12.8	6.3	6.4	4.0	9.2	3.0	6.9

^aESB mort. = Trees killed by Engelmann spruce beetles

^bbasal area in square feet

TABLE 2. Density and basal area of subalpine fir in each two-inch diameter class on the Deadman study area

Diameter class (inches DBH)	6-8	8.1-10	10.1-12	12.1-14	14.1-16	16.1-18	18.1-20	20.1-22	22.1-24	24.1-26
Trees/acre	23.2	8.7	5.1	5.0	1.7	1.6				0.4
Total dead/acre	1.6	0.7		0.7	0.7					
Total live/acre	21.6	8.0	5.1	4.3	1.0	1.6				0.4
Basal area/acre ^b	6.2	3.9	3.4	4.6	2.1	2.5				1.3
Basal area of mort./acre	0.4	0.3		0.7	0.9					
Basal area of live/acre	5.8	3.6	3.4	3.9	1.2	2.5				1.3

^b basal area in square feet

TABLE 3. Density and basal area of lodgepole pine in each two-inch diameter class on the Deadman study area

Diameter class (inches DBH)	6-8	8.1-10	10.1-12	12.1-14	14.1-16	16.1-18	18.1-20	20.1-22	22.1-24
Trees/acre	20.8	23.2	17.3	10.9	9.4	5.0	1.5	1.9	1.4
Total dead/acre	1.8	3.0	2.6	1.2	2.9	1.2			0.4
Total live/acre	19.0	20.2	14.7	9.7	6.5	3.8	1.5	1.9	1.0
Basal area/acre ^b	5.6	10.2	11.4	10.1	11.5	7.9	3.0	4.6	4.0
Basal area of mort./acre	0.5	1.3	1.7	1.1	3.6	1.9			1.2
Basal area of live/acre	5.1	8.9	9.7	9.0	7.9	6.0	3.0	4.6	2.8

^bbasal area in square feet

are similar to values published by Oosting and Reed (1952) for a mature spruce-fir forest in the Medicine Bow Range of the Snowy Mountains in Wyoming. The estimates for the lodgepole pine are higher than those found by Oosting and Reed; in addition, there were fewer Engelmann spruce and subalpine fir in the larger diameter classes at Deadman than in the Snowy Mountains. These considerations plus the discovery of numerous old pieces of fire-charred wood and an occasional logged stump in the forest interior suggest that the forest at Deadman had been sufficiently disturbed to reduce significantly the maturity of the forest.

Temperature

The maximum and minimum temperature records from the forest interior are presented in Figures 2 and 3, and from the lookout tower in Figures 4 and 5. Temperatures for the years 1963, 1964 and 1965, are graphed only for the period June 10 to December 27, because the data are most complete for this interval.

The lowest temperature recorded for the study was -32° F during the winter of 1962-1963; -13° F and -19° F were the lows recorded for the winters of 1963-1964 and 1964-1965, respectively. Overwinter highs, occurring sometime between early to mid-December and late March to early April, were 41° , 43° and 42° F, respectively. All overwinter temperatures are from the forest interior because the thermometer on the tower was taken inside each winter.

Wind Thrown Trees

Two hundred-fourteen blowdowns were found during the period June 10, 1963 to August 15, 1965. More than half, or 127, of these

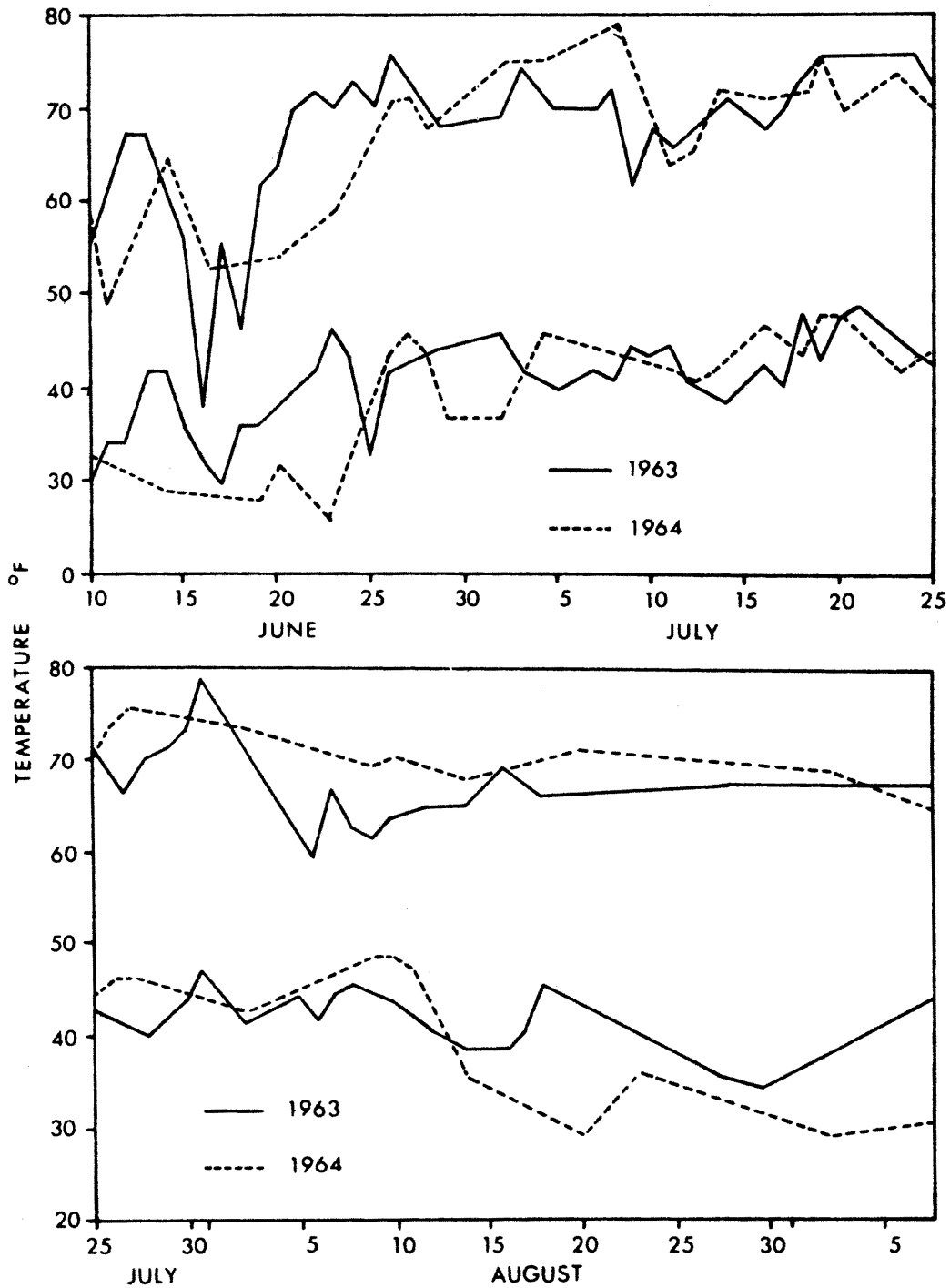


Figure 2. Temperatures recorded within the forest on the Deadman study area for the months June through September. Upper lines represent maxima and lower lines represent minima.

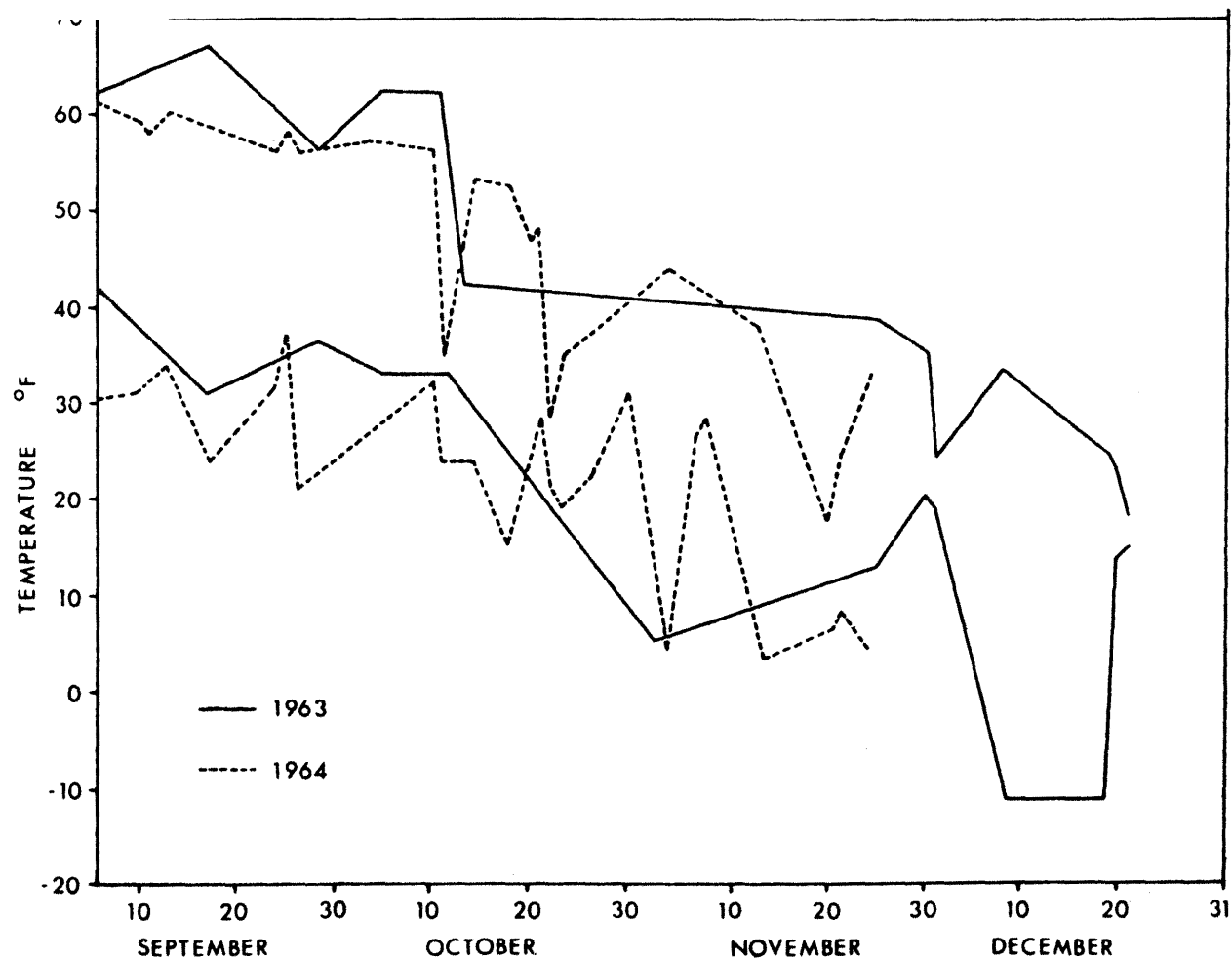


Figure 3. Temperatures recorded within the forest on the Deadman study area for the months September through December. Upper lines represent maxima and lower lines represent minima.

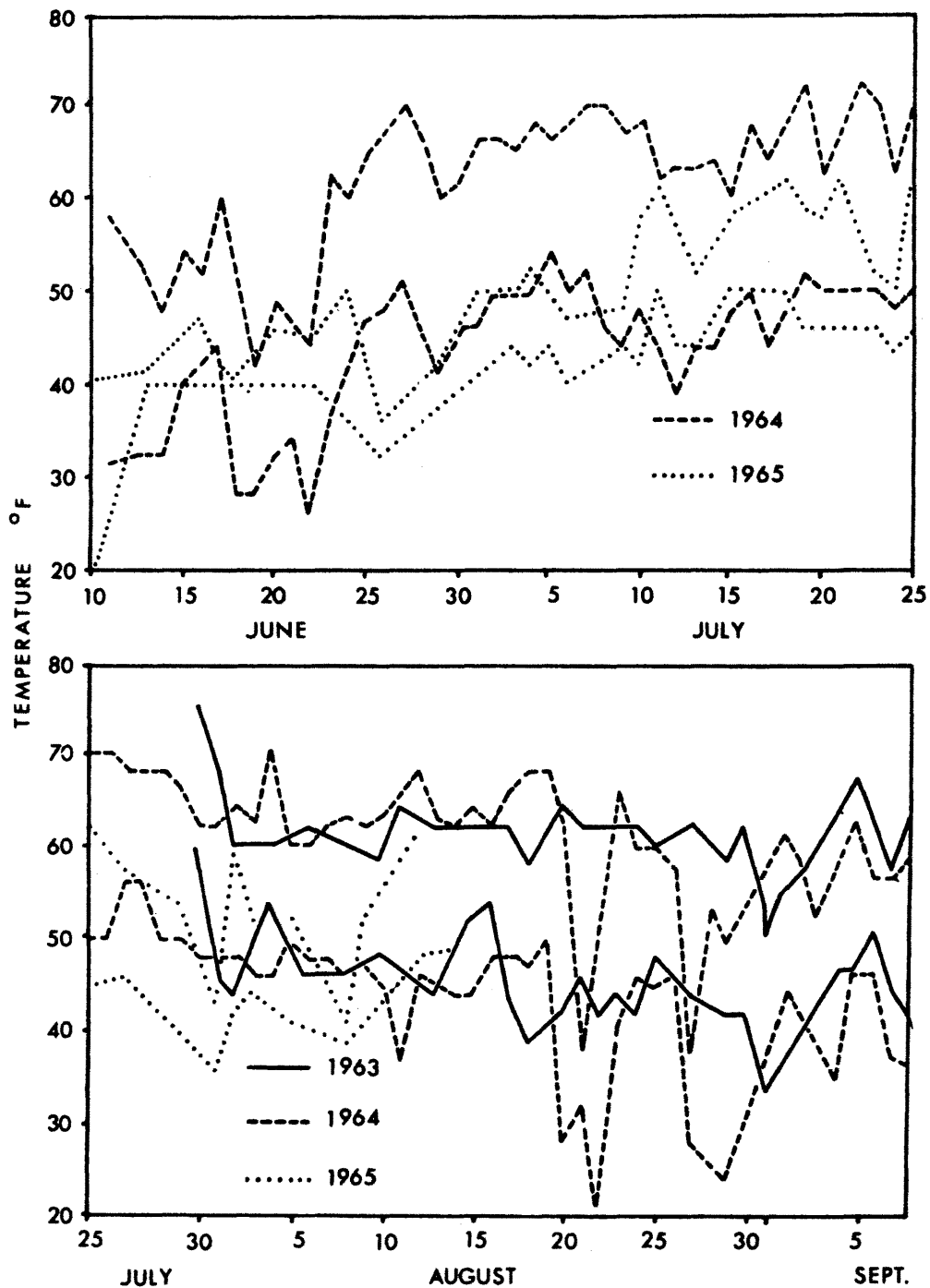


Figure 4. Temperatures recorded on the lookout tower on the Deadman study area for the months June through early September. Upper lines represent maxima and lower lines represent minima.

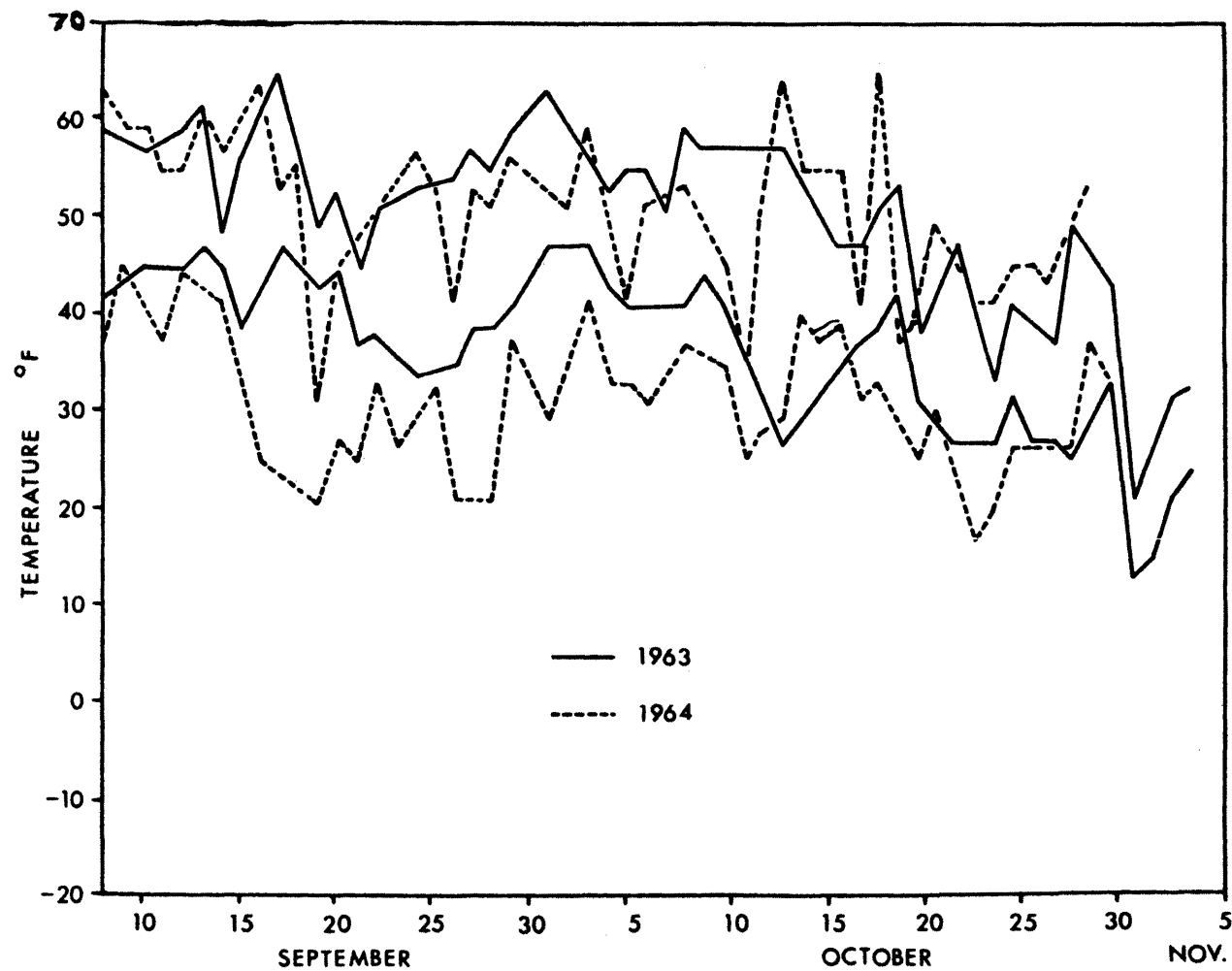


Figure 5. Temperatures recorded on the lookout tower on the Deadman study area for the months September through early December. Upper lines represent maxima and lower lines represent minima.

were encountered on the windward, northwest, edge of the small census plot; 40 were noted on the north and east edges of other clearcuts; only 10 were found on the south and west edges; and the remaining 37 were discovered in widely scattered positions throughout the interior of the forest on the study area.

Table 4 presents the data by species for the year during which a given blowdown was initially invaded by bark beetles.

Bark-Beetle Populations

Figure 6 summarizes the results of the Engelmann spruce beetle censuses. Ninety-five per cent confidence estimates of the mean number of larvae per six-inch sample are shown, and the survival of one-year old and two-year old brood is depicted by the line interconnecting the average value for fall with the average value for spring, which in turn is connected with the average for the following spring. The higher averages for spring represent estimates of the number of larvae surviving beneath areas of bark protected from woodpeckers.

Fall estimates for 1962 and 1963 broods are based upon 13 and 11 samples, respectively. Spring estimates for the 1962 trap trees are based upon 20 pairs of samples for 1963 and 1964, respectively. Spring estimates for the 1963 trap trees are based upon 11 pairs of samples for 1964 and 12 pairs for 1965.

Pairing the samples permitted the use of the sign test, a "strong" nonparametric statistic (Dixon and Massey, 1957), to compare directly the number of larvae in each sample pair. In order to make the sample size as large as possible, all of the brood counts were

TABLE 4. Relative location and year of initial invasion by bark beetles of blowdowns discovered on the Deadman study area

Year invaded by bark beetles	Species of tree wind thrown	Number of trees			
		NW edge of small census plot	North and east edges of other clearcuts	South and west edges of clearcuts	Forest interior
1963	Spruce	29			2
	Fir	6			
	Lodgepole pine	5			
1964	Spruce	23			8
	Fir	5	2		1
	Lodgepole pine	9		1	3
1965	Spruce	31	13	6	6
	Fir	5	15	1	3
	Lodgepole pine	14	10	2	12

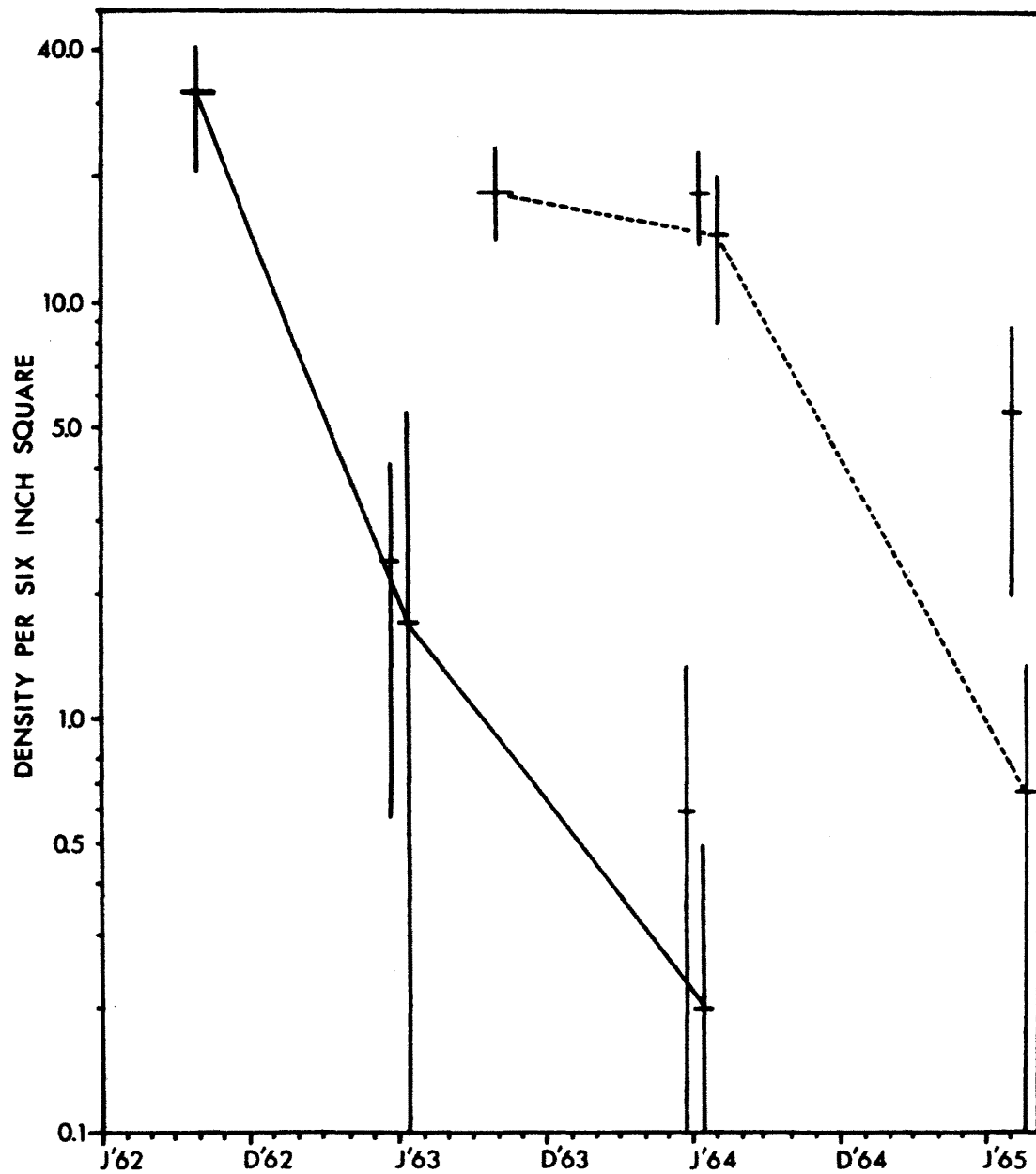


Figure 6. Semilog graph of the densities of Engelmann spruce beetle larvae in trap trees felled on the Deadman study area. Horizontal lines indicate mean values. Vertical lines represent 95 per cent confidence estimates of the means. Lines touching the abscissa extend to 0.

pooled. The sign test is based upon the frequency of signs obtained from sample pairs of unequal size; sample pairs of equal size are excluded, thus reducing the sample size. Nine of the 43 sample pairs were equal, reducing the sample size to 34.

It must be determined if more beetles survived inside than outside the exclosures, in which case the null hypothesis that there are 50 per cent or fewer plus signs can be rejected. Twenty-nine samples of larvae inside the exclosures were larger than those outside, i.e., there were 29 plus and five minus signs. The hypothesis is rejected at less than the .005 per cent level of significance, since this is the level when $N = 34$ and there are only nine or fewer minus signs.

Experiments conducted by Massey and Wygant (1954) showed that 90 to 100 per cent of the larvae of the Engelmann spruce beetle were killed when exposed to subcortical temperatures at or colder than -30° F. Thus the -32° F temperature which occurred during the winter of 1962-1963 is presumably responsible for the first year mortality of 92 per cent, $\frac{30.1 - 2.4}{30.1}$, recorded for the 1962 brood (Figure 6). The brood which emerged during the spring of 1963 must have been similarly affected because fall samples of the 1963 brood revealed an average larval density only two-thirds as large as was found for the 1962 brood (Figure 6).

In any event, all attempts to induce a rising infestation of the Engelmann spruce beetle failed. Beetles emerging from the bolts of spruce lashed to the trees entered the trees as was expected, but they attracted less than a dozen adults emerging from the 1962 trap logs and blowdowns. Other scolytids invading trees damaged by a

ground fire in the fall of 1962, however, provided a rising food supply which attracted the feeding attention of the woodpeckers.

The fire, accidentally set by Forest Service personnell while burning cull logs, killed or injured about ten acres of timber along the perimeters of the clearcuts west and southwest of the smaller woodpecker census plot. Shot holes possibly made by the ambrosia beetle, Trypodendron sp., in the stems of the fire-damaged spruce trees were noted July 29, 1963. On the same date, Ips pilifrons galleries were found in the bark on the exposed portions of the roots of these trees. Woodpeckers were first noted pecking on the fire-damaged trees on September 5, 1963. No further activity was detected until May 8, 1964, when flakes of bark were found in the snow at the base of the snags, indicating feeding attention during the previous winter. The next activity was witnessed on July 9, 1964, when a bird was seen pecking on the stem of a fire damaged spruce; thereafter woodpeckers were observed with increasing regularity on these snags. It was not until early August 1964, however, that it was realized woodpeckers were concentrating on the snags. At this time one of the spruce snags was felled and its insect brood reared to adulthood. Ips pilifrons was the most numerous scolytid in the stem and Pityophthorous sp. the most numerous in the branches. In addition, Scierus annectens Lec. and a hymenopteran, Coeloides sp. were reared out of bolts from the stem.

Subalpine fir and lodgepole pine snags killed by the fire were not checked for bark beetles.

Woodpecker Populations

Eighty-nine variable-width strip and 89 fixed width plot--63 on the small plot and 26 of the large plot--censuses were conducted on the Deadman study area during the period June 1962 to August 1965. Deep, powdery snow prevented access to the study area each winter; subsequent early spring access was possible only by snow vehicle or by snowshoes, and once the area was reached censuses had to be conducted on snowshoes. These difficulties resulted in a lack of data for the months January through March and in limited data for April and May. The results of the woodpecker censuses are summarized in Tables 5, 6, and 7. The data for each month or, in cases of limited data, series of months have been combined. For example, Table 5 shows for the month of August 1963, that 1185.8 acres were censused and 24 Northern Three-toed Woodpeckers were observed. These data are the result of eight strip censuses and three plot censuses for each of the large and small census plots. The values represent cumulative totals, since a woodpecker observed on one census could be detected on subsequent censuses, thus the number of woodpeckers reported for a census period represents total observations and not necessarily total number of individuals observed. Dividing the number of birds observed by the number of acres censused resulted in estimates of the average number of woodpeckers per acre for each census period.

Table 5 summarizes the results of all the census data for woodpeckers, Table 6 presents the results of only the censuses or partial censuses outside the area of the 1962 fire, and Table 7 shows the results of the censuses or partial censuses within the area of the 1962 burn.

TABLE 5. Number of acres censused and woodpeckers observed per census period on the Deadman study area

Census period	Northern-3-toed		Hairy		Downy	
	Acres censused	No. of obs.	Acres censused	No. of obs.	Acres censused	No. of obs.
July '62	212.5	2			143.3	1
Aug-Dec '62	191.7	5	211.4	1		
April-June '63	465.8	3	504.1	1		
July '63	985.4	16	1007.9	5		
August '63	1185.8	24	1033.0	15		
Sept. '63	396.1	8	392.7	7		
Oct. '63	180.1	1	191.5	2		
Nov. & Dec. '63	369.8	4				
Apr. & May '64	347.2	2	480.6	4		
June '64	441.9	1	682.5	1		
July '64	1595.3	21	870.7	5		
August '64	267.2	29	198.9	3		
Sept. '64	385.0	43	436.1	17		
Oct. '64	531.9	27	601.5	3	437.5	3
Nov. '64	486.2	17	502.8	4	440.8	2
Dec. '64	211.9	13	226.0	1	159.4	3
April & May '65	407.5	19			327.2	1
June '65	195.0	2				
July '65	227.7	5				
August '65	228.4	4	271.3	1		

TABLE 6. Number of acres censused and woodpeckers observed per census period outside the area of the 1962 fire

Census period	Northern-3-toed		Hairy		Downy	
	Acres censused	No. of obs.	Acres censused	No. of obs.	Acres censused	No. of obs.
July '62	200.3	2			143.3	1
Aug-Dec '62	186.5	4	206.2	1		
Apr.-June '62	457.4	3	495.2	1		
July '63	925.3	13	952.0	4		
August '63	1104.1	16	963.4	13		
Sept. '63	357.7	3	354.8	7		
Oct. '63	167.3	1	177.9	2		
Nov. & Dec. '63	351.0	2				
Apr. & May '64	306.1	1	429.9	1		
June '64	395.5	0	612.1	1		
July '64	1382.8	13	806.7	5		
August '64	220.0	3	167.6	1		
Sept. '64	313.0	1	350.7	4		
Oct. '64	328.9	1	367.8	0	291.4	1
Nov. '64	345.0	3	301.7	4	303.4	1
Dec. '64	123.7	2	91.5	1	93.4	0
Apr. & May '64	334.2	4			275.4	0
June '65	144.6	1				
July '65	136.5	1				
August '65	170.5	0	194.4	0		

TABLE 7. Number of acres censused and woodpeckers observed per census period within the area of 1962 fire

Census period	Northern-3-toed		Hairy		Downy	
	Acres censused	No. of obs.	Acres censused	No. of obs.	Acres censused	No. of obs.
July '62	12.2	0				
Aug-Dec '62	5.2	1	5.2	0		
Apr-June '63	8.4	0	8.9	0		
July '63	60.1	3	55.9	1		
August '63	81.7	8	69.6	2		
Sept. '63	38.4	5	37.9	0		
Oct. '63	12.8	0	13.6	0		
Nov. & Dec. '63	18.8	2				
Apr. & May '64	41.1	1	50.7	3		
June '64	46.4	1	70.4	0		
July '64	207.5	8	64.0	0		
August '64	47.2	26	31.3	2		
Sept. '64	72.0	42	85.4	13		
Oct. '64	203.0	26	233.7	3	146.1	2
Nov. '64	141.2	14	201.1	0	137.4	1
Dec. '64	88.2	11	98.0	0	66.0	3
Apr. & May '64	73.3	15			51.8	1
June '65	50.4	1				
July '65	91.2	4				
August '65	57.9	4	76.9	1		

The disparity in the number of acres censused for each species of woodpecker in the tables is due to the fact that, during strip censuses, Hairy Woodpeckers were usually perceived at greater distances than Northern Three-toed Woodpeckers, which in turn were perceived at greater distances than Downy Woodpeckers. The average distance of initial perception for each of these species was 1.90, 1.65 and 1.11 chains, respectively. The area censused for a given species of woodpecker could not be estimated unless individuals of that species were observed during the census period involved.

The distance at which woodpeckers were initially detected during strip censuses varied from about 16 feet to an estimated one-quarter mile. This variability is the result of whether the initial detection was by sight or by sound, and if by sound, upon the relative loudness of background noise created by wind blowing through the trees. Visual detections constituted only 18.5 per cent of the total 184 detections. The distance of initial detection by sight varied from about 16 to 330 feet, while the distance of initial detection by sound ranged from 16 feet to one-quarter mile. The variability in distance of detection by sight was a function of the distance at which woodpeckers flushed and whether the birds flushed from within a forested or clearcut area, i.e., birds flushing within forests. The variability in distances of detection by sound was more complicated. Typically, vocalizing woodpeckers could be heard further than drumming woodpeckers; drumming woodpeckers were detectable at greater distances than pecking woodpeckers. Wind velocity further increased the variability of the distance of

detection by sound. For example, the longest auditory detection of one-quarter mile for a vocalizing woodpecker was made on an extremely calm day; the shortest auditory detections involved pecking birds and were made on very windy days.

Figure 7 summarizes the results of the woodpecker censuses and shows a dramatic increase in their numbers during the late summer and fall of 1964. The numbers remained high but decreased gradually throughout the remainder of the winter until the spring of 1965, when they stabilized at a level comparable to former years.

A comparison of Figures 8 and 9 shows that the increase in numbers of the woodpeckers was the result of a numerical response by the birds to the insect prey attracted to the trees killed and damaged by the fire in 1962. The intensity of the response was greatest in the Northern Three-toed Woodpecker and least in the Downy Woodpecker. The Northern Three-toed and Downy Woodpeckers remained on the study area throughout the winter, while the Hairy Woodpecker disappeared between December 1964 and April 1965.

Foraging Behavior

Tables 8 through 11 summarize the observations on the relative use made of each type of tree and on feeding positions occupied by each species of woodpecker. Contingency test analyses (Simpson, et al., 1960: 314-324) were used to determine statistically significant differences. The observations were segregated into two non-nesting periods, one prior to the appearance of Downy Woodpeckers on the study area--mid-July to mid-October--and the other when Downy Woodpeckers were being observed--mid-October to mid-May. These periods

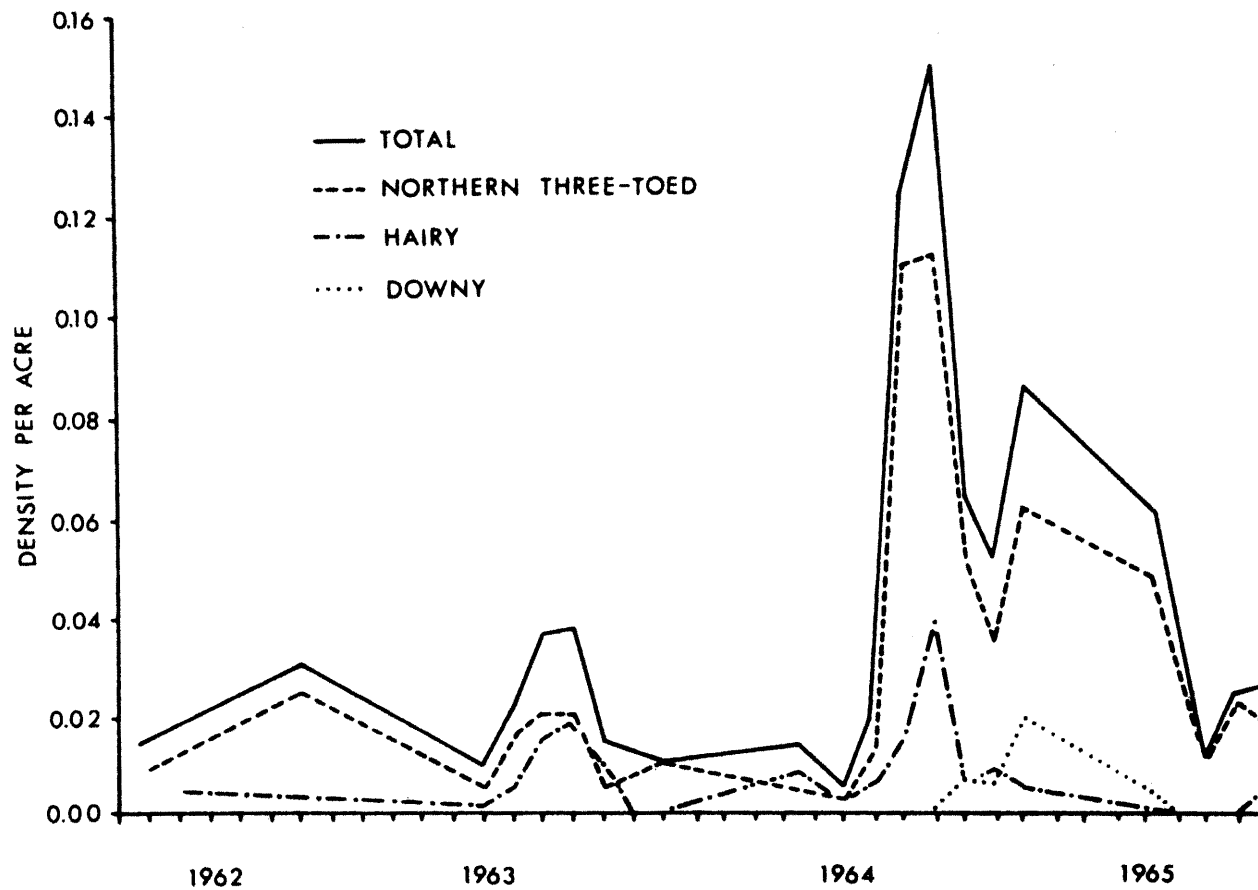


Figure 7. Woodpecker densities on the Deadman study area during the period June 1962 through August 1965.

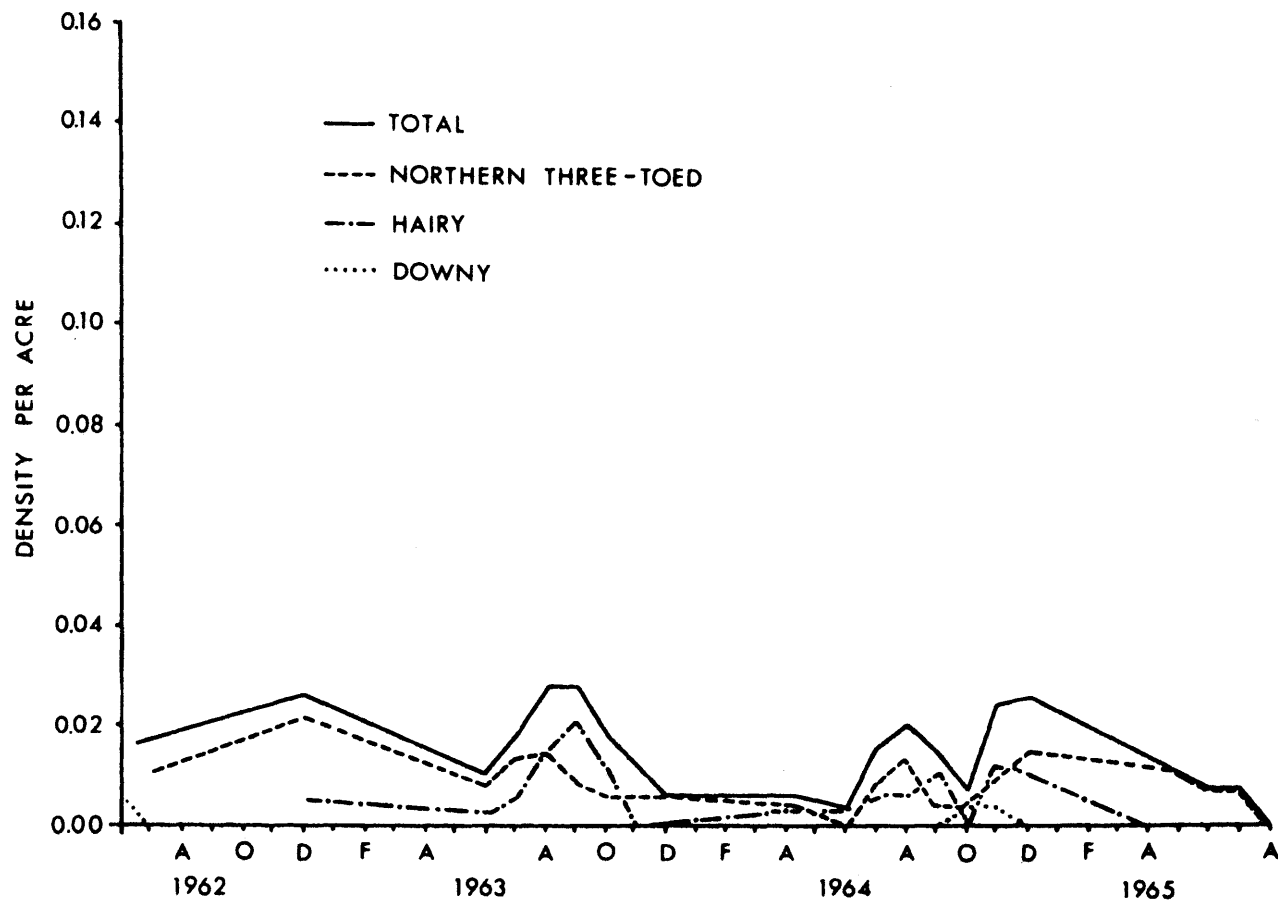


Figure 8. Woodpecker densities on the Deadman study area outside the 1962 burn

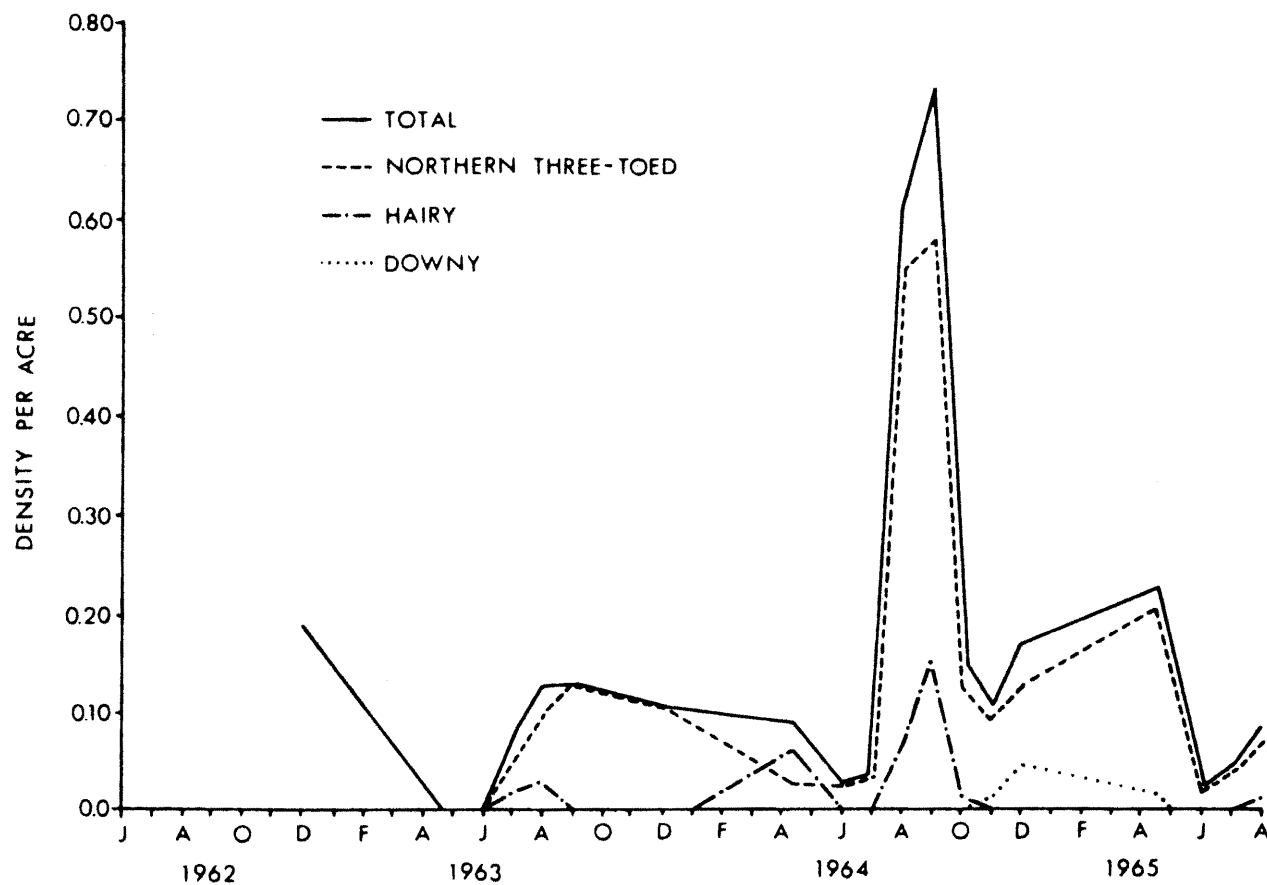


Figure 9. Woodpecker densities on the Deadman study area within the 1962 burn.

TABLE 8. Comparisons of relative use of tree types and of foraging positions within trees for Northern Three-toed (N3T) and Hairy (HW) Woodpeckers for the period July 16 to October 15, 1962 to 1965

Feeding category	N3T		HW		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	94	75.2	19	38.0	37.2 ^a
Subalp. fir	14	11.2	18	36.0	24.8 ^a
Lodgep. pine	17	13.6	13	26.0	12.4 ^d
Total	125	100.0	50	100.0	74.4
Stem	103	91.2	42	82.4	8.8 ^d
Branches	10	8.8	8	15.7	N.S. ^e
Twigs	0	0.0	1	1.9	N.S. ^e
Total	113	100.0	51	100.0	8.8
Height					
0'-14'	49	60.5	8	34.8	N.S. ^e
15'-29'	20	24.7	5	21.7	N.S. ^e
30'+	12	14.8	10	43.5	28.7 ^a
Total	81	100.0	23	100.0	28.7
Green	7	5.1	2	3.5	N.S. ^e
Dead w/bark	122	89.8	28	49.1	40.7 ^a
Dead w/out bark	7	5.1	27	47.4	42.3 ^a
Total	136	100.0	57	100.0	83.0
Upright	113	83.1	51	89.5	N.S. ^e
Prostrate	23	16.9	6	10.5	N.S. ^e
Total	136	100.0	57	100.0	0.0

^a difference significant at .005 level

^b difference significant at .010 level

^c difference significant at .025 level

^d difference significant at .050 level

^e difference not significant

TABLE 9. Comparisons of relative use of tree types and of feeding positions within trees for Northern Three-toed (N3T) and Hairy (HW) Woodpeckers for the period October 16 to May 10, 1962 to 1965

Feeding category	N3T		HW		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	73	76.8	6	60.0	N.S.
Subalp. fir	10	10.5	3	30.0	N.S.
Lodgep. pine	12	12.7	0	0.0	N.S.
Limber pine	0	0.0	1	10.0	N.S.
Total	95	100.0	10	100.0	0.0
Stem	71	81.6	6	54.5	N.S.
Branches	10	11.5	3	27.3	N.S.
Twigs	6	6.9	2	18.2	N.S.
Total	87	100.0	11	100.0	0.0
Height					
0'-14'	34	43.6	2	25.0	N.S.
15'-29'	20	25.6	3	37.5	N.S.
30'+	24	30.8	3	37.5	N.S.
Total	78	100.0	8	100.0	0.0
Green	4	4.1	0	0.0	N.S.
Dead w/bark	92	93.9	7	63.6	30.3 ^b
Dead w/out bark	2	2.0	4	36.4	34.4 ^a
Total	98	100.0	11	100.0	64.7
Upright	84	85.7	10	90.9	N.S.
Prostrate	14	14.3	1	9.1	N.S.
Total	98	100.0	11	100.0	0.0

^adifference significant at .005

^bdifference significant at .010

TABLE 10. Comparisons of relative use of tree types and foraging positions within trees for Northern Three-toed (N3T) and Downy (DW) Woodpeckers for the period October 16 to May 10, 1964-1965

Feeding category	N3T		DW		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	68	78.2	14	93.3	N.S. ^e
Subalp. fir	10	11.5	0	0.0	N.S. ^e
Lodgep. pine	9	10.3	1	6.7	N.S. ^e
Total	87	100.0	15	100.0	0.0
Stem	69	83.1	0	0.0	83.1 ^a
Branches	8	9.6	0	0.0	N.S. ^e
Twigs	6	7.3	16	100.0	92.7 ^a
Total	83	100.0	16	100.0	175.8
Height					
0'-14'	29	42.0	1	7.6	34.4 ^d
15'-29'	18	26.1	6	46.2	N.S. ^e
30'+	22	31.9	6	46.2	N.S. ^e
Total	69	100.0	13	100.0	34.4
Green	3	3.3	0	0.0	N.S. ^e
Dead w/bark	85	94.5	17	100.0	N.S. ^e
Dead w/out bark	2	2.2	0	0.0	N.S. ^e
Total	90	100.0	17	100.0	0.0
Upright	80	88.9	16	94.1	N.S. ^e
Prostrate	10	11.1	1	5.9	N.S. ^e
Total	90	100.0	17	100.0	0.0

^adifference significant at .005 level

^ddifference significant at .050 level

^edifference not significant

TABLE 11. Comparisons of relative use of tree types and of foraging positions within trees for Hairy (HW) and Downy (DW) Woodpeckers for the period October 16 to May 10, 1964-1965

Feeding category	HW		DW		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	4	57.1	14	93.3	36.2 ^d
Subalp. fir	2	28.6	0	0.0	28.6
Lodgep. pine	0	0.0	1	6.7	N.S. ^e
Limber pine	1	14.3	0	0.0	N.S. ^e
Total	7	100.0	15	100.0	64.8
Stem	4	57.1	0	0.0	57.1 ^a
Branches	3	42.9	0	0.0	42.9 ^a
Twigs	0	0.0	16	100.0	100.0 ^a
Total	7	100.0	16	100.0	200.0
Height					
0'-14'	2	33.3	1	7.6	N.S. ^e
15'-29'	3	50.0	6	46.2	N.S. ^e
30'+	1	16.7	6	46.2	N.S. ^e
Total	6	100.0	13	100.0	0.0
Green	0	0.0	0	0.0	0.0
Dead w/bark	4	50.0	17	100.0	50.0 ^a
Dead w/out bark	4	50.0	0	0.0	50.0 ^a
Total	8	100.0	17	100.0	100.0
Upright	7	87.5	16	94.1	N.S. ^e
Prostrate	1	12.5	1	5.9	N.S. ^e
Total	8	100.0	17	100.0	0.0

^adifference significant at .005 level

^ddifference significant at .050 level

^edifference not significant

are also times of relatively high and low food abundances, respectively. So few woodpeckers were seen during the nesting season, roughly from mid-May to mid-July, that foraging data could not be presented for that period.

Tables 12 through 15 compare the time spent by each species on each of the trees and in the various foraging positions. The differences shown are maximal, since statistical analyses were not conducted because of unequal sample sizes. Time is a continuous variable, requiring a parametric statistic for analytical purposes; a factorial analysis of variance, extremely difficult to perform with unequal sample sizes, is called for in this case.

Tables 8 and 12 show that when food resources were most abundant, the Northern Three-toed Woodpecker fed mostly on insects in the basal portions of the stems of spruce snags and the Hairy Woodpecker fed mostly on insects in the middle and upper portions of the stems of all three species of snags, more or less in direct proportion to the relative abundances of the trees at Deadman (Tables 1-3). Both species of woodpeckers fed mostly on insects in the stems of freshly killed snags, but the Hairy Woodpecker fed on older snags to a greater extent than did the Northern Three-toed Woodpecker.

Tables 9 and 13 show that when food resources were less abundant, the Northern Three-toed and Hairy Woodpeckers fed at higher positions on the stems and out onto smaller branches and twigs. The Hairy Woodpecker shifted the majority of its feeding activities from the older snags to the freshly-killed Engelmann spruce snags. The Northern Three-toed Woodpecker fed mostly upon freshly killed spruce snags.

TABLE 12. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Northern Three-toed (N3T) and Hairy (HW) Woodpeckers for the period July 16 to October 15, 1962 to 1965

Feeding category	N3T		HW		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	1,598	80.7	159	32.2	40.5
Subalp. fir	91	4.6	124	25.1	20.5
Lodgep. pine	291	14.7	211	42.7	28.0
Total	1,980	100.0	494	100.0	97.0
Stem	1,574	89.8	384	79.5	10.3
Branches	178	10.2	47	9.7	0.5
Twigs	0	0.0	52	10.8	10.8
Total	1,752	100.0	483	100.0	21.6
Height					
0'-14'	712	67.3	47	22.5	44.8
15'-29'	205	19.4	34	16.2	3.2
30'+	141	13.3	128	61.3	48.0
Total	1,058	100.0	209	100.0	96.0
Green	66	3.2	11	2.2	1.0
Dead w/bark	1,937	93.5	341	67.9	25.6
Dead w/out bark	69	3.3	150	29.9	26.6
Total	2,072	100.0	502	100.0	53.2
Upright	1,752	84.6	483	96.2	11.6
Prostrate	320	15.4	19	3.8	11.6
Total	2,072	100.0	502	100.0	23.2

TABLE 13. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Northern Three-toed (N3T) and Hairy (HW) Woodpeckers for the period October 16 to May 10, 1962 to 1965

Feeding category	N3T		HW		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	1,246	85.6	63	88.8	3.2
Subalp. fir	110	7.6	4	5.6	2.0
Lodgep. pine	100	6.8	0	0.0	6.8
Limber pine	0	0.0	4	5.6	5.6
Total	1,456	100.0	71	100.0	17.6
Stem	1,135	90.3	4	5.6	84.7
Branches	93	7.4	12	16.9	9.5
Twigs	29	2.3	55	77.5	75.2
Total	1,257	100.0	71	100.0	169.4
Height					
0'-14'	607	51.4	4	6.0	45.4
15'-29'	220	18.6	8	12.0	6.6
30'+	355	30.0	55	82.0	52.0
Total	1,182	100.0	67	100.0	104.0
Green	13	0.9	0	0.0	0.9
Dead w/bark	1,472	98.9	64	90.1	8.8
Dead w/out bark	4	0.2	7	9.9	9.7
Total	1,489	100.0	71	100.0	19.4
Upright	1,231	82.7	70	98.6	15.9
Prostrate	258	17.3	1	1.4	15.9
Total	1,489	100.0	71	100.0	31.8

TABLE 14. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Northern Three-toed (N3T) and Downy (DW) Woodpeckers for the period October 16 to May 10, 1964-1965

Feeding category	N3T		DW		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	1,235	85.5	136	84.5	0.1
Subalp. fir	110	7.6	0	0.0	7.6
Lodgep. pine	100	6.9	25	15.5	8.6
Total	1,445	100.0	161	100.0	16.3
Stem	1,108	92.4	0	0.0	92.4
Branches	62	5.2	0	0.0	5.2
Twigs	29	2.4	161	100.0	97.6
Total	1,199	100.0	161	100.0	195.2
Height					
0'-14'	596	52.3	33	24.3	28.0
15'-29'	215	18.9	49	36.0	17.1
30'+	329	28.8	54	39.7	10.9
Total	1,140	100.0	136	100.0	56.0
Green	13	0.9	0	0.0	0.9
Dead w/bark	1,430	98.8	161	100.0	1.2
Dead w/out bark	4	0.3	0	0.0	0.3
Total	1,447	100.0	161	100.0	2.4
Upright	1,199	82.9	156	96.9	14.0
Prostrate	248	17.1	5	3.1	14.0
Total	1,447	100.0	161	100.0	28.0

TABLE 15. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by Hairy (HW) and Downy (DW) Woodpeckers during the period October 16 to May 10, 1964-1965

Feeding category	HW		DW		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	8	50.0	136	84.5	34.5
Subalp. fir	4	25.0	0	0.0	25.0
Lodgep. pine	0	0.0	25	15.5	15.5
Limber pine	4	25.0	0	0.0	25.0
Total	16	100.0	161	100.0	100.0
Stem	5	29.4	0	0.0	29.4
Branches	12	70.6	0	0.0	70.6
Twigs	0	0.0	161	100.0	100.0
Total	17	100.0	161	100.0	200.0
Height					
0'-14'	4	33.3	33	24.3	9.0
15'-29'	8	66.7	49	36.0	30.7
30'+	0	0.0	54	39.7	39.7
Total	12	100.0	136	100.0	79.4
Green	0	0.0	0	0.0	0.0
Dead w/bark	9	52.9	161	100.0	47.1
Dead w/out bark	8	47.1	0	0.0	47.1
Total	17	100.0	161	100.0	94.2
Upright	16	94.1	156	96.9	2.8
Prostrate	1	5.9	5	3.1	2.8
Total	17	100.0	161	100.0	5.6

Tables 10, 11, 14 and 15 show that during the period when Downy Woodpeckers were present at Deadman, the birds fed on insects only in the twigs of freshly killed spruce snags at heights in excess of 15 feet above the ground. The feeding behavior of the Northern Three-toed and Hairy Woodpeckers was essentially the same as described from Tables 9 and 13, except that the Hairy Woodpecker devoted about as much of its feeding attention to older snags as it did to freshly killed ones, and it was not observed to feed on smaller branches and twigs.

Tables 16 through 23 summarize the frequencies of utilization and the amounts of time spent by the sexes of the Northern Three-toed and Hairy Woodpeckers on each species of tree and on each feeding position within the trees. Analysis of intersexual foraging behavior of the Hairy Woodpecker during the interval October 16 to May 10 was not possible, because of the limited number of birds observed, so data for the period July 16 to October 15 and data from the whole study, including the latter period, were analyzed. Also, the numbers of Downy Woodpeckers seen throughout the study were so few that an analysis of the differences in foraging behavior between the sexes was impossible.

Differences in foraging behavior between the sexes of the Northern Three-toed Woodpecker were least when the insect prey was most abundant (Tables 16 and 20), and greatest when the prey was less abundant (Tables 17 and 21). Differences in foraging behavior between the sexes of the Hairy Woodpecker were less pronounced (Tables 18, 19, 22 and 23). The most consistent differences in both species, even though non-significant in the Hairy Woodpecker, involved

TABLE 16. Comparisons of relative use of tree types and foraging positions within trees for female (F) and male (M) Northern Three-toed Woodpeckers for the period July 16 to October 15, 1962-1965

Feeding category	F		M		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	60	71.4	34	82.9	N.S. ^e
Subalp. fir	9	10.7	5	12.2	N.S. ^e
Lodgep. pine	15	17.9	2	4.9	N.S. ^e
Total	84	100.0	41	100.0	0.0
Stem	71	88.8	32	97.0	N.S. ^e
Branches	9	11.2	1	3.0	N.S. ^e
Twigs	0	0.0	0	0.0	N.S. ^e
Total	80	100.0	33	100.0	0.0
Height					
0'-14'	28	53.8	21	72.4	N.S. ^e
15'-29'	16	30.8	4	13.8	N.S. ^e
30'+	8	15.4	4	13.8	N.S. ^e
Total	52	100.0	29	100.0	0.0
Green	5	5.5	2	4.4	N.S. ^e
Dead w/bark	81	89.0	41	91.2	N.S. ^e
Dead w/out bark	5	5.5	2	4.4	N.S. ^e
Total	91	100.0	45	100.0	0.0
Upright	80	87.9	33	73.3	N.S. ^e
Prostrate	11	12.1	12	26.7	N.S. ^e
Total	91	100.1	45	100.0	0.0

^edifference not significant

TABLE 17. Comparisons of relative use of tree types and foraging positions within trees for female (F) and male (M) Northern Three-toed Woodpeckers for the period October 16 to May 10, 1962-1965

Feeding category	F		M		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	30	71.5	43	81.2	N.S. ^e
Subalp. fir	4	9.5	6	11.3	N.S. ^e
Lodgep. pine	8	19.0	4	7.5	N.S. ^e
Total	42	100.0	53	100.0	0.0
Stem	23	61.9	48	100.0	38.1 ^a
Branches	10	23.8	0	0.0	23.8 ^a
Twigs	6	14.3	0	0.0	14.3 ^d
Total	39	100.0	48	100.0	76.2
Height					
0'-14'	14	38.9	20	47.6	N.S. ^e
15'-29'	8	22.2	12	28.6	N.S. ^e
30'+	14	38.9	10	23.8	N.S. ^e
Total	36	100.0	42	100.0	0.0
Green	3	7.1	1	1.8	N.S. ^e
Dead w/bark	39	92.9	53	94.6	N.S. ^e
Dead w/out bark	0	0.0	2	2.6	N.S. ^e
Total	42	100.0	56	100.0	0.0
Upright	36	85.7	48	85.7	N.S. ^e
Prostrate	6	14.3	8	14.3	N.S. ^e
Total	42	100.0	56	100.0	0.0

^adifference significant at .005 level

^ddifference significant at .050 level

^edifference not significant

TABLE 18. Comparisons of relative use of tree types and of foraging positions within trees for female (F) and male (M) Hairy Woodpeckers for the period July 16 to October 15, 1962-1965

Feeding category	F		M		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	9	33.3	10	43.5	N.S. ^e
Subalp. fir	12	44.5	6	26.1	N.S. ^e
Lodgep. pine	6	22.2	7	30.4	N.S. ^e
Total	27	100.0	23	100.0	0.0
Stem	24	85.7	18	78.3	N.S. ^e
Branches	3	10.7	5	21.7	N.S. ^e
Twigs	1	3.6	0	0.0	N.S. ^e
Total	28	100.0	23	100.0	0.0
Height					
0'-14'	3	30.0	5	38.5	N.S. ^e
15'-29'	3	30.0	2	15.4	N.S. ^e
30'+	4	40.0	6	46.1	N.S. ^e
Total	10	100.0	13	100.0	0.0
Green	0	0.0	2	7.7	N.S. ^e
Dead w/bark	17	54.8	11	42.3	N.S. ^e
Dean w/out bark	14	45.2	13	50.0	N.S. ^e
Total	31	100.0	26	100.0	0.0
Upright	28	90.3	23	88.5	N.S. ^e
Prostrate	3	9.7	3	11.5	N.S. ^e
Total	31	100.0	26	100.0	0.0

^edifference not significant

TABLE 19. Comparisons of relative use of tree types and foraging positions within trees for female (F) and male (M) Hairy Woodpeckers for the period July 16 to May 10, 1962-1965

Feeding category	F		M		% Difference
	No. in sample	% of sample	No. in sample	% of sample	
Eng. spruce	13	39.4	12	44.4	N.S. ^e
Subalp. fir	13	39.4	8	29.6	N.S. ^e
Lodgep. pine	6	18.2	7	26.0	N.S. ^e
Limber pine	1	3.0	0	0.0	N.S. ^e
Total	33	100.0	27	100.0	0.0
Stem	27	77.1	21	77.8	N.S. ^e
Branches	5	14.3	6	22.2	N.S. ^e
Twigs	3	8.6	0	0.0	N.S. ^e
Total	35	100.0	27	100.0	0.0
Height					
0'-14'	5	31.3	5	33.3	N.S. ^e
15'-29'	4	25.0	4	26.7	N.S. ^e
30'+	7	43.7	6	40.0	N.S. ^e
Total	16	100.0	15	100.0	0.0
Green	0	0.0	2	6.8	N.S. ^e
Dead w/bark	22	57.9	14	46.6	N.S. ^e
Dead w/out bark	16	42.1	14	46.6	N.S. ^e
Total	38	100.0	30	100.0	0.0
Upright	34	89.5	27	90.0	N.S. ^e
Prostrate	4	10.5	3	10.0	N.S. ^e
Total	38	100.0	30	100.0	0.0

^edifference not significant

TABLE 20. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female (F) and male (M) Northern Three-toed Woodpeckers for the period July 16 to October 15, 1962-1965

Feeding category	F		M		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	924	75.3	674	89.5	14.2
Subalp. fir	42	3.4	49	6.5	3.1
Lodgep. pine	261	21.3	30	4.0	17.3
Total	1,227	100.0	753	100.0	34.6
Stem	986	85.4	588	98.3	12.9
Branches	168	14.6	10	1.7	12.9
Twigs	0	0.0	0	0.0	0.0
Total	1,154	100.0	598	100.0	25.8
Height					
0'-14'	377	57.6	335	83.1	25.5
15'-29'	186	28.4	19	4.7	23.7
30'+	92	14.0	49	12.2	1.8
Total	655	100.0	403	100.0	51.0
Green	46	3.5	20	2.6	0.9
Dead w/bark	1,205	92.9	732	94.6	1.7
Dead w/out bark	47	3.6	22	2.8	0.8
Total	1,298	100.0	774	100.0	3.4
Upright	1,154	88.9	598	77.3	11.6
Prostrate	144	11.1	176	22.7	11.6
Total	1,298	100.0	774	100.0	23.2

TABLE 21. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female (F) and male (M) Northern Three-toed Woodpeckers for the period October 16 to May 10, 1962-1965

Feeding category	F		M		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	688	81.8	558	90.7	8.9
Subalp. fir	58	6.9	52	8.5	1.6
Lodgep. pine	95	11.3	5	0.8	10.5
Total	841	100.0	615	100.0	21.0
Stem	528	81.2	607	100.0	18.8
Branches	93	14.3	0	0.0	14.3
Twigs	29	4.5	0	0.0	4.5
Total	650	100.0	607	100.0	37.6
Height					
0'-14'	268	40.1	339	66.0	25.9
15'-29'	106	15.9	114	22.2	6.3
30'+	294	44.0	61	11.8	32.2
Total	668	100.0	514	100.0	64.4
Green	13	1.5	0	0.0	1.5
Dead w/bark	859	98.5	613	99.4	0.9
Dead w/out bark	0	0.0	4	0.6	0.6
Total	872	100.0	617	100.0	3.0
Upright	624	71.6	607	98.4	26.8
Prostrate	248	28.4	10	1.6	26.8
Total	872	100.0	617	100.0	53.6

TABLE 22. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female (F) and male (M) Hairy Woodpeckers for the period July 16 to October 15, 1962-1965

Feeding category	F		M		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	60	18.9	99	56.3	37.4
Subalp. fir	85	26.7	39	22.2	4.5
Lodgep. pine	173	54.4	38	21.5	32.9
Total	318	100.0	176	100.0	74.8
Stem	231	73.1	153	91.6	18.3
Branches	33	10.4	14	8.4	2.0
Twigs	52	16.5	0	0.0	16.5
Total	316	100.0	167	100.0	37.0
Height					
0'-14'	10	9.0	37	37.8	28.8
15'-29'	16	14.4	18	18.4	4.0
30'+	85	76.6	43	43.9	32.7
Total	111	100.0	98	100.0	65.5
Green	0	0.0	11	6.3	6.3
Dead w/bark	229	70.2	112	63.6	6.6
Dead w/out bark	97	29.8	53	30.1	0.3
Total	326	100.0	176	100.0	13.2
Upright	316	96.9	167	94.9	2.0
Prostrate	10	3.1	9	5.1	2.0
Total	326	100.0	176	100.0	4.0

TABLE 23. Comparisons of total amount of time, in minutes, each tree type and foraging position was occupied by female (F) and male (M) Hairy Woodpeckers for the period July 16 to May 10, 1962-1965

Feeding category	F		M		% Difference
	Min. in sample	% of sample	Min. in sample	% of sample	
Eng. spruce	120	31.4	102	55.7	24.3
Subalp. fir	85	22.3	43	23.5	1.2
Lodgep. pine	173	45.3	38	20.8	24.5
Limber pine	4	1.0	0	0.0	1.0
Total	382	100.0	183	100.0	51.0
Stem	231	60.8	157	90.2	29.4
Branches	42	11.1	17	9.8	1.3
Twigs	107	28.1	0	0.0	28.1
Total	380	100.0	174	100.0	58.8
Height					
0'-14'	15	8.5	37	36.6	28.1
15'-29'	21	11.9	21	20.8	8.9
30'+	140	79.6	43	42.6	37.0
Total	176	100.0	101	100.0	74.0
Green	0	0.0	11	6.0	6.0
Dead w/bark	289	74.1	116	63.4	10.7
Dead w/out bark	101	25.9	56	30.6	4.7
Total	390	100.0	183	100.0	21.4
Upright	380	96.4	174	95.1	1.3
Prostrate	14	3.6	9	4.9	1.3
Total	394	100.0	183	100.0	2.6

the increased feeding attention of females upon insects in terminal branches and twigs, while males fed only on insects in the stems and larger branches.

Brewer (1963) proposed summing the differences between the percentages of foraging categories to obtain an index to the degree of distinctiveness of foraging behavior between two species. This technique can also be used to analyze sexual differences (Selander, 1966). Each of the columns of percentage difference in Tables 8 through 23 were summed and then averaged--divided by 500--to obtain values comparable to Brewer's; the results are presented in Tables 24 and 25. An index of 200 signifies no overlap whatsoever and is an expression of the maximum difference possible under Brewer's scheme. An index of 200 was assigned to the species-pairs in Table 24 involving the Downy Woodpecker and either the Northern Three-toed or Hairy Woodpeckers for those periods when no Downy Woodpeckers were observed at Deadman.

The maximum differences in foraging behavior are at the interspecific level, between the Hairy and Downy Woodpeckers (Table 24); and the minimum differences at the intraspecific level, between the sexes of the Hairy Woodpecker (Table 25).

Food Habits

The results of the stomach content analyses are summarized in Tables 26 through 31. Only data for the Northern Three-toed Woodpecker (Tables 26-28) were sufficient to permit comparisons among birds feeding on endemic, epidemic and post-epidemic populations of the Engelmann spruce beetle. Only four Hairy Woodpecker stomachs

TABLE 24. Indices of differences in foraging behavior between Northern Three-toed (N3T), Hairy (HW), and Downy (DW) Woodpeckers

Species pair		Percentage differences		
		July 16 to October 15	October 16 to May 10	July 16 to May 10
N3T-HW	numbers	39	13	26.0
	minutes	58	68	63.0
N3T-DW	numbers	200	42	121.0
	minutes	200	60	130.0
HW-DW	numbers	200	73	136.5
	minutes	200	96	148.0

TABLE 25. Indices of differences in foraging behavior between the sexes of the Northern Three-toed (N3T) and Hairy (HW) Woodpeckers

Species		Percentage differences		
		July 16 to October 15	October 16 to May 10	July 16 to May 10
N3T	numbers	0	15	7.5
	minutes	28	36	32.0
HW	numbers	0	-	0.0
	minutes	40	-	41.4

TABLE 26. Stomach content analyses of 24 Northern Three-toed Woodpeckers collected in spruce-fir forests supporting endemic populations of the Engelmann spruce beetle (Data courtesy of Dr. Paul H. Baldwin)

	No. of stomachs with prey	% of 24 stomachs with prey	Total no. of prey in stomachs	% of total no. of prey in 24 stomachs
<u>Dendroctonus</u> <u>obesus</u>	7	29	44	7.4
<u>Ips</u> sp	5	21	14	2.4
<u>Pityogenes</u> sp	2	8	9	1.5
<u>Pityophthorus</u> sp	3	13	21	3.5
Other Scolytidae	14	58	211	5.5
Cerambycidae	19	79	173	29.1
Buprestidae	4	17	9	1.5
Cleridae	10	42	18	3.0
Formicidae	5	21	20	3.4
Other Hymenoptera	3	13	4	0.7
Arachnida	12	50	24	4.0
Other	12	50	46	7.8
Total	24		593	100.0

TABLE 27. Stomach content analyses of 56 Northern Three-toed Woodpeckers collected in spruce-fir forests supporting epidemic populations of the Engelmann spruce beetle (Data courtesy of Dr. Paul H. Baldwin)

	No. of stomachs with prey	% of 56 stomachs with prey	Total no. of prey in stomachs	% of total no. of prey in 56 stomachs
<u>Dendroctonus</u> <u>obesus</u>	33	59	636	28.1
<u>Ips</u> sp	19	34	52	2.3
<u>Pityogenes</u> sp	18	33	398	17.6
<u>Pityophthorus</u> sp	10	18	91	4.0
Other Scolytidae	34	61	630	27.8
Cerambycidae	38	68	316	14.0
Buprestidae	1	2	1	0.1
Cleridae	23	41	35	1.5
Formicidae	7	13	8	0.4
Other Hymenoptera	12	21	14	0.6
Arachnida	17	30	23	1.0
Other	27	48	59	2.6
Total	56		2,263	100.0

TABLE 28. Stomach content analyses of 32 Northern Three-toed Woodpeckers collected in spruce-fir forests supporting post-epidemic populations of the Engelmann spruce beetle (Data courtesy of Dr. Paul H. Baldwin)

	No. of stomachs with prey	% of 32 stomachs with prey	Total no. of prey in stomachs	% of total no. of prey in 32 stomachs
<u>Dendroctonus</u> <u>obesus</u>	17	53	292	32.7
<u>Ips</u> sp	4	13	5	0.6
<u>Pityogenes</u> sp	6	19	111	12.4
<u>Pityophthorus</u> sp	3	9	11	1.2
Other Scolytidae	13	40	164	18.4
Cerambycidae	22	69	204	22.8
Buprestidae	3	9	8	0.9
Cleridae	13	40	23	2.6
Formicidae	1	3	11	1.2
Other Hymenoptera	6	19	7	0.8
Arachnida	14	44	23	2.6
Other	15	47	34	3.8
Total	32		893	100.0

TABLE 29. Stomach content analyses of 18 Hairy Woodpeckers collected in spruce-fir forests supporting endemic populations of the Engelmann spruce beetle (Data courtesy of Dr. Paul H. Baldwin)

	No. of stomachs with prey	% of 18 stomachs with prey	Total no. of prey in stomachs	% of total no. of prey in 18 stomachs
<u>Dendroctonus</u> <u>obesus</u>	1	6	5	1.5
<u>Ips</u> sp	1	6	9	2.6
<u>Pityogenes</u> sp				
<u>Pityophthorus</u> sp				
Other Scolytidae	2	11	40	11.8
Cerambycidae	13	72	67	19.7
Buprestidae				
Cleridae	3	17	4	1.2
Formicidae	13	72	179	52.6
Other Hymenoptera	3	17	4	1.2
Arachnida	7	39	6	1.8
Other	5	28	26	7.6
Total	18		340	100.0

TABLE 30. Stomach content analyses of 21 Hairy Woodpeckers collected in spruce-fir forests supporting epidemic populations of the Engelmann spruce beetle (Data courtesy of Dr. Paul H. Baldwin)

	No. of stomachs with prey	% of 21 stomachs with prey	Total no. of prey in stomachs	% of total no. of prey in 21 stomachs
<u>Dendroctonus</u> <u>obesus</u>	9	43	149	13.6
<u>Ips</u> sp	4	19	35	3.2
<u>Pityogenes</u> sp				
<u>Pityophthorus</u> sp				
Other Scolytidae	10	48	667	60.8
Cerambycidae	7	33	28	2.6
Buprestidae	2	10	6	0.5
Cleridae				
Formicidae	5	24	24	2.2
Other Hymenoptera	3	14	5	0.4
Arachnida	5	24	10	0.9
Other	7	33	173	15.8
Total	21		1,097	100.0

TABLE 31. Stomach content analyses of 16 Downy Woodpeckers collected in spruce-fir forests supporting epidemic populations of the Engelmann spruce beetle (Data courtesy of Dr. Paul H. Baldwin)

	No. of stomachs with prey	% of 16 stomachs with prey	Total no. of prey in stomachs	% of total no. of prey in 16 stomachs
<u>Dendroctonus</u> <u>obesus</u>	5	25	50	4.4
<u>Ips</u> sp	3	19	24	2.1
<u>Pityogenes</u> sp				
<u>Pityophthorus</u> sp	10	63	256	22.8
Other Scolytidae	13	81	666	59.0
Cerambycidae	1	6	1	0.1
Buprestidae				
Cleridae	4	25	5	0.4
Formicidae	7	44	119	10.5
Other Hymenoptera	3	19	4	0.3
Arachnida	1	6	1	0.1
Other	4	25	4	0.3
Total	16		1,130	100.0

were available from forests supporting post-epidemic populations of the spruce beetle; these were combined with the stomachs from epidemic populations. Two Downy Woodpecker stomachs from forests harboring endemic populations of the spruce beetle were combined with the stomachs from epidemic populations; no Downy Woodpeckers were available from forests supporting post-epidemic populations of the spruce beetle.

In forests supporting endemic populations of the Engelmann spruce beetle, the Northern Three-toed Woodpecker preyed mainly upon scolytids and cerambycids (Table 26), while the Hairy Woodpecker preyed mainly upon formicids (Table 29). In forests supporting epidemic populations of the spruce beetle, all three species of woodpeckers preyed predominantly upon scolytids (Tables 27 and 31); and in forests with post-epidemic populations of the spruce beetle, the Northern Three-toed Woodpecker continued to prey heavily upon scolytids, and increased its use of cerambycids (Table 28). Thus, of the three species of woodpecker, the Northern Three-toed Woodpecker is the most consistent predator of scolytids, including the Engelmann spruce beetle.

Northern Three-toed and Hairy Woodpeckers both consumed more Engelmann spruce beetles in forests supporting epidemic populations of the beetle than in forests supporting endemic populations (Tables 26-30); since Downy Woodpeckers were not regularly observed in spruce-fir forests supporting endemic populations of bark beetles (Figures 7-9), it can be inferred that this woodpecker also consumed more spruce beetles in forests supporting epidemic populations. Thus, all three species of woodpeckers demonstrate a direct functional

response to prey density.

Only the stomachs of the Northern Three-toed Woodpecker were sufficiently numerous to permit a differential analysis of the contents on a sexual basis. Two types of commonly consumed beetles, Cerambycidae and Scolytidae, the former being the larger, were selected to conduct the analysis. Of the 112 stomachs available, 63 contained either cerambycids or scolytids, the remainder had both. The statistical significance of the differences in the number of stomachs containing remains of one or the other of these families of beetles was checked by means of the Chi-square contingency test (Table 32).

Linear Measurements of Morphological Characters

No overlap exists in either the measurements of the culmen lengths or the weights of the adult Downy and Northern Three-toed Woodpeckers, or of the adult Downy and Hairy Woodpeckers; on the other hand, overlap of varying amounts does exist between these measurements in the Northern Three-toed and Hairy Woodpeckers (Table 33 and Figure 10). Average values for four other linear measurements, obtained from Ridgway (1914), are included in Table 33 to demonstrate that interspecific and intersexual divergence in the measurements of the trophic structure are greater than the measurements of the non-trophic structures.

Coefficients of difference (Mayr, et al., 1953), providing a measure of the amounts of joint nonoverlap among variables, were calculated for the culmen length and linear weight measurements by the formula $\frac{L - S}{s_1 + s_2}$, where L is the larger and S the smaller of two

TABLE 32. Comparison of the numbers of stomachs of male and female Northern Three-toed Woodpeckers containing scolytids and cerambycids

	No. of female stomachs	%	No. of male stomachs	%	% Difference
Scolytidae	19	40	10	16	24 ^a
Cerambycidae	9	19	25	39	20 ^b
Both	20	41	29	45	
Total	48	100.0	64	100.0	44

^aDifference significant at less than .01 level

^bDifference significant at less than .05 level

TABLE 33. Measurements of six linear characters from adult female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers. Weight in grams; all other measurements in mm

	Mean culmen l.	N	SE	³ Mean wt	N	SE	Mean wing l.	Mean tail l.	Mean tarsus l.	Mean toe IV	N
F-DW	13.6	71	.062	2.96	13	.019	100.9	63.9	16.2	10.3	10 ^a
M-DW	14.1	63	.073	2.97	17	.016	99.3	62.3	16.5	10.5	10 ^a
F-N3T	22.4	14	.300	3.79	9	.006	121.5	76.1	20.6	10.6	10 ^b
M-N3T	24.0	25	.200	3.91	20	.018	123.3	75.2	20.9	10.8	10 ^b
F-HW	23.5	12	.210	4.13	8	.024	131.1	79.8	22.1	14.3	8 ^c
M-HW	26.4	15	.370	4.24	12	.020	133.3	82.5	22.7	14.7	10 ^c

^aDendrocopos pubescens homorus

^bPicoides americanus dorsalis

^cDendrocopos villosus monticola

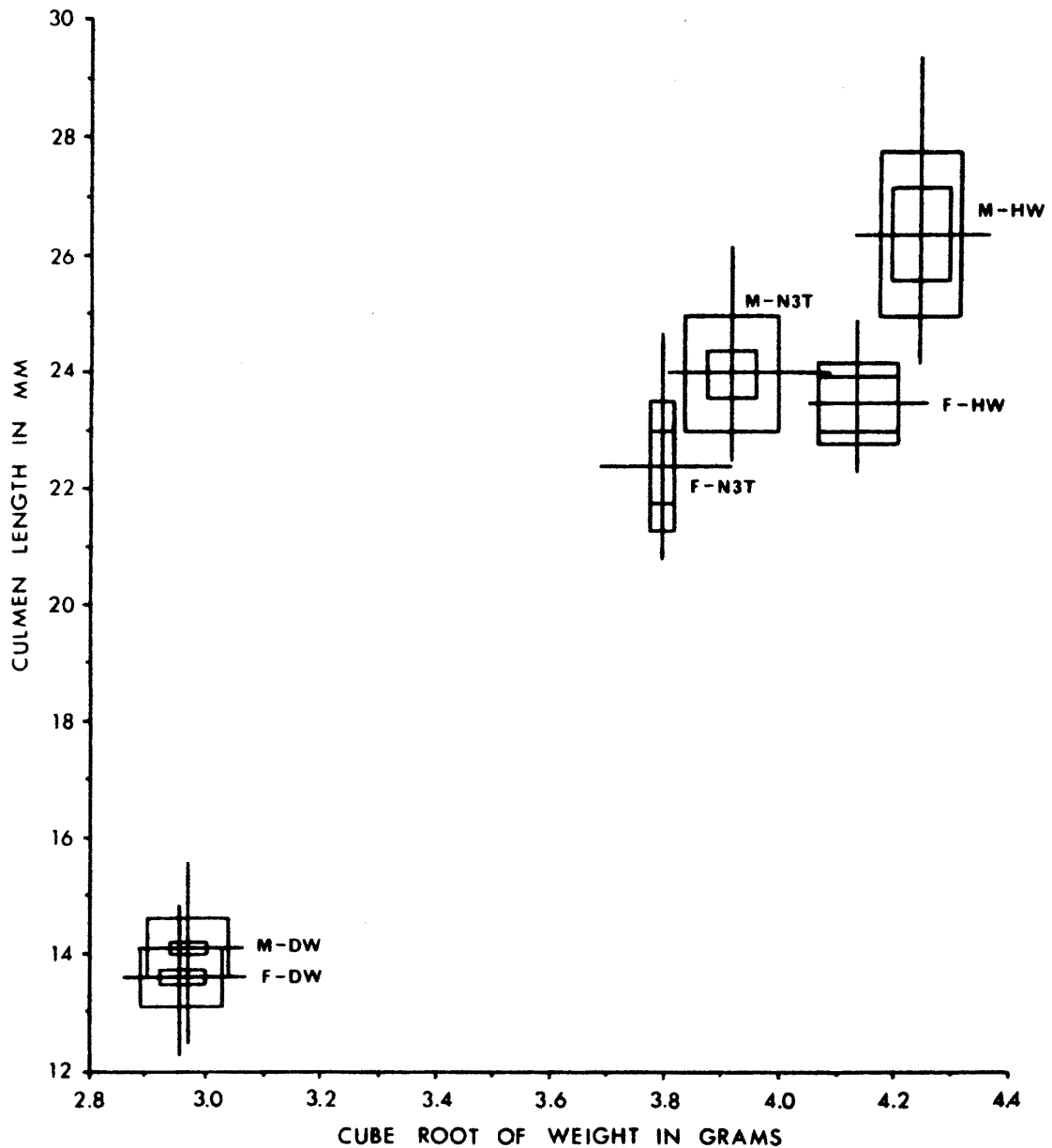


Figure 10. Culmen lengths of female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers plotted as functions of the cube roots of their weights. Lines span the range of measurements and intersect at average values. Small quadrangles represent 95 per cent confidence estimates of population means, and large quadrangles, one standard deviation on either side of the average.

averages, and s_1 and s_2 the standard deviations of the large and small averages, respectively (Table 34). And with the exception of the weight measurements for the Northern Three-toed Woodpecker which are probably biased by sampling error, the percent nonoverlap in measurements of linear weight between the sexes of the woodpeckers is less than the nonoverlap in the measurements of their culmen lengths.

Ratios of character difference (Schoener, 1965) calculated by the formula L/S (Hutchinson, 1959) and ratios of percentage difference calculated by $\frac{L - S}{L}$, presented in Tables 35 and 36, respectively, also show that interspecific and intersexual differences in the measurements of trophic structure are greater than interspecific and intersexual differences in non-trophic structures. It should be noted that ratios of percentage difference are only half as large as Brewer's (1963) indices of percentage difference.

Energetics

In comparative studies it is desirable to have a base for purposes of reference; standard metabolic rate, because it is the lowest rate possible, functions as a reference point against which the energetic costs of different levels of activity can be compared. Accordingly, standard metabolic rates were determined for ten woodpeckers and the results are presented in Table 37, along with rates calculated from their weights by two of the four equations discussed by King and Farner (1961), and Lasiewski and Dawson (1967). The observed data are statistically similar to values predicted by the Brody-Proctor equation ($M=89.0 W^{.64}$) but different from the other four. The Brody-Proctor equation has been widely accepted by

TABLE 34. Coefficients of difference (C.D.) among culmen lengths and cube roots of weight of female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers. Percent nonoverlap of Downy with the other two woodpeckers is 100

		F-DW		F-N3T		M-N3T		F-HW	
		C.D.	% non-overlap	C.D.	% non-overlap	C.D.	% non-overlap	C.D.	% non-overlap
M-DW	³ wt	0.08	53						
	Culmen	0.45	67						
M-N3T	³ wt			1.21	88				
	Culmen			0.74	77				
F-N3T	³ wt			3.89	100	1.48	93		
	Culmen			0.59	72	0.29	61		
M-HW	³ wt			4.95	100	2.17	98	0.79	78
	Culmen			1.56	94	0.99	84	1.34	91

TABLE 35. Ratios of character difference among female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers

		F-DW	M-DW	F-N3T	M-N3T	F-HW
M-DW	Wing	1.02				
	Tail	1.02				
	Tarsus	1.02				
	Toe IV	1.02				
	3 wt.	1.00				
	Culmen	1.04				
F-N3T	Wing	1.20	1.23			
	Tail	1.19	1.22			
	Tarsus	1.27	1.25			
	Toe IV	1.03	1.01			
	3 wt.	1.28	1.28			
	Culmen	1.65	1.59			
M-N3T	Wing	1.23	1.25	1.02		
	Tail	1.18	1.21	1.01		
	Tarsus	1.29	1.27	1.02		
	Toe IV	1.05	1.03	1.02		
	3 wt.	1.32	1.32	1.03		
	Culmen	1.76	1.70	1.07		

TABLE 35.---Continued

		F-DW	M-DW	F-N3T	M-N3T	F-HW
F-HW	Wing	1.30	1.32	1.08	1.06	
	Tail	1.25	1.28	1.05	1.06	
	Tarsus	1.36	1.34	1.07	1.10	
	Toe IV	1.39	1.36	1.35	1.32	
	³ wt.	1.40	1.40	1.09	1.06	
	Culmen	1.73	1.67	1.05	1.02	
M-HW	Wing	1.32	1.34	1.10	1.08	1.02
	Tail	1.29	1.32	1.08	1.10	1.03
	Tarsus	1.40	1.38	1.10	1.09	1.03
	Toe IV	1.43	1.40	1.39	1.36	1.03
	³ wt.	1.43	1.43	1.12	1.08	1.03
	Culmen	1.94	1.87	1.18	1.10	1.12

TABLE 36. Percentage difference ratios calculated by $(L - S)/L$ among female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers

		F-DW	M-DW	F-N3T	M-N3T	F-HW
M-DW	Wing	1.6				
	Tail	2.5				
	Tarsus	1.8				
	Toe IV	1.9				
	³ wt.	0.3				
	Culmen	3.5				
F-N3T	Wing	17.0	18.3			
	Tail	16.0	18.1			
	Tarsus	21.4	19.9			
	Toe IV	2.9	0.9			
	³ wt.	21.9	21.9			
	Culmen	39.3	37.1			
M-N3T	Wing	18.2	19.5	1.8		
	Tail	15.0	17.2	1.2		
	Tarsus	22.5	21.1	1.4		
	Toe IV	4.6	2.7	1.9		
	³ wt.	24.3	24.3	3.1		
	Culmen	43.3	41.3	6.7		

TABLE 36.--Continued

		F-DW	M-DW	F-N3T	M-N3T	F-HW
F-HW	Wing	23.0	24.3	7.3	5.9	
	Tail	19.9	21.9	4.6	5.8	
	Tarsus	26.7	25.3	4.6	5.4	
	Toe IV	28.0	26.6	25.9	24.5	
	³ wt.	28.3	28.3	8.2	5.3	
	Culmen	42.1	40.0	4.7	2.1	
M-HW	Wing	24.3	25.5	8.9	7.5	1.7
	Tail	22.5	24.5	7.6	8.8	3.3
	Tarsus	28.6	27.3	7.8	7.9	2.6
	Toe IV	29.9	28.6	27.9	26.5	2.7
	³ wt.	30.2	30.2	10.6	7.8	2.6
	Culmen	48.5	46.6	15.2	9.1	11.0

TABLE 37. Standard metabolic rates (M) in kilocalories per day for female (F) and male (M) Downy (DW) and Hairy (HW) Woodpeckers. W represents weight in kilograms

Sex and species	Wt in kg	Chamber temp °C	Observed rate (M)	Estimated rates (M)	
				$78.3W^{.723}$	$89.0W^{.64}$
M-DW	.026	27.1	12.86	5.55	8.40
F-HW	.054	27.4	17.02	9.47	13.71
F-HW	.055	27.2	11.61	9.62	13.91
F-HW	.056	24.0	19.20	9.74	14.28
F-HW	.060	28.3	18.65	10.18	14.62
M-HW	.059	24.2	22.78	10.17	14.61
M-HW	.061	28.2	19.07	10.38	14.86
M-HW	.063	27.7	16.74	10.55	15.09
M-HW	.072	26.0	20.74	11.72	16.43
M-HW	.076	28.3	17.95	12.12	16.61

ornithologists for birds weighing less than one kilogram; however, King and Farner (op cit.) logically question its validity. Lasiewski (1963) has shown that standard metabolic rates for the smallest of birds, the hummingbirds, fit the King-Farner equation ($M = 74.3W^{.744}$), which is statistically indistinguishable from the equations for mammals ($M = 69.0W^{.756}$) and nonpasserines ($M = 78.3W^{.723}$), so that it becomes unnecessary to invoke metabolic mechanisms for nonpasserine birds which are different from those of mammals. Lasiewski and Dawson (1967) have shown that passerines exhibit higher weight-specific metabolic rates than nonpasserines and mammals, although weight exponents--the logarithmic slopes, or b values--of all three groups are nearly identical. Thus, the observed values in Table 37 are too high. Two reasons for this divergence are that metabolic determinations were made during late August when the birds were molting and also when they were suffering from a salmonella infection. It is also possible that oxygen consumptions were measured under subthermoneutral conditions, as there were no means for systematically varying temperature to determine rates of relative oxygen utilization throughout a range of temperatures.

The Lasiewski-Dawson equation for nonpasserines ($M = 78.3W^{.723}$) was employed to calculate the standard metabolic rates of the three species of woodpeckers (Figure 11) from the data on weight statistically summarized in Table 38. The variances in weight of the sexes of each species were similar (determined by the F-test), so they were pooled to achieve a larger sample size and a correspondingly better estimate of population mean.

Caloric values determined for insects and for woodpecker

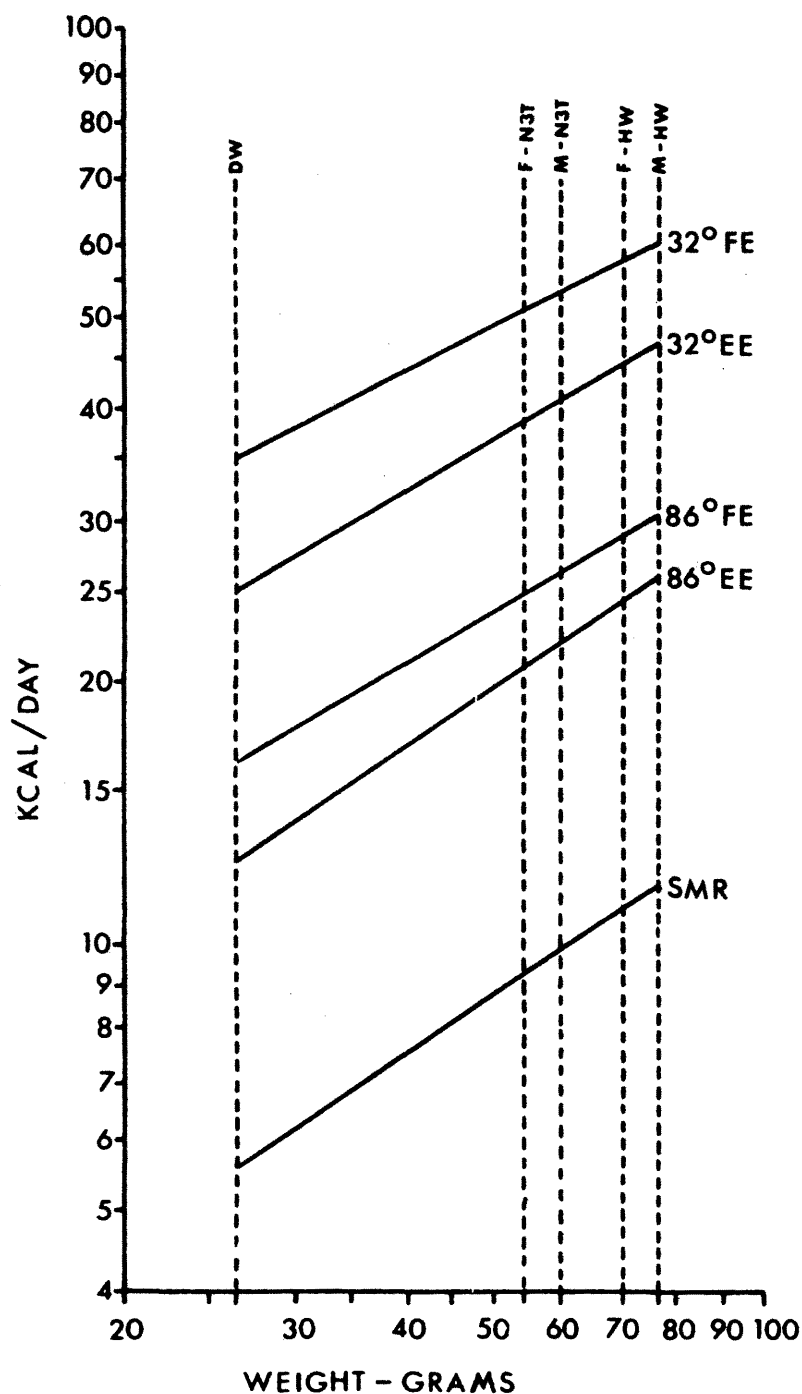


Figure 11. Log graph of standard metabolic rate (SMR), and existence (EE) and exercise (FE) energies at 32° F and 86° F plotted as functions of the average weights of female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers.

TABLE 38. Weights of woodpeckers and the existence energies calculated from them. M is metabolic rate in kilocalories per day, and w is weight in grams

Sex and species	Avg wt \pm 95% confidence estimate of mean wt	N	Existence energy, 32° F $M=3.858w^{.550}$	Existence energy, 86° F $M=1.586w^{.601}$
F-DW	26.3 \pm .57	13	23.30 \pm .29	11.32 \pm .14
M-DW	26.3 \pm .57	17	23.30 \pm .29	11.32 \pm .14
F-N3I	54.6 \pm .68	9	34.82 \pm .24	17.55 \pm .13
M-N3I	59.9 \pm .68	20	36.64 \pm .23	18.56 \pm .12
F-HW	70.7 \pm 1.81	8	40.14 \pm .56	20.50 \pm .32
M-HW	76.2 \pm 1.81	12	41.83 \pm .55	21.45 \pm .31

excreta are presented in Table 39. The caloric values for Tenebrio and the excreta were utilized in the calculations of gross and excrement energy for the feeding experiments. Five woodpeckers were utilized for a total of 27 feeding experiments; however, eight of the experiments could not be included with the results in Table 40 because they involved juveniles that were gaining weight.

The data in Table 40 for the Northern Three-toed Woodpecker, when plotted with temperature as the abscissa and energy as the ordinate, are not linear and are, accordingly, problematical. The energetic values determined for Hairy and Downy Woodpeckers, however, do plot as linear functions of temperature. This makes it possible, therefore, to estimate for the latter two species energetic values over a temperature gradient by projecting the lines to the desired temperatures. Caloric values were so estimated for 32° F, then plotted as logarithmic functions of weight; subsequently, the expected metabolic rates of Northern Three-toed Woodpeckers were calculated for this temperature from their weights. The energetic rates at 50° F for all three species when plotted as logarithmic functions of weight were approximately linear, so it was possible to trust the observed energetic values for this temperature. Combining these two sets of figures, i.e., the 32° F estimates and the 50° F determinations, permitted estimation of metabolic rates as a logarithmic function of weight for these two temperatures. It was then possible to estimate energetic rates as a linear function of temperature. The results of these calculations are presented in Tables 41 and 42.

Existence energies were calculated from the average weights

TABLE 39. Caloric values of insects and of woodpecker excreta

	No./gm dry wt	Kcal/gm dry wt	Kcal/ individual
<u>Dendroctonus obesus</u> , larvae	309.2	5.806	0.019
<u>Dendroctonus obesus</u> , adults	195.9	5.929	0.030
<u>Ips pilifrons</u> , larvae	480.4	5.938	0.012
<u>Ips pilifrons</u> , adults	304.3	5.514	0.018
<u>Tenebrio</u> sp., larvae	20.6	6.500	0.315
Woodpecker excreta	--	3.500	--

TABLE 40. Caloric values from the feeding experiments for female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers

Sex and species	Wt in gms	Temp., °F	Kcal gross energy per day	Kcal excrement energy per day	Kcal metabolic energy per day
M-DW	27.6	60	29.538	3.697	25.841
M-DW	26.6	50	30.827	4.581	26.246
M-DW	27.7	40	34.943	4.772	30.171
F-N3T	49.4	60	34.110	7.152	26.958
F-N3T	46.2	50	41.269	7.830	33.439
F-N3T	49.8	40	34.578	6.242	28.336
M-N3T	51.9	60	36.461	6.684	29.777
M-N3T	53.8	50	45.107	7.637	37.470
M-N3T	47.9	40	41.610	7.180	34.430
M-N3T	53.1	30	39.476	7.841	31.635
M-N3T	56.2	60	33.723	7.899	25.824
M-N3T	56.2	50	41.751	7.197	34.554
M-N3T	55.4	40	37.419	9.126	28.293
F-HW	63.6	50	49.324	7.810	41.514
F-HW	57.1	25	52.001	8.184	43.817
F-HW	51.2	8	54.924	9.395	45.519
M-HW	72.2	50	49.653	8.867	40.786
M-HW	67.1	25	58.251	9.979	48.272
M-HW	67.6	8	68.331	11.718	56.613

TABLE 41. Equations to estimate energetics (M) of cage activity from weight (w) for three temperatures. M is metabolic rate in kilocalories per day and w is weight in grams

Temperature	Gross energy	Metabolic energy	Excrement energy
32° F	$M = 7.430w^{.479}$	$M = 7.089w^{.446}$	$M = 0.5838w^{.663}$
50° F	$M = 6.250w^{.488}$	$M = 5.703w^{.464}$	$M = 0.637w^{.617}$
86° F	$M = 3.601w^{.538}$	$M = 2.809w^{.546}$	$M = 0.753w^{.519}$

TABLE 42. Equations to estimate energetics (M) of cage activity from temperature (T) for female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers. M is metabolic rate in kilocalories per day, and T is temperature in degrees Fahrenheit

Species	Gross energy	Metabolic energy	Excrement Energy
F-DW	$M = 43.240 - .260T$	$M = 37.790 - .245T$	$M = 5.483 - .016T$
M-DW	$M = 43.240 - .260T$	$M = 37.790 - .245T$	$M = 5.483 - .016T$
F-N3T	$M = 61.969 - .359T$	$M = 52.342 - .317T$	$M = 9.626 - .042T$
M-N3T	$M = 64.703 - .373T$	$M = 54.488 - .328T$	$M = 10.273 - .046T$
F-HW	$M = 69.894 - .399T$	$M = 58.436 - .346T$	$M = 11.624 - .056T$
M-HW	$M = 72.438 - .413T$	$M = 60.294 - .354T$	$M = 12.156 - .058T$

in Table 38 by means of unpublished equations kindly provided by Dr. S. C. Kendeigh. A comparison of exercise and existence energies shows that the exercise energies have higher weight-specific metabolic rates than the existence energies (Figure 11). In addition, the weight exponents of both energy levels are smaller at 32° F than at 86° F. Finally, there is a consistent increase in the value of the weight exponent from the energetically most demanding activity--exercise at 32° F--to the energetically least demanding activity--standard metabolic rate.

These considerations suggest that the equations in Tables 41 and 42, while undoubtedly not as accurate as Kendeigh's equations because they were derived from a much smaller sample, consistently predict, over a wide range of temperatures, the trends of the energetics of a higher level of activity than has been measured previously.

Figure 11 summarizes the metabolic energy expenditures of the three species of woodpeckers for several levels of activity at several different temperatures. The lines are not parallel, due to the fact that the weight exponent decreases with each increase in activity or decrease in temperature. This is because smaller birds exert proportionately larger amounts of energy than do larger birds, on a unit weight basis (Figures 12 and 13).

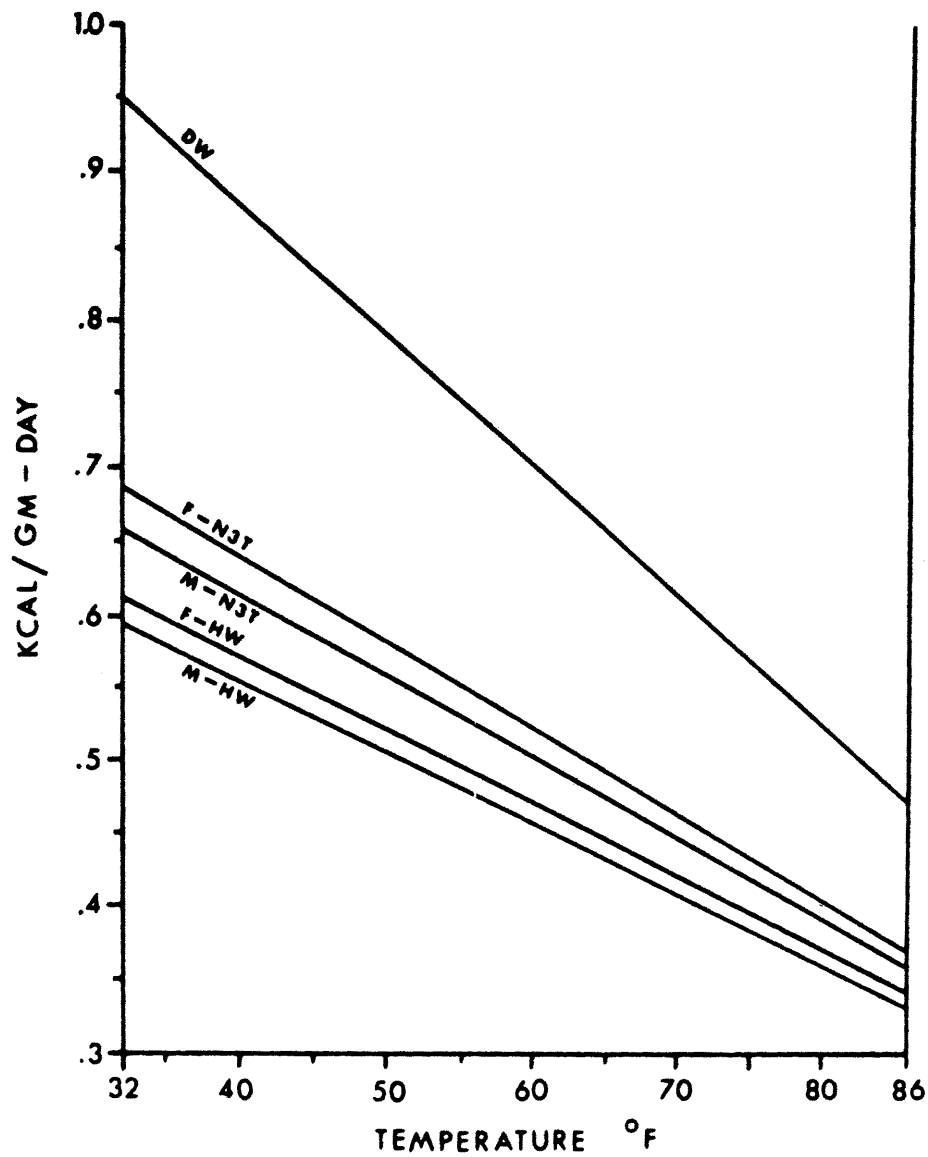


Figure 12. Existence energy per gram body weight of female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers plotted as functions of temperature.

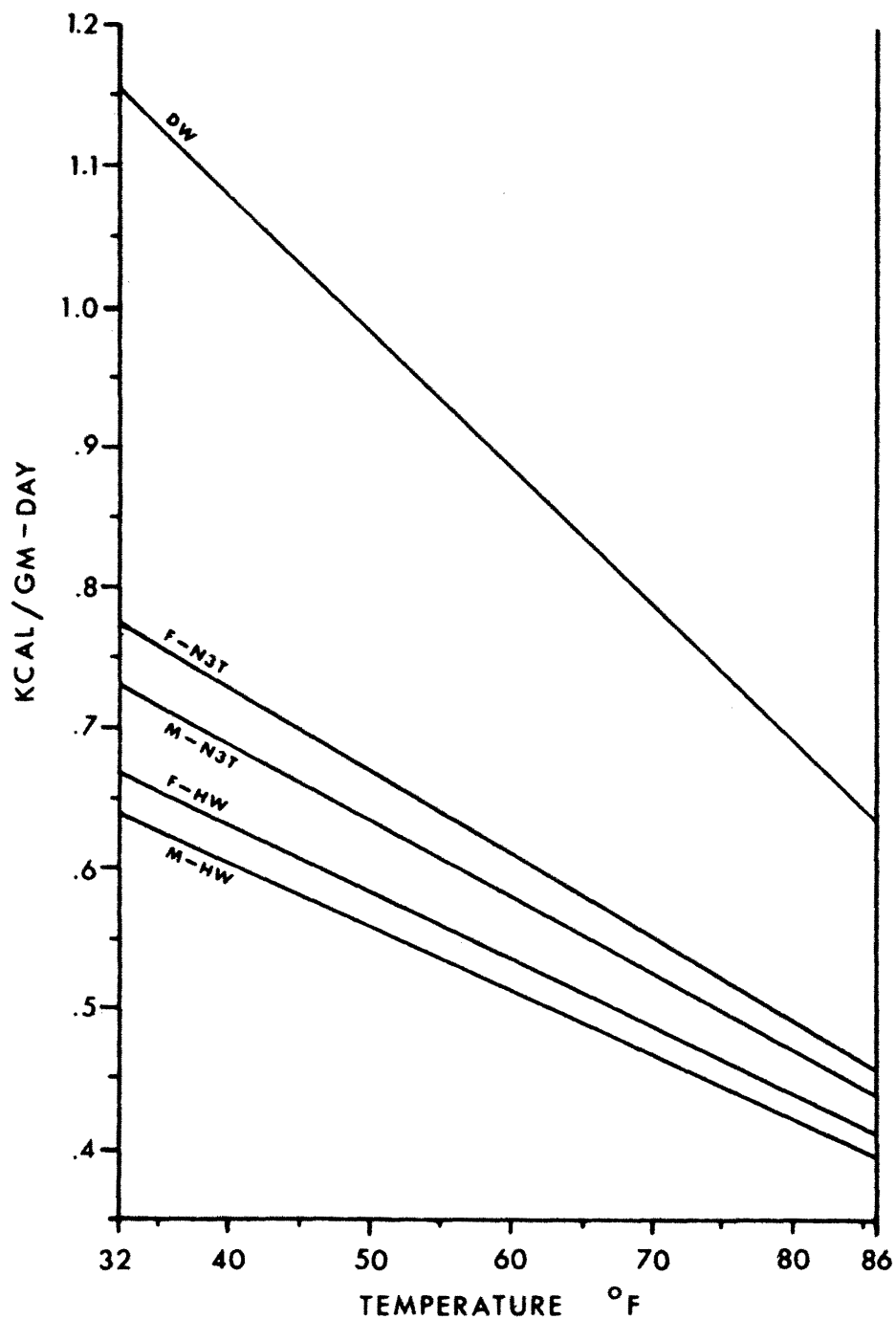


Figure 13. Exercise energy per gram body weight of female (F) and male (M) Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers plotted as functions of temperature.

DISCUSSION

It is now possible to compare and contrast the study reported herein with other studies to point out those aspects of the predator-prey system between woodpeckers and the Engelmann spruce beetle which fit into the previously developed predator-prey theory, as well as those aspects which are unique to the system. The concepts of niche, competition and the principle of competitive exclusion will aid in the interpretation of the differences in predator-pressure exerted upon populations of the spruce beetle by the different species of woodpeckers.

Components of Character Displacement

The spatial, temporal, dietary and morphological differences, often cited as evidences indicative of competitive exclusion in comparative ecological studies, may be thought of as components of character displacement. Conversely, spatial, temporal, dietary and morphological similarities may be thought of as components of character overlap.

Several techniques have been proposed recently as means of quantifying differences or similarities within some of the components. One of these, the index of distinctiveness proposed by Brewer (1963) for quantifying differences in the spatial component, has already been mentioned. Since the maximal value with Brewer's index is 2.00, halving the index provides an index of spatial difference that ranges from 0.00 at no overlap to 1.00 at complete overlap.

Differences within the temporal component can be expressed similarly. Horn (1966), in a review of indices of overlap in the dietary component of character displacement, pointed out that Morisita's (1959) index of overlap, an extension of Simpson's (1949) index of diversity, is one of probability and is, therefore, a measure of the differential availability of food items in a given habitat. Alternatively, the Shannon-Wiener (Shannon and Weaver, 1949) index of dietary overlap is based upon information theory and measures the choices made among equally available food items. Both indices of overlap within the dietary component can range from 0.00 to 1.00. Finally, ratios of percentage difference, as shown in Table 36, provide indices of difference within morphological components, and the spectrum of values can range, theoretically at least, from 0.00 to 1.00. Indices of difference of one or approaching one within a morphological component are possible only when S --the smaller of two averages--equals or approaches zero, an obvious impossibility; therefore, an index of one within a morphological component is possible in theory only. Thus, the range of values for expressing the amount of difference or similarity within each of the components of character displacement or character overlap is the same.

It is the components of character displacement that are of interest, so the remainder of the discussion will be devoted to indices of difference. However, any desired index of overlap can be calculated by subtracting the index of difference from one.

Spatial and Temporal Differences

The average indices of difference in foraging behavior for both periods of observation, presented in Tables 8 through 15,

provided the data for the computation of indices of difference within the spatial (microhabitat) and temporal components of the niches of the woodpeckers studied at Deadman lookout. Thus, the index of difference in the spatial components of the niches of the Northern Three-toed and Hairy Woodpeckers is $.26/2 = .13$, and the index of difference in the temporal component is $.63/2 = .32$. Indices of spatial and temporal difference for the remaining species-pairs in Tables 8 through 15 as well as for several other species-pairs, included for the sake of comparison, are presented in Table 43.

The indices of spatial difference in Table 43 were calculated from differences statistically significant to at least the five per cent level. The differences were tested, as were those in Tables 8 through 11 and 16 through 19, by means of Chi-square contingency tests.

The number of foraging categories in Table 43 is equivalent to the number of categories utilized in the calculations of the indices of temporal difference for each species-pair. Tables 12 and 13, for example, include the categories: spruce, subalpine fir, lodgepole pine, limber pine, stem, . . . upright and prostrate, for a total of 15 categories utilized by either the Northern Three-toed Woodpecker or the Hairy Woodpecker. Only those categories that were significantly different (at or less than the five per cent level of significance) were utilized in the calculations of the indices of spatial difference. Thus, the number of foraging categories included in the indices of spatial difference is generally less than the number listed. Table 8 shows significant differences in only seven of the possible 14 foraging categories and Table 9 shows significant

TABLE 43. Indices of interspecific difference in spatial and temporal components of character difference

Species-pair	Total no. of foraging categories	Index of spatial difference	Index of temporal difference	Source
<u>Picoides tridactylus</u> <u>Dendrocopos villosus</u>	15	0.13	0.32	This study
<u>Picoides tridactylus</u> <u>Dendrocopos pubescens</u>	14	0.62	0.65	This study
<u>Dendrocopos villosus</u> <u>D. pubescens</u>	12	0.68	0.74	This study
<u>Dendrocopos villosus</u> <u>Sphyrapicus thyroideus</u>	25	0.40	0.90	Stallcup, 1966
<u>Sitta carolinensis</u> <u>S. pygmaea</u>	30	0.54	0.75	Stallcup, 1966
<u>Sitta carolinensis</u> <u>S. canadensis</u>	27	0.67	0.70	Stallcup, 1966
<u>Sitta pygmaea</u> <u>S. canadensis</u>	17	0.60	0.65	Stallcup, 1966

TABLE 43.--Continued

Species-pair	Total no. of foraging categories	Index of spatial difference	Index of temporal difference	Source
<u>Dendroica castanea</u> <u>D. tigrina</u>	14	0.57	0.76	MacArthur, 1958
<u>Dendroica castanea</u> <u>D. virens</u>	15	0.14	0.36	MacArthur, 1958
<u>Dendroica castanea</u> <u>D. coronata</u>	15	0.20	0.48	MacArthur, 1958
<u>Dendroica tigrina</u> <u>D. fusca</u>	11	0.14	0.27	MacArthur, 1958
<u>Parus atricapillus</u> <u>P. carolinensis</u>	9	0.07	--	Brewer, 1963

differences in only two of the possible 15 foraging categories. Thus, there were significant differences in only nine of the possible 15 categories.

With the exception of the parids, all of the species-pairs listed in Table 43 are at least seasonally sympatric. The parids are contiguously allopatric except for a zone several miles wide in western Illinois and eastern Missouri where they are sympatric. The index of spatial difference shown in Table 43 was obtained from a study by Brewer (1963) of the ecological relationships of the two chickadees in the zone of sympatry. The index of spatial difference between the chickadees is the smallest listed in Table 43, implying, as suggested by Brewer, that the ecological dynamics of the two species are so similar that sympatry is possible only within the narrow strip where the geographic ranges of the two species are juxtaposed. Brewer provided evidence suggesting that reproductive isolation of the two parids has not been achieved; thus, interspecific differences that might otherwise accumulate and bring about competitive exclusion are swamped out by hybridization in the zone of geographic overlap.

The remaining indices of difference in Table 43 are at least twice as large as the index of spatial difference for the allopatric parids, indicating that divergence of foraging behavior in each species-pair is sufficient to permit at least seasonal sympatry. Except in the case of Dendroica castanea and D. tigrina, the indices of spatial and temporal difference between the parulids are equivalent to the smaller indices of difference between the other congeneric species-pairs. Parulids are migratory and able to take advantage of

insect prey in different geographic areas at times when the prey in these areas is likely to be most abundant. It is reasonable to assume, then, that the five congeneric species of warblers are exposed to foods that are fairly abundant, and the birds are, consequently, able to tolerate more spatial and temporal overlap than the resident sympatric, congeneric picids and sittids, which are exposed to foods that are relatively less abundant on a year-round basis. The indices of spatial and temporal difference in Table 43 support this postulate.

With the exception of Picoides tridactylus and Dendrocopos villosus, the intergeneric indices of difference listed in Table 43 are comparable to the congeneric indices of difference listed for the picids and sittids. The indices of difference between the Northern Three-toed and Hairy Woodpeckers are equivalent to the smaller congeneric indices of difference listed for the parulids, suggesting more spatial and temporal overlap between the Northern Three-toed and Hairy Woodpeckers than between the other intergeneric species-pairs. The Northern Three-toed and Hairy Woodpeckers are able to tolerate this large amount of spatial and temporal overlap because of important differences in the foraging techniques of the two woodpeckers. The average amount of time expended per feeding effort is one manifestation of the foraging techniques of a given species; summing the largest totals for each species of woodpecker in Tables 12 and 13, and dividing the resultant values by the sum of the largest totals for each species in Tables 8 and 9 provides the average amount of time expended per feeding effort. Thus, the Northern Three-toed Woodpecker expended an average of

$\frac{2072 + 1489}{136 + 98} = 15.2$ minutes per feeding effort and the Hairy Woodpecker an average of $\frac{502 + 71}{57 + 11} = 8.4$ minutes per feeding effort, suggesting that the Northern Three-toed Woodpecker is almost twice as sedentary as the Hairy Woodpecker. This suggestion is supported by Spring's (1965) study on the morphological and behavioral feeding adaptations of the genera Dendrocopos and Picoides. Spring concluded that Picoides is adapted for stationary feeding and that Dendrocopos is adapted for vertical climbing, feeding more or less on the move. Dividing the larger totals in Tables 14 and 15 by the larger totals in Tables 10 and 11-- $\frac{161}{17} = 9.5$ minutes per feeding effort--shows a foraging technique for the Downy Woodpecker that is more similar to that of the Hairy Woodpecker than that of the Northern Three-toed Woodpecker. This is in keeping with Spring's postulate that the genus Dendrocopos is better adapted for climbing than is Picoides.

Tables 26 and 29 also provide indirect evidence to support the hypothesis that Dendrocopos is better adapted for climbing than Picoides. Table 29 shows that ants comprised more than 50 per cent of the items in the diet of Hairy Woodpeckers in spruce-forests supporting endemic populations of the Engelmann spruce beetle. It is expected that ants would be gleaned from trunk surfaces or pecked from the relatively soft wood of decaying snags; thus, ants could be obtained by an agile woodpecker with a minimum of effort. Table 26, on the other hand, shows that scolytids and cerambycids comprised almost 80 per cent of the items in the diet of Northern Three-toed Woodpeckers in spruce-fir forests supporting endemic populations of the spruce beetle. Scolytids inhabit cortical and subcortical regions of bark, and cerambycids inhabit subcortical regions of

bark and sapwood. A woodpecker feeding on bark and wood-boring insects has to obtain its prey by pecking, and adaptations for pecking are inversely correlated with adaptations for climbing (Spring, 1965). Thus, the foraging techniques of the Northern Three-toed and Hairy Woodpeckers are correlated with the summaries of their diets in Tables 26 and 29.

The high proportion of scolytids in the diets of Hairy and Downy Woodpeckers in spruce-fir forests supporting epidemic populations of the spruce beetle (Tables 30 and 31) is inconsistent with the notion that Dendrocopos is a genus adapted for climbing and not particularly well adapted for pecking. Hairy and Downy Woodpeckers must receive relatively less energy than they expend in obtaining bark beetles when the beetle populations are distributed at endemic densities. When the beetle populations are at epidemic levels, however, the insects must be abundant enough to represent a utilizable resource for even these relatively inefficient predators of bark beetles. The Northern Three-toed Woodpecker as a relatively more efficient predator of bark beetles, does not displace competitively the Hairy and Downy Woodpeckers because of the ceiling imposed upon increase in numbers of the superior competitor by nesting territoriality.

An implication from the foregoing is that in spruce-fir forests Hairy and Downy Woodpeckers are fugitive species, in the sense proposed by Hutchinson (1951 and 1965), where one of several related species is competitively superior and the inferior or fugitive species must rely upon their dispersal mechanisms to occupy newly arisen habitats created by temporary food surpluses.

Indices of spatial and temporal difference between the sexes of the Northern Three-toed and Hairy Woodpeckers were calculated by halving the indices of difference in foraging behavior in Table 25 for the period July 16 to May 10, and the results together with the results of similar calculations from other woodpecker studies are presented in Table 44. Indices of spatial difference between the sexes of the Hairy Woodpecker are widely divergent, probably because of the greater degree of complexity and concomitant number of foraging strata available in the eastern versus the western forests in which the observations on foraging behavior were made. The remaining indices of difference in Table 44 are smaller than or comparable to the smallest indices of interspecific difference in Table 43.

Centurus striatus is an insular woodpecker, and the comparatively large magnitude of the indices of spatial and temporal difference between its sexes is correlated with the absence of interspecific competitors on the islands this bird inhabits (Selander, 1966; Selander and Giller, 1963). It is more difficult to suggest an hypothesis to account for the extremely large index of spatial difference between the sexes of the Hairy Woodpecker studied by Kilham (1965) in New England. As pointed out by Selander (1965), the Hairy Woodpecker is an unusually dimorphic woodpecker, exhibiting non-overlap in bill lengths between the sexes of from 91 per cent for Dendrocopos villosus monticola (Table 34) to 95 per cent for D. v. leucothorectis. The extreme sexual dimorphism in trophic structure of the Hairy Woodpecker together with the large index of spatial difference calculated from Kilham's data strongly support the hypothesis that sexual dimorphism is an adaptation alleviating

TABLE 44. Indices of intersexual difference in spatial and temporal components of character difference

Species	Total no. of foraging categories	Index of spatial difference	Index of temporal difference	Source
<u>Picoides tridactylus</u>	14	0.04	0.16	This study
<u>Dendrocopos villosus</u>	15	0.00	0.20	This study
<u>Dendrocopos villosus</u>	8	0.61	--	Kilham, 1965
<u>Centurus striatus</u>	14	0.10	0.34	Selander, 1966
<u>Centurus aurifrons</u>	12	0.00	--	Selander, 1966

intersexual competition for food (Selander, 1966). The indices of difference calculated for the Hairy Woodpecker from the results of the present study, however, do not support the postulate that sexual dimorphism alleviates intersexual competition for food. These indices are somewhat misleading however, because, as shown in Figures 7 and 9, the Hairy Woodpecker was most numerous at Deadman during the late summer and early fall when insect prey was most abundant, and least numerous during the winter and spring when insects were least abundant. The Northern Three-toed Woodpecker exhibited a similar but much less pronounced decline; comparisons of the largest totals in Tables 8 and 9, show that the ratio of the number of Northern Three-toed Woodpeckers to the number of Hairy Woodpeckers increased from $136:57 = 2.4:1.0$, when food resources at Deadman were highest, to $98:11 = 8.9:1.0$, when food resources were lower.

The disproportionate numerical decrease can be accounted for in two ways: differential mortality or differential emigration, neither of which is mutually exclusive. Differential mortality by factors other than predation cannot be discounted, but it seems likely that the relatively sedentary Northern Three-toed Woodpecker would be exposed to a higher rate of mortality by predation than would the more active Hairy Woodpecker. Thus, predators such as the marten (Martes americana) and the Goshawk (Accipiter gentilis), both of which were observed at Deadman, should be more important sources of mortality for the Northern Three-toed Woodpecker than for the Hairy Woodpecker. Therefore, differential mortality seems unlikely to be the mechanism causing the disproportionate numerical decrease

of the Hairy Woodpecker. Differential emigration, on the other hand, is a perfectly plausible explanation and, as discussed earlier, long-range movements of banded Hairy Woodpeckers have been documented.

Numerical decrease by either mechanism would accomplish the same end result--the presence of fewer individuals among which to partition the available food. Numerical decrease by emigration, however, could be a response to declining prey (Lack, 1954b), in which case, emigration would be a mechanism decreasing intersexual competition for food by the Hairy Woodpecker.

It appears, then, as if spruce-fir forests offer so few foraging strata for the Hairy Woodpecker that sexual dimorphism is of little adaptive value to it in reducing intersexual competition for food. Thus, emigration and concomitant numerical reduction was the mechanism reducing intersexual competition for food by Hairy Woodpeckers in the subalpine forest of the Rocky Mountains; whereas, differential niche utilization within a common habitat, where the sexes were able to forage in different strata (Selander, 1966), was the mechanism reducing intersexual competition for food by Hairy Woodpeckers in New England (Kilham, 1965).

The indices of difference in Table 25 suggest that there was little or no competition for food between the sexes of the Northern Three-toed Woodpecker at Deadman when prey was most abundant (Table 16), and that differential niche utilization within a common habitat, where the sexes were able to forage in different strata (Table 17), was the mechanism reducing competition for food between the sexes of the Northern Three-toed Woodpecker at Deadman when prey was less abundant.

Dietary Differences

Interspecific indices of dietary difference were calculated for North American woodpeckers from the data in Tables 26 through 31 and for Finnish woodpeckers from data provided by Pynnonen (1943); in addition, because it is one of the few studies with data suitable for both treatments, intraspecific as well as interspecific indices of difference were calculated for three species of accipiters from information provided by Storer (1966). The indices of difference (Tables 45 and 46) are the converse, $1 - C\lambda$, of Morisita's index of overlap, $C\lambda$, calculated from the formula,

$$C\lambda = \frac{2 \sum_{i=1}^S X_i Y_i}{(\lambda_x + \lambda_y) XY},$$

based upon characteristic food samples $|X_o|$ and $|Y_o|$ composed of a total of S species in both samples, where species i (or the lowest identifiable taxonomic level) is represented X_i times in $|X_o|$ and Y_i times in $|Y_o|$,

$$X = \sum_{i=1}^S X_i,$$

$$Y = \sum_{i=1}^S Y_i,$$

$$\lambda_x = \frac{\sum_{i=1}^S X_i (X_i - 1)}{X (X - 1)}, \text{ and}$$

TABLE 45. Indices of interspecific difference in the dietary component of character displacement. Parenthetical values were calculated from weight class differences

Species-pair	Status of prey populations	Total no. of dietary constituents (S)	Index of dietary difference	Source
<u>Picoides tridactylus</u> <u>Dendrocopos villosus</u>	endemic	12	0.55	This study
<u>Picoides tridactylus</u> <u>Dendrocopos villosus</u>	epidemic	12	0.36	This study
<u>Picoides tridactylus</u> <u>Dendrocopos pubescens</u>	epidemic	12	0.45	This study
<u>Dendrocopos villosus</u> <u>D. pubescens</u>	epidemic	11	0.11	This study
<u>Dendrocopos major</u> <u>D. minor</u>	endemic	58	0.95	Pynnönen, 1943
<u>Dendrocopos major</u> <u>Dryocopus martius</u>	endemic	57	0.90	Pynnönen, 1943

TABLE 45.--Continued

Species-pair	Status of prey populations	Total no. of dietary constituents (S)	Index of dietary difference	Source
<u>Dendrocopos minor</u> <u>Dryocopus martius</u>	endemic	49	0.98	Pynnonen, 1943
<u>Accipiter gentilis</u> <u>A. cooperi</u>	?	32(19)	0.95(0.53)	Storer, 1966
<u>Accipiter cooperi</u> <u>A. striatus</u>	?	29(14)	0.65(0.14)	Storer, 1966
<u>Accipiter striatus</u> <u>A. gentilis</u>	?	32(17)	0.99(0.75)	Storer, 1966

TABLE 46. Indices of intersexual difference in the dietary component of character displacement of North American Accipiters, calculated from weight-class differences. (Data from Storer, 1966)

Species of <u>Accipiter</u>	Total no. of dietary constituents (S)	Index of dietary difference
<u>A. striatus</u>	8	0.06
<u>A. cooperi</u>	14	0.08
<u>A. gentilis</u>	15	0.15

$$\lambda_y = \frac{\sum_{i=1}^s Y_i(Y_i - 1)}{Y(Y - 1)} .$$

Morisita's technique was adopted as the method for computing the indices because, as previously discussed, the different species of woodpeckers have different foraging adaptations; consequently, a given species of prey has a differential probability of being selected by a given species, and to a lesser extent even a given sex, of woodpecker. Morisita's technique was also used for analyzing the accipitrine data, since the larger prey items, available to the larger species and sexes of raptors, are largely unavailable to smaller raptors because of the latter's inabilities to capture and subdue the larger prey. Smaller prey is more available to smaller raptors, because the smaller raptors are morphologically and behaviorally better adapted for selecting smaller prey (Holling, 1964).

The indices of interspecific difference (Table 45) calculated from the results of this study are lower than the indices calculated from the data provided by Pynnonen (1942) and Storer (1966). This is because there was less resolution in the identification of prey remains reported on in this study than in the other two studies. With the exception of two to four genera of prey, most of the dietary constituents in Tables 26 through 31 were identified only to the family level; whereas, the taxonomic determinations of the other two studies were usually carried to the generic level. Thus, the indices of difference calculated from the results of this study are undoubtedly

lower than they should be, i.e.,--there are more differences among the dietary components of the Northern Three-toed, Hairy and Downy Woodpeckers than indicated by the indices shown in Table 45.

The indices of difference in the dietary components among the three species of woodpeckers studied in Colorado, even though too low, do indicate trends. Thus, the index of dietary difference between the Northern Three-toed and Hairy Woodpeckers from spruce-fir forests supporting endemic populations of bark beetles is less than that from forests supporting epidemic populations of bark beetles. Because Downy Woodpeckers are not regular inhabitants of spruce-fir forests supporting endemic populations of bark beetles (Figures 7-9), differences in the dietary components of the Downy Woodpecker and the other two woodpeckers from spruce-fir forests supporting endemic populations of bark beetles are greater than those from spruce-fir forests supporting epidemic populations of bark beetles.

The indices of dietary difference between the sexes of the accipiters (Table 46) had to be calculated from differences in weights of the prey; therefore, they are not comparable to the interspecific indices which were calculated from taxonomic differences of the prey. It was possible to calculate interspecific indices of dietary difference for the accipiters using both taxonomic and weight-class differences, and indices calculated from weight-class differences are smaller than those calculated from taxonomic differences (Table 45), probably because of the smaller number of constituents used in the weight class calculations. Even though the indices calculated from weight class differences are too small, they reflect the trends shown by indices calculated from taxonomic differences. Thus, the smallest

index of dietary difference, calculated by either method, is between Accipiter cooperi and A. striatus; the largest, between A. striatus and A. gentilis. By the same token, the intersexual indices of dietary difference, while undoubtedly low, suggest that the least difference in diet occurs between the sexes of A. striatus and the greatest difference occurs between the sexes of A. gentilis, while the difference between the sexes of A. cooperi, is intermediate. The only data available for intersexual dietary differences in woodpeckers are those for the Northern Three-toed Woodpecker in Table 32. These data are incomplete, so it is impossible to calculate an index of dietary difference for the Northern Three-toed Woodpecker that is comparable to those for the accipiters in Table 46.

The intersexual dietary difference in the Northern Three-toed Woodpecker shows a positive correlation between size of sex and size of prey selected (Table 32). As mentioned earlier, a positive correlation exists between size of Accipiter and size of prey selected; thus, the smallest Accipiter, males of striatus, select the highest proportion of the smallest prey taken by accipiters; and the largest Accipiter, females of gentilis, select the highest proportion of the largest prey taken by accipiters (Storer, 1966). One would predict a similar correlation between size of woodpecker and size of prey selected; Tables 26 through 31 show that the Downy Woodpecker selected a higher proportion of the small scolytid, Pityophthorus sp., than the other two woodpeckers, and that the Northern Three-toed Woodpecker selected a higher proportion of the larger scolytid, Dendroctonus engelmanni, than the other two woodpeckers. It is not possible to determine from the tables whether

the Hairy Woodpecker selected the largest prey, but Table 29 shows that formicids form a majority of the diet of Hairy Woodpeckers in spruce-fir forests supporting endemic populations of bark beetles; most of the formicids are carpenter ants, Camponotus sp., which are larger than scolytids. Thus, while the information for these woodpeckers is much more sketchy than that for the accipiters, the correlation between size of predator and size prey selected by the predator seems to hold for the woodpeckers as well as for the raptors.

Morphological Differences

There are several patterns of difference within the linear measurements presented in Table 33. Some of the patterns are correlated with previously mentioned differences in foraging behavior and dietary habits, and others convey implications for some additional and, as yet, unmentioned differences in dietary habits. As previously shown, there is a correlation both between the size of the woodpecker and the dimensional properties of its foraging substratum and between the size of a woodpecker and the size of prey it selects. It is the latter phenomenon that is of interest here and the one now to be considered.

One of the most striking patterns is the disproportionate difference in the sizes between the smallest and the intermediate-sized woodpeckers and the intermediate and largest-sized woodpeckers, the difference between the latter species-pair being less than that between the former (Figure 10). These differences in size are adaptive, serving to alleviate interspecific competition for food, especially between the congeneric species. A corroboration of this postulate is found in the disproportionate divergence in trophic

structure over non-trophic structure as seen between the smallest and each of the two larger species. Ratios of average values (large: small) between male Northern Three-toed Woodpeckers and male Downy Woodpeckers range from 1.03 to 1.32, and between male Downy Woodpeckers and male Hairy Woodpeckers from 1.32 to 1.43 for non-trophic measurements; whereas ratios of average culmen lengths for the same species-pairs are 1.70 and 1.87, respectively (Table 35). Ratios of average values for females of the same species-pairs are consistently smaller than ratios for the males: 1.03 to 1.28 and 1.25 to 1.40 for non-trophic measurements, and 1.65 to 1.73 for culmen lengths, respectively (Table 35). This implies greater interspecific competition between females than between males (whether this implication has any validity or not is completely speculative). Ratios of interspecific difference in trophic structure between the same sexes of the Northern Three-toed and Hairy Woodpeckers are mostly less than the ratios of difference between their non-trophic structures; however, the ratio of interspecific difference in culmen length between the male Northern Three-toed Woodpecker and the female Hairy Woodpecker is smaller than any other ratio of difference for this species pair (Table 35).

The differences between the means in Table 33 have been expressed as percentage differences (Table 36). Percentage differences reflect the same patterns as the ratios of small to large means, but are more readily converted to indices of morphological difference comparable to the indices of spatial, temporal and dietary difference. For example, the indices of difference in non-trophic measurements between male Downy and male Hairy Woodpeckers range from

0.25 (0.245) to 0.30 (0.302), and the index of difference in their culmen lengths is 0.47 (0.466). Comparing the indices and ratios of difference in mean culmen length for several species-pairs (Table 47) shows that the magnitude of interspecific difference in trophic structure between the Northern Three-toed and Hairy Woodpeckers is less than that of any other species-pair of woodpecker, and is comparable to that of the contiguously allopatric parids and the sympatric parulids.

Implications in the foregoing are the competition for food is minimal between the Downy Woodpecker and each of the other two woodpeckers and that competition could occur for food between the Northern Three-toed and Hairy Woodpeckers, especially between males of the former and females of the latter. However, as was discussed earlier, differences in foraging adaptations between the Northern Three-toed and Hairy Woodpeckers reduce the amount of competition for food implied, first by spatial overlap, and now by morphological overlap.

Schoener (1965) recently discussed the theoretical implications of differences in bill size among sympatric, congeneric species of birds. He concluded that species-pairs exhibiting small ratios of difference in bill size--large:small bill ratios, less than 1.14--eat foods that are fairly abundant and are able, therefore, to tolerate more dietary overlap than forms exhibiting large differences in bill size--large:small bill ratios, greater than 1.14. The latter forms, because of the relative scarcity of their food, achieve sympatry by selecting foods of different sizes. The ratios of difference in mean culmen length between the congeneric

TABLE 47. Indices of interspecific difference in mean culmen lengths of adult male birds. (S is the smaller and L the larger average of a given species pair)

Species-pair	Mean culmen length (mm)		Ratio of difference S/L	Index of difference (L - S)/L
	S	L		
<u>Parus carolinensis</u> -- <u>P. atricapillus</u>	8.3	9.0	1.08	0.08
<u>Dendroica coronata</u> -- <u>D. tigrina</u>	9.8	9.8	1.00	0.00
<u>D. tigrina</u> -- <u>D. virens</u>	9.8	9.9	1.01	0.01
<u>D. virens</u> -- <u>D. castanea</u>	9.9	10.0	1.10	0.09
<u>D. tigrina</u> -- <u>D. castanea</u>	9.8	10.9	1.11	0.10
<u>Sitta pygmaea</u> -- <u>S. canadensis</u>	14.0	14.7	1.05	0.05
<u>S. canadensis</u> -- <u>S. carolinensis</u>	14.7	19.1	1.30	0.26
<u>S. pygmaea</u> -- <u>S. carolinensis</u>	14.0	19.0	1.36	0.27
<u>Picoides tridactylus</u> -- <u>P. arcticus</u>	28.0	34.5	1.23	0.19
<u>Dendrocopos pubescens</u> -- <u>P. tridactylus</u>	14.1*	24.0*	1.70	0.41

TABLE 47.--Continued

Species-pair	Mean culmen length (mm)		Ratio of difference S/L	Index of difference (L - S)/L
	S	L		
<u>P. tridactylus</u> -- <u>D. villosus</u>	24.0*	26.4*	1.10	0.09
<u>D. pubescens</u> -- <u>D. villosus</u>	14.1*	26.4*	1.87	0.47
<u>D. minor</u> -- <u>D. medius</u>	12.4	17.9	1.44	0.31
<u>D. medius</u> -- <u>D. major</u>	17.9	23.8	1.33	0.25
<u>D. minor</u> -- <u>D. major</u>	12.4	23.8	1.92	0.48
<u>Accipiter striatus</u> -- <u>A. cooperi</u>	10.8	15.2	1.41	0.29
<u>A. cooperi</u> -- <u>A. gentilis</u>	15.2	19.7	1.30	0.23
<u>A. striatus</u> -- <u>A. gentilis</u>	10.8	19.7	1.81	0.45

* culmen length from anterior edge of nostril

Downy and Hairy Woodpeckers greatly exceed 1.14 (Table 47), and the two birds also select foods of different size; thus, the morphological and behavioral relationships of these two woodpeckers conform to Schoener's thesis. The ratios of difference in bill length between the Downy and Northern Three-toed Woodpeckers exceed 1.14, and the birds also select foods of different size; the ratios of difference in bill lengths between the Northern Three-toed and Hairy Woodpeckers, however, are less than 1.14, but the two birds take foods of different size. Thus, as might be expected, it appears as if differences in bill size within associations of closely related, yet intergeneric, species cannot be trusted to predict dietary differences within the associations.

The relatively small difference in the culmen lengths of the Red- and White-breasted Nuthatches (Table 47) implies a partitioning of food in this species-pair by some means other than size. Indeed, the Red-breasted Nuthatch seems to be spatially and temporally isolated from the White-breasted Nuthatch during the reproductive season, and also the species-pair exhibits a high degree of spatial and temporal difference (Table 43) during the post-reproductive season (Stallcup, 1966); thus, while the two birds may be taking foods of similar size, they are taking them in different places.

A second and equally striking pattern is the increase in degree of sexual dimorphism associated with the increase in body size. Although females of all three species average smaller than males, the sexual difference in size is least in the smallest species and greatest in the largest species (Table 33 and Figure 10). As was the case for the interspecific morphological differences, there

is a disproportionate degree of dimorphism in trophic structure. With the exception of measurements of weight for the Northern Three-toed Woodpeckers which, as mentioned earlier, are probably biased by sampling error, the percent of nonoverlap in the cube roots of the weights of the sexes is less than the nonoverlap in their culmen lengths (Figure 10 and Table 34). Furthermore, the per cent nonoverlap in culmen lengths is least, 67 per cent, between the sexes of the smallest species and greatest, 91 per cent, between the sexes of the largest species (Table 34). Comparisons of averages show this pattern most clearly: ratios of large to small averages for non-trophic measurements are fairly constant, ranging from 1.00-1.02 in the smallest species to 1.02-1.03 in the largest species, while ratios for trophic measurements range from 1.04 in the smallest species to 1.12 in the largest (Table 35).

The two facts of correlation between size of sex and size of prey selected by Northern Three-toed Woodpeckers (Table 32) and the disproportionate degree of sexual dimorphism in trophic structure can only be interpreted to mean that the dimorphism in trophic structure is adaptive in this species, serving to alleviate competition for food between the sexes.

An increase in the degree of sexual dimorphism in bill size associated with an increase in body size seems to be characteristic of the genus Dendrocopos, yet may not be characteristic of the genus Picoides (Table 48); although evidence on the latter point is inconclusive. P. arcticus is larger but apparently no more sexually dimorphic than P. tridactylus, and D. villosus is larger and apparently no more dimorphic than D. stricklandi (Table 48); yet

TABLE 48. Indices and ratios of intersexual difference in mean culmen lengths of adult female (F) and male (M) woodpeckers. Listed in order from the smallest to largest species

Species	Mean culmen length (mm)		Ratio of difference M/F	Index of difference (M - F)/F	Source
	F	M			
<u>Dendrocopos pubescens</u>	13.6*	14.1*	1.04	0.04	This study
<u>D. nuttallii</u>	19.3	20.8	1.08	0.07	Ridgway, 1914
<u>D. scalaris cactophilus</u>	19.8	22.7	1.15	0.13	Ridgway, 1914
<u>D. stricklandi arizonae</u>	19.3*	22.4*	1.16	0.14	Davis, 1965
<u>D. borealis</u>	20.3	21.4	1.05	0.05	Ridgway, 1914
<u>D. villosus monticola</u>	23.5*	26.4*	1.12	0.11	This study
<u>Picoides tridactylus</u>	22.4*	24.0*	1.07	0.07	This study
<u>P. arcticus</u>	30.7	33.0	1.07	0.07	Ridgway, 1914

* culmen length from anterior edge of nostril

D. v. leucothorectis, similar in size to D. v. monticola, exhibits a ratio of difference in mean culmen length of 1.19 and an index of difference in mean culmen length of 0.16. Thus, the question of whether P. arcticus is more sexually dimorphic than P. tridactylus will have to await the acquisition of more specimens throughout the geographic ranges of both species.

An interspecific size effect, especially among insectivorous birds, paralleling the intersexual size effect has been demonstrated by Schoener (1965). The effect is based upon a presumed inverse relationship between size and density of prey. Thus, smaller sympatric congeneric species exhibit more overlap in trophic structure than do larger species, because the smaller species feed on smaller prey which are more abundant than larger prey.

The assumption of an inverse relationship between size and density of prey has some validity because, if nothing else, younger and smaller instars of insects are generally more numerous than older and larger instars, which in turn are more numerous than the still larger imagoes and adults (Figure 6). Also, there is undoubtedly much more bark area on the branches and twigs than on the stems of snags; branches and twigs are inhabited by smaller species of bark beetles to a much greater extent than is the stem. Thus, there is reason to believe that the disproportionate increase in degree of sexual dimorphism in trophic structure associated with an increase in the body size of Dendrocopos and possibly Picoides is associated with an inverse relationship between size and density of their prey.

Components of Predation

Interrelating the population dynamics revealed in this study with those revealed by Amman (1958) and Baldwin (1960), who reported on woodpecker densities during an initial spruce beetle outbreak covering about one square mile, and Hutchison (1951), who reported on woodpecker densities during a catastrophic epidemic covering thousands of square miles (Knight, 1950), permits an analysis of the components of predation (Holling, 1959) of this predator-prey system.

Spruce Beetle Densities

One of the variables affecting population size of the Engelmann spruce beetle is the proportional relationship between the number of beetles emerging as adults and the number of prostrate trees available for breeding sites. Endemic populations of the spruce beetle are maintained at levels where the number of emerging adults does not greatly exceed the capacity of the downed material to absorb them. If, as was apparently the case in the White River National Forest, an unusual amount of downed material becomes available, spruce beetle numbers can build to epidemic levels, and when the downed trees become saturated, the beetles proceed to attack living trees. The rate at which spruce trees are killed by endemic populations of the spruce beetle is unknown, but four trees killed by spruce beetles during the spring of 1962 were found within an 800 acre area at Deadman, suggesting a rate of 0.005 spruce trees per acre per year being killed by endemic populations of the insect.

It is possible to obtain density estimates of endemic spruce beetle populations from the data provided in Table 4 and Figure 7. Fall estimates are the most meaningful because this is the time of

the year when larvae first become large enough to count easily and fall is also the time of the year when woodpeckers begin feeding on scolytid larvae. Table 4 shows that 31 spruce trees were thrown by wind during each of the years 1963 and 1964; if 31 is an accepted annual rate, there were 31 blowdowns plus the 22 trap trees felled in October 1961, or a total of 53 prostrate spruce trees available for spruce beetle occupancy during the spring of 1962. Most field observations were conducted within an area of about 800 acres; thus, there was a calculated density of 0.07 ($53/800$) prostrate trees per acre. Figure 7 shows that there was an average of 120 (4×30) spruce beetle larvae per square foot of habitable bark on these trees in the fall of 1962.

No beetle counts were obtained from standing trees, but it can be argued that 66 larvae per square foot of bark is a reasonable figure, because there is a minimum spruce beetle density which can successfully kill a tree; if this density does not materialize, then the physiological resistance of the tree causes a "pitch out" of the attack, i.e., the trauma of the attack causes an increased flow of pitch which literally drowns the beetles in their egg galleries (Dr. N. D. Wygant, pers. comm.). The smallest number of brood found in trees killed by the spruce beetle was 66 larvae per square foot (Massey and Wygant, 1954); this is very likely the minimum larval density resulting from a successful attack.

Spruce beetles inhabit the bark of the average stem of trap trees from the base to a length of 58 feet, at which point the stem averages five inches in diameter (Massey and Wygant, 1954); the basal diameter of 31 spruce blowdowns at Deadman averaged 16 inches. The

stems of spruce trees are cone-shaped, consequently, the average amount of available bark per log was calculated by the formula for the frustum of a right cone, resulting in an average of 161.2 square feet of bark area per stem. Spruce beetles prefer the lateral and bottom surfaces of stems, their presence in upper surfaces being directly related to the amount of shading from the sun (Nagel, et al., 1957). If at least half the bark surface of the average log is habitable, then the amount of bark occupied is 80.6 square feet per stem.

All four of the standing trees killed by spruce beetles at Deadman were approximately 24 inches d.b.h., a diameter class which, according to Massey and Wygant (1954), becomes infested to an average height of 31 feet. The 31 spruce blowdowns at Deadman had an average taper of 0.86 inches in 16 feet (e.g., a tree with a 10-inch d.b.h. has an 8.6-inch diameter at 16 feet above the ground). Thus, trees which tapered to 20.6 inches in 16 feet are supposed to have tapered proportionately to 17.4 inches in 31 feet, resulting in a calculated 150.4 square feet of habitable bark area per tree.

Combining the foregoing calculations results in an estimated 680 larvae per acre in the bark of the 1962 trap trees and blowdowns, and an estimated 50 larvae per acre in the bark of standing trees killed by the spruce beetle in 1962 (Table 49). These larvae represent first-year brood; but since the Engelmann spruce beetle has a two-year life cycle, second-year brood from the infestation of blowdowns and standing trees in 1961 was also present at Deadman during the fall of 1962.

TABLE 49. Estimated densities of Engelmann spruce beetle (ESB) brood per acre, calculated from the average number found per square foot of infested bark on prostrate and standing trees

Location	No. trap logs per acre	No. infested trees per acre	Ave. no. sq. ft. inhabited per log or tree	Ave. no. ESB brood per sq. ft.	No. 1st year ESB brood per acre	No. 2nd year ESB brood per acre	Total no. ESB brood per acre
Deadman, Fall 1962	.07		80.6	120	680		
	.04		80.6	85		274	
		.005	150.4	66	50		
		.005	150.4	11		8	1,012
Deadman, Fall 1963	.06		80.6	74	360		
	.07		80.6	7		40	
		.005	150.4	3		2	402
Wolf Creek Pass, Fall 1956		7.0	108.6	181	137,596		
		7.0	108.6	30		22,806	160,402
Rabbit Ears Pass, Fall 1949		40.7	86.7	316	1,115,066		
		42.5	86.7	42		523,235	1,638,300

In the absence of more suitable data, the same calculated number of blowdowns and standing trees are assumed to have been infested by the spruce beetle at Deadman during 1961. It is also assumed that during the fall of 1961 there were 120 and 66 larvae per square foot of habitable bark on blowdowns and standing trees, respectively. It is further assumed that brood in the blowdowns suffered an overwinter mortality of 29 per cent, the same reduction exhibited by the relatively more "normally affected" 1963 brood (Figure 6) and that brood in the standing trees suffered a first-year mortality of 83 per cent, the rate necessary to decrease the brood count to 11 larvae per square foot. This was the number found by Knight (1958) in bark lightly disturbed by woodpeckers in the course of their feeding activities; lightly disturbed bark contained brood resulting from the minimal number of parental spruce beetles required to kill a tree.

Cold during the winter of 1962-1963 reduced first-year survival of the 1962 brood to approximately seven (4×1.7) larvae per square foot (Figure 6), and it so reduced second year survival of the 1961 brood, emerging and reproducing in the spring of 1963, that larvae were found in the 1963 trap logs during the fall count at the relatively low density of 74 (4×18.6) per square foot of bark (Figure 6). If the cold killed the same proportion of 1962 brood in the standing trees as in the logs (92 per cent), then there were seven larvae per square foot of bark in logs and four per square foot in standing trees during the fall of 1963. There were 20 trap logs and 31 spruce blowdowns (Table 4) available for breeding habitat during the spring of 1963. No trees killed by spruce beetles

in 1963 were found; the relative abundance of prostrate material in relation to the small number of spruce beetles emerging in 1963 undoubtedly accounts for this fact.

The density of infested trees in a local outbreak of the Engelmann spruce beetle at Wolf Creek Pass, Mineral County, Colorado, was estimated to be 14 per acre (Amman, 1958). It is assumed that seven trees per acre contained first-year brood of the spruce beetle and the other seven, second-year brood. This assumption is based upon the fact that Hutchison found approximately half the infested trees at Rabbit Ears Pass, Routt County, Colorado, contained first-year brood and the other half second-year brood. The amount of infested bark per tree was calculated from data on basal diameters provided by Amman (1958), on height of infestation from Massey and Wygant (1954) and on taper of the stem from the 31 spruce blowdowns at Deadman. Knight (1958) found an average of 181 larvae per square foot in bark protected from predation by woodpeckers; in the absence of more suitable data, this is assumed to have been the fall density of first-year brood at Wolf Creek Pass. The number of second-year brood averaged 30 per square foot of infested bark.

Hutchison (1951) determined the relative frequencies of infested spruce trees in the catastrophic epidemic near Rabbit Ears Pass, but he failed to estimate their density. Amman (1958), however, ascertained densities of trees in a nearby area, presumed comparable, so the two sources of information were combined, yielding an estimated density of 83.2 infested spruce trees per acre. Hutchison determined the average amount of infested bark per tree and estimated an average fall density of 316 first-year and 142 second-year larvae

per square foot of infested bark.

These considerations, summarized in Table 49 suggest fall densities of approximately 400 to 1,000 larvae per acre in areas supporting endemic populations of the Engelmann spruce beetle and 160,000 to 1,600,000 larvae per acre in areas supporting epidemic populations of the beetle.

Numerical Response of Woodpeckers to Prey Density

Average fall densities of the woodpecker population on the Deadman study area were estimated to be 0.03 and 0.02 birds per acre in 1962 and 1963, respectively (Table 5 and Figure 8); fall densities of woodpeckers at Wolf Creek Pass and Rabbit Ears Pass, 1.35 and 1.26 per acre, respectively (Amman, 1958; Baldwin, 1960; and Hutchison, 1951). The factors responsible for the similarity in densities of the woodpecker populations at Wolf Creek Pass and Rabbit Ears Pass are obscure, but they may be related to the fact that the beetle epidemic at Wolf Creek Pass covered much less area, resulting in a concentration of the woodpecker population there, while the population in the more extensive epidemic at Rabbit Ears Pass is expected to have been more uniformly distributed. The composition of these two populations differed also: relative frequencies of the three species were approximately equal at Wolf Creek Pass (Baldwin, 1960), while the Northern Three-toed Woodpecker was the most prevalent species at Rabbit Ears Pass (Hutchison, 1951). Thus, there was an average of 0.45 Northern Three-toed Woodpeckers per acre at Wolf Creek Pass and 0.92 per acre at Rabbit Ears Pass. The latter figure is an estimate necessitated because Hutchison (1951) lumped all species of woodpeckers

the figure is based upon the fact that, of the woodpeckers located at Deadman during each fall and at Wolf Creek Pass during the fall of 1957, approximately 73 per cent were Northern Three-toed Woodpeckers. Average frequencies of occurrence of the three species of woodpeckers at Deadman were almost identical to the average frequencies at Wolf Creek Pass, implying that the observed frequencies are representative of the composition of fall populations of woodpeckers in spruce-fir forests in general. Thus, average values of the observed frequencies of occurrence were used to estimate the composition of the fall population of woodpeckers at Rabbit Ears Pass. In addition to 0.92 Northern Three-toed Woodpeckers per acre, it is estimated that 0.04 Downy and 0.30 Hairy Woodpeckers per acre also were present at Rabbit Ears Pass.

In summary, average densities of 0.02 to 0.03, 1.35, and 1.26 woodpeckers per acre have been found in areas supporting densities of approximately 400-1,000, 160,000, and 1,600,000 larvae per acre, respectively, in the fall. Otvos (1964) estimated densities of Hairy and Downy Woodpeckers in forests containing endemic and epidemic populations of Dendroctonus brevicomis Lec., and reported averages of 0.01 Downy and 0.05 Hairy Woodpeckers per acre in the endemic infestations, and 0.04 Downy and 0.11 Hairy Woodpeckers per acre in the epidemic infestation. Thus, it can be concluded that woodpeckers exhibit a numerical response to prey density. The dynamics of the numerical response warrant consideration, however.

Even though information on densities of insects in the trees killed and damaged at Deadman by the fire in 1962 is lacking, the situation is instructive because it represents the appearance of a

food surplus; the numerical response of woodpeckers to the food surplus was studied. The insects were not attractive until the summer of 1964, as evidenced by the concentration of woodpeckers present from that time until the following spring (Figures 7-9); it is certain that this concentration was the result of drift and aggregation and that increased reproduction was not involved.

A thorough search of four square miles in the vicinity of Deadman Lookout turned up evidence of three woodpecker nests, or approximately 0.01 nests per acre, during the spring of 1963. A similar search of the 800-acre area encompassing the majority of the Deadman study plot during the spring of 1964, disclosed one nest, or approximately 0.01 per acre. Thus, nesting densities of the two years are similar, and it can be concluded that the rather small-scale food supply provided by insects in the ten acres of burned forests at Deadman did not induce an increased rate of reproduction in the resident woodpecker population.

The largest number of Northern Three-toed Woodpeckers observed in the burned area at any one time was 11, the largest number of Hairy Woodpeckers was four, and the largest number of Downy Woodpeckers was two, representing calculated densities of 1.10, 0.40, and 0.20 birds per acre respectively.

An accumulation of 11 Northern Three-toed Woodpeckers would involve movements of all birds previously distributed at 0.01 to 0.02 birds per acre--the average density of Northern Three-toed Woodpeckers in the fall of 1962 and 1963 (Figure 7)--within a radius of 2,760 to 3,900 feet ($3.1414 \times 2,760^2$ to $3,900^2$ feet = 550 to 1,100 acres). Average densities of the Hairy Woodpecker in the fall

of 1962 and 1963 were 0.005 to 0.015 individuals per acre, respectively; for this bird to achieve a concentration of 0.40 birds per acre would entail movements within a radius of 1,920 to 3,330 feet ($3.1414 \times 1,920^2$ to $3,330^2$ feet = 267 to 800 acres). The limited information on previous densities of the Downy Woodpecker makes it difficult to estimate the distances travelled by them in the fall of 1964 in achieving a concentration of 0.20 birds per acre.

A total of five nestlings was in two nests of the Northern Three-toed Woodpecker found at Deadman; all five were banded, and all five fledged. The banded young were frequently observed at distances up to 0.6 mile (about 3,200 feet) from the nest trees. These movements are commensurate with those required to effect the aggregation of Northern Three-toed Woodpeckers observed in the burned area at Deadman. First-hand information on distances moved by Hairy and Downy Woodpeckers is lacking; however, Staebler (1949) has assembled data on movements for these two birds from records of banding returns in the files of the U. S. Fish and Wildlife Service. One Hairy Woodpecker was recovered 48 miles from where it was banded and three others were recovered at distances approximately 20 miles from where they were banded. All four movements are well within the distances required to bring about the concentration of Hairy Woodpeckers noted in the burned area at Deadman. Three Downy Woodpeckers were recovered at distances of 50 to 185 miles from where they were banded. Downy Woodpeckers are known to nest in and regularly frequent montane forests in Colorado; montane vegetation exists within 6.5 to 10.5 airline miles from Deadman, distances well within the movements recorded for banded Downy Woodpeckers. Thus it

can be concluded that the numerical response of woodpeckers to short-term food surpluses, such as occurred in the burned area at Deadman in 1964 and 1965, is effected by aggregation. Aggregation is probably the initial response of woodpeckers--indeed, of mobile predators in general (Craighead and Craighead, 1956; Craighead, 1962)--to a newly arisen food surplus.

The numerical response of at least the Northern Three-toed Woodpecker to longer-term food surpluses is enhanced by an increase in nesting density. Baldwin (1960 and pers. comm.) found evidence of six Northern Three-toed Woodpecker nests within the one-square-mile epidemic at Wolf Creek Pass. He was unable to determine brood sizes of the six nests, but even if brood size remained unchanged, the number of nests per unit area was approximately nine times that found at Deadman, since the density was 0.09 nests per acre at Wolf Creek Pass and about 0.01 nests per acre at Deadman. The net affect is at least a ninefold increase in the number of young produced per 100 acres at Wolf Creek Pass over the number of young produced at Deadman.

Functional Response of Woodpeckers to Prey Density

Tables 26 and 29 show that spruce beetles comprised an average of 5.3 per cent (49/933) of the total number of prey recorded in the stomachs of the woodpeckers collected in forests supporting endemic populations of the beetle. Tables 27, 28, 30 and 31 show that the beetle represented 20.9 per cent (1127/5383) of the prey in stomachs from woodpeckers collected at Wolf Creek Pass during the spruce beetle epidemic there during 1956 and 1957. Spruce beetles formed 99 per cent of the prey from woodpeckers collected in the catastrophic

epidemic at Rabbit Ears Pass (Hutchison, 1951). It is not readily apparent as to why the functional response of the woodpeckers to the spruce beetle epidemic at Wolf Creek Pass was less pronounced than the functional response of the birds to the epidemic at Rabbit Ears Pass, but is probably related to differences in the nature of the build-up of the two epidemics. The epidemic at Wolf Creek Pass had gone through a gradual build-up over a period of years, whereas the epidemic at Rabbit Ears Pass was one that started explosively from spruce beetles moving in from elsewhere (N. D. Wygant, pers. comm.). In the former situation the dead trees from previous years would have attracted a variety of secondary beetles which functioned as alternative prey and reduced the proportion of spruce beetles consumed, while in the latter situation the recency of the invasion meant that mainly spruce beetles were available for consumption.

Spruce Beetle Mortality from Woodpecker Predation

It is possible to measure the impact of predation by woodpeckers upon populations of spruce beetle by combining the numerical and functional responses. This is accomplished by multiplying the number of beetles consumed per day at each density of the prey by the number of effective woodpecker-days. A woodpecker-day is defined as the normal feeding activities of one woodpecker for one day (24 hour period). In order to estimate the number of beetle larvae consumed per woodpecker-day, it is first necessary to establish the rate of turnover in numbers of beetles per stomach per day. This can be accomplished by solving the formula:

$$T_{OR} = \frac{M_{GE}}{(N_{S1})(KCN_1) + (N_{S2})(KCN_2) + \dots + (N_{Sn})(KCN_n)},$$

where:

T_{OR} = turnover rate per stomach per day,

M_{GE} = intake of gross energy by woodpeckers, in kilocalories per day,

N_{S1} = number of insects of species 1 per stomach,

N_{S2} = number of insects of species 2 per stomach,

N_{Sn} = number of insects of species n per stomach,

KC_{N1} = kilocalories of energy per individual of species 1,

KC_{N2} = kilocalories of energy per individual of species 2, and

KC_{Nn} = kilocalories of energy per individual of species n.

M_{GE} is a function of temperature and can be calculated for the three species of woodpeckers from the formulae in Table 42, N_S is a function of stomach capacity and an unknown, and KC_N is a constant for each species of prey, having the values for the insects listed in Table 39.

N_S can be estimated from data provided by Hutchison (1951), who analyzed the contents of 77 stomachs from woodpeckers collected in the spruce-beetle epidemic at Rabbit Ears Pass. He counted the number of insects found in each stomach and reported that spruce beetles constituted 99 per cent of the contents. Thus, it can be safely assumed that the stomachs contained only larvae of spruce beetles and the formula for rate of turnover simplifies to

$$T_{OR} = \frac{M_{GE}}{(N_S)(KC_N)}, \text{ where:}$$

T_{OR} = the number of larval spruce beetles per stomach, and

KC_N = kilocalories of energy per larva.

Hutchison stratified his results according to sex but not species because, "... it was found that the number of Downy and Hairy

Woodpeckers killed was not large enough to compare with the number of . . . Three-toed Woodpeckers . . ." He found a total of 3,969 larvae, or an average of 52 per stomach.

Setting the temperature at 0° F and solving for T_{OR} , given the value of M_{GE} for the Northern Three-toed Woodpecker to be 63.336--i.e., the average gross energy for males and females, $\frac{64.703 + 61.969}{2} = 63.336$ --results in a value of 63.95, which is the number of times during a 24 hour period when a woodpecker feeding solely on spruce beetles would have to accumulate 52 spruce beetle larvae. This is also the average rate at which larvae are digested when the temperature is 0° F, regardless of the number of larvae involved at any one time. If a bird will digest groups of 52 larvae 63.95 times every 24 hours, it follows that the bird will digest 52 larvae 2.6 ($63.95/24$) times every hour. It is suggested, furthermore, that a bird feeding on a variety of foods should digest individual larvae of the spruce beetle at the same average rate of 2.6 larvae per hour when temperature is 0° F. Thus, an estimate of the turnover rate T_{OR} , of any digestible item is of heuristic value, for it permits estimation of the average number of items an animal would be expected to consume per unit time at any given temperature.

Rate of turnover, or digestive rate, of homoiotherms is a function of the physiological mechanisms maintaining body temperature and should, therefore, be a constant at any given temperature for phylogenetically related organisms. Consequently, T_{OR} should be a constant at any given temperature for all three species of woodpeckers, and N_S should vary directly with the size and the concomitant metabolic demands of a given species of woodpecker. Thus, N_S was

calculated for the three species of woodpeckers, given $T_{OR} = 63.95$, with these results: Downy Woodpeckers = 35.6, Northern Three-toed Woodpecker = 52.6, and Hairy Woodpecker = 58.5 larvae per stomach.

Having estimates for N_S and KC_N permits a re-expression of the formula for rate of turnover as a function of temperature. Reference to Table 42 shows that the generalized formula for gross energy is:

$$M_{GE} = Y_{int.} + kT, \text{ where:}$$

$Y_{int.}$ = expenditure of gross energy when temperature equals

$0^{\circ} F$,

k = slope,

T = temperature in $^{\circ}F$.

Therefore,

$$\begin{aligned} T_{OR} &= \frac{Y_{int.} + kT}{(N_S)(KC_N)} \\ &= \frac{Y_{int.}}{(N_S)(KC_N)} + \frac{k}{(N_S)(KC_N)} T. \end{aligned}$$

It has been shown that an approximation of $\frac{Y_{int.}}{(N_S)(KC_N)} = 63.95$; it remains for $\frac{k}{(N_S)(KC_N)}$ to be estimated. This can be accomplished by dividing the slopes, k , in the formulae for gross energy in Table 42, by the appropriate values of $(N_S)(KC_N)$. For example, the slope, k , for Downy Woodpeckers equals .260, $N_S = 36$ and $KC_N = .019$; thus $\frac{k}{(N_S)(KC_N)} = 0.38$. Similar computations for the other two species produced the following: Northern Three-toed Woodpecker 0.37, and Hairy Woodpecker 0.36, or an average of 0.37 for all three species. Thus, the generalized formula for rate of turnover of larvae as a function of temperature is : $T_{OR} = 63.95 - 37T$; Figure 14 is a graphic representation of the rate of turnover throughout the range

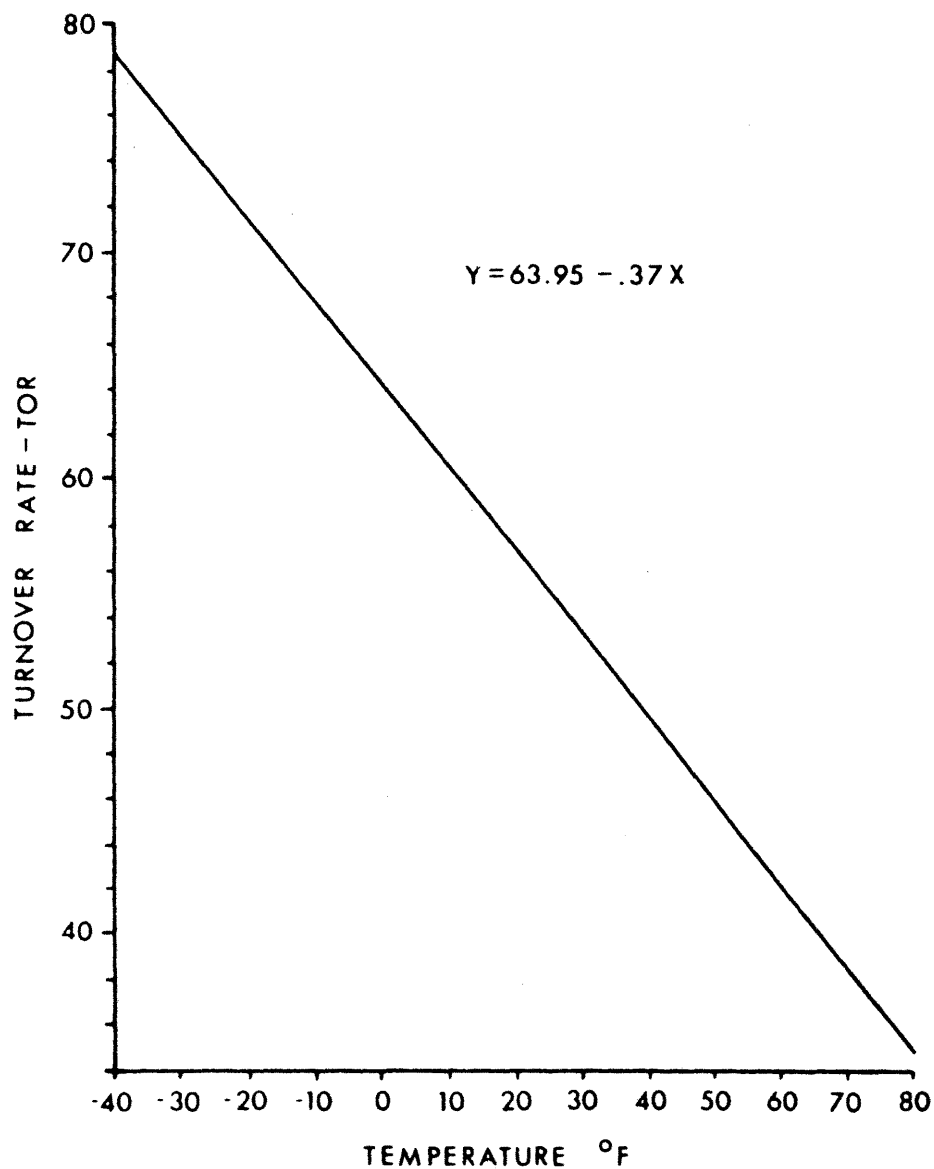


Figure 14. Daily rates of turnover or number of larvae of the Engelmann spruce beetle digested per day per woodpecker throughout the range of temperatures recorded on the Deadman study area.

of ambient temperatures recorded at Deadman.

Data on temperature are not available for spruce-fir forests, consequently, it is assumed that the temperatures summarized in Figures 2 through 5 are representative of spruce-fir forests in Colorado; weekly, biweekly, monthly or trimonthly averages of the data provided the basis for the calculated seasonal rates of turnover presented in Table 50.

The numbers of larvae of the Engelmann spruce beetle annually consumed per acre at Deadman, Wolf Creek Pass and Rabbit Ears Pass were estimated by multiplying the seasonal rates of turnover in Table 50 by the average number of larvae found per stomach from woodpeckers collected in these or comparable areas. The resultant values in turn were multiplied by the number of days the woodpeckers were known, or estimated to have been in these areas; finally, the latter values were multiplied by the average number of woodpeckers per acre for each time interval.

The average number of larvae per woodpecker stomach was determined for Deadman and Wolf Creek Pass from the data in Tables 18 and 19, and for Rabbit Ears Pass from data provided by Hutchison (1951) and Massey and Wygant (1954). Densities of woodpeckers were estimated for Deadman from the data in Table 5 and Figure 7, for Wolf Creek Pass from data provided by Amman (1958) and Baldwin (1960), and for Rabbit Ears Pass from data provided by Hutchison (1951). Hutchison did not census woodpeckers throughout a full year, therefore, average densities of woodpeckers were used for those months for which there were no census data.

TABLE 50. Seasonal rates of turnover, or rates at which larvae of the Engelmann spruce beetle are digested by woodpeckers for average conditions of temperature in spruce-fir forests

Dates	Time interval	Ave. temp. °F for interval	T _{OR}
July 29 to Aug. 5	7 days	57.4	42.7
Aug. 6 to Aug. 12	" "	53.7	44.1
Aug. 13 to Aug. 19	" "	53.6	44.1
Aug. 20 to Aug. 26	" "	48.9	45.9
Aug. 27 to Sept. 2	" "	46.2	46.9
Sept. 3 to Sept. 9	" "	51.1	45.0
Sept. 10 to Sept. 16	" "	47.5	46.4
Sept. 17 to Sept. 23	" "	42.7	48.2
Sept. 24 to Sept. 30	" "	43.0	48.0
Oct. 1 to Oct. 7	" "	44.9	47.3
Oct. 8 to Oct. 14	" "	41.2	48.7
Oct. 15 to Oct. 21	" "	40.1	49.1
Oct. 22 to Oct. 28	" "	37.7	50.0
Oct. 29 to Nov. 4	" "	27.2	53.9
Nov. 5 to Nov. 18	14 days	27.0	54.0
Nov. 19 to Dec. 2	" "	19.8	56.6
Dec. 3 to Dec. 21	" "	14.0	58.8
Dec. 22 to April 3	103 days	13.3	59.0
April 4 to April 26	23 days	20.3	56.4
April 27 to May 10	14 days	29.1	53.2
May 11 to June 14	35 days	38.3	49.8
June 15 to June 21	7 days	43.9	47.7
June 22 to June 28	" "	55.3	43.5
June 29 to July 5	" "	55.8	43.3
July 6 to July 12	" "	54.3	43.9
July 13 to July 19	" "	57.9	42.5
July 20 to July 28	9 days	59.0	42.1

Calculations of the number of larvae consumed during the months of January through May were not included for Deadman, since throughout this period of time all fallen trees were buried under snow. Calculations of the number of larvae consumed during June and most of July are not included for either Deadman or Wolf Creek Pass, since woodpeckers were not then feeding upon spruce beetles to any extent. That is, the earliest that woodpeckers at Deadman began flaking bark from the trap logs was July 29; Tables 26 through 31 include only three stomachs with remains of spruce beetles from a total of 37 collected in June and July. Calculations of the number of larvae consumed at Rabbit Ears Pass include every month of the year. However, Massey and Wygant (1954) found averages of only 2.6, 1.4 and 12.4 larvae per stomach from a total of 115 woodpeckers collected during July, August and September, respectively. Thus, larvae of the spruce beetle although preyed upon by woodpeckers throughout the year at Rabbit Ears Pass, were preyed upon to a much lesser extent during the summer than during the winter.

Table 51 summarizes the estimated number of larvae of the spruce beetle consumed annually at Deadman, Wolf Creek Pass and Rabbit Ears Pass, respectively. A comparison of Tables 49 and 51 shows that predation by woodpeckers would have killed 20 to 50, 84, and 59 per cent of the total estimated number of larvae at Deadman, Wolf Creek Pass and Rabbit Ears Pass, respectively. These estimates are in quite close agreement with estimates made by comparing the number of larvae surviving in bark protected from woodpeckers with the number surviving in bark exposed to woodpeckers. Figure 7 shows that predation by woodpeckers accounted for $2 \left(\left(\frac{30.1-1.7}{30.1} \right) - \left(\frac{30.1-2.4}{30.1} \right) \right)$

TABLE 51. Estimated number of Engelmann spruce beetle larvae consumed per acre per year as a result of woodpecker predation

Woodpecker	No. of larvae consumed/acre		
	Deadman	Wolf Creek Pass	Rabbit Ears Pass
Downy	--	19,685	19,867
Northern Three-toed	183	71,553	692,916
Hairy	16	44,055	246,304
Total	199	135,293	959,087

per cent of the first-year and $23 \left(\frac{1.7-0.2}{1.7} \right) - \left(\frac{1.7-0.6}{1.7} \right)$ per cent of the second-year mortality of the 1962 brood; and $20 \left(\frac{18.6-14.9}{18.6} \right)$ per cent of the first-year and $32 \left(\frac{14.9-0.7}{14.9} \right) - \left(\frac{14.9-5.5}{14.9} \right)$ per cent of the second-year mortality of the 1963 brood at Deadman. Knight (1958) showed that predation by woodpeckers at Wolf Creek Pass reduced survival of spruce beetles an average of 83 per cent, and Hutchison (1951) estimated that woodpeckers killed approximately 55 per cent of the spruce beetles at Rabbit Ears Pass. The close agreement between the two techniques implies that the metabolic technique is a valid one.

Without sampling data, it is not possible to state definitely that the population of spruce beetles at Wolf Creek Pass declined between the falls of 1956 and 1957. Amman (1958), however, reported that the woodpeckers declined from an average density of 1.35 birds per acre in the fall of 1956 to an average density of 0.13 birds per acre by the fall of 1957, suggesting a concomitant decline in numbers of spruce beetles. Thus, it is entirely possible that predation by woodpeckers was sufficient to limit the number of Engelmann spruce beetles at Wolf Creek Pass, in which case it could be said that the consumption by woodpeckers of 83 to 84 per cent of the brood is sufficient to check the further increase of epidemic populations of the beetle existing at densities in the fall of approximately 160,000 larvae per acre.

The smaller per cent reduction of the population of the spruce beetle at Rabbit Ears Pass as a result of predation by woodpeckers, and the fact that the infestation continued unabated suggest that populations with fall densities greater than 160,000 larvae per acre

but less than 1,600,000 larvae per acre are so large that woodpeckers become relatively ineffective in suppressing them. That is, there is a density or range of densities of the spruce beetle above which the limiting influence of predation by woodpeckers seems to be less effective, and this critical density may be somewhere between 160,000 and 1,600,000 larvae per acre.

Factors Regulating the Effectiveness of Predation by Woodpeckers

Figure 15 pictorially summarizes the effects of the numerical and functional responses of woodpeckers on the three densities of the prey found at Deadman, Wolf Creek Pass and Rabbit Ears Pass, and it shows that the Northern Three-toed Woodpecker is the most effective predator and the Downy Woodpecker the least effective. The figure suggests that there is an optimal density of prey--or probably a range of densities as found by Holling (1959)--where predation by woodpeckers is most effective, with proportionately fewer spruce beetles being consumed above and below this level. Decreased effectiveness of predation at the higher densities of prey is undoubtedly due to adaptive mechanisms which tend to limit woodpeckers at or below certain densities, regardless of how large a surplus of food is available. Decreased effectiveness of predation at lower densities of prey is due to several factors, including the relative densities of alternative prey and the adaptive mechanisms responsible for utilization of the alternative prey by the different species of woodpeckers.

A number of other factors indirectly influence the effectiveness of woodpeckers as predators of beetles. For example, snow,

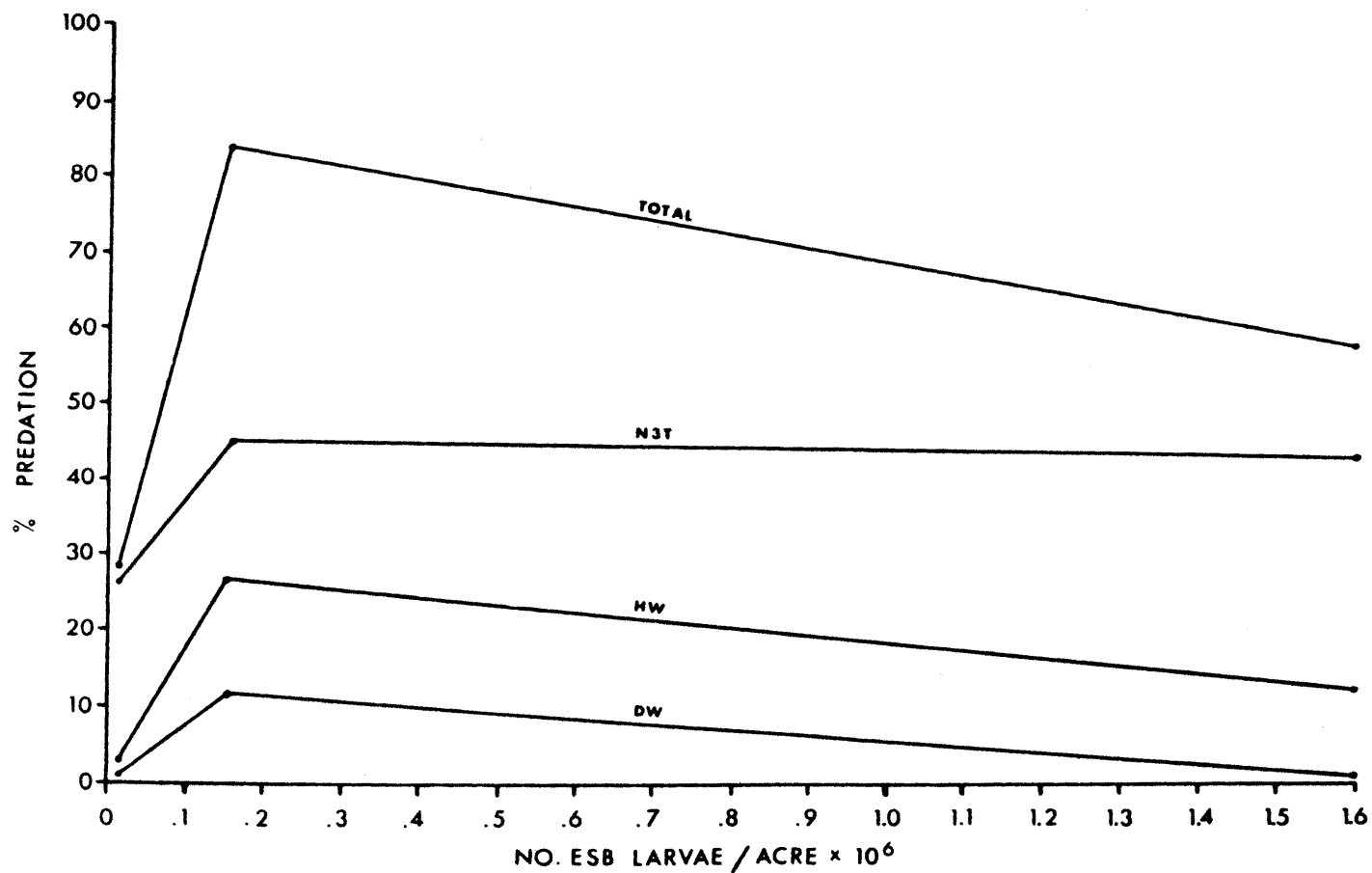


Figure 15. Functional and numerical responses combined to show percentages of the total number of Engelmann spruce beetle (ESB) larvae consumed per year (per cent predation) by Downy (DW), Northern Three-toed (N3T) and Hairy (HW) Woodpeckers at various larval densities.

covering the blowdowns and the basal portions of snags, decreases the effectiveness of woodpeckers in obtaining the prey, regardless of the densities of the prey so protected. At higher densities of prey, woodpeckers in the course of their feeding activities often flake away so much bark that larvae otherwise protected by the overlying bark are killed by dessication (Massey and Wygant, 1954) and by exposure to hymenopterous parasites with short ovipositors (Otvos, 1965). While it is realized that the indirect factors are important variables influencing the effectiveness of predation by woodpeckers, it is the influence of the adaptive mechanisms previously established for woodpeckers that is of main concern in this study.

Nesting Territoriality

Wynne-Edwards (1964) proposed that, ". . . the average population level of at least some vertebrates is set by the long-term food resources A system of behavioral conventions acts as homeostatic machinery that prevents the growth of the population from departing too far from the optimal density. Fluctuations from this average can be explained as being due . . . to the working of the homeostatic machinery itself, which allows the population density to build up when food yields are good and thins it down when the yields fall below average . . ." Thus, woodpeckers, which are territorial during the breeding season, are expected to conform to this principle; given adequate resources, the upper level that populations of woodpeckers will attain is dependent upon the amount of crowding tolerated during the breeding season. As previously mentioned, the Northern Three-toed Woodpecker at Wolf Creek Pass tolerated crowding to the

extent of at least six nests per square mile. In another local epidemic of the Engelmann spruce beetle on Beaver Creek, in the San Isabel National Forest, Custer County, Colorado, Dr. Paul H. Baldwin (pers. comm.) found 3.0 pairs of Northern Three-toed Woodpeckers and 3.3 pairs of Hairy Woodpeckers per square mile, or an average density of 6.3 nests per square mile. Thus, six nests per square mile is probably approaching the upper limit of nesting density of woodpeckers in spruce-fir forests.

The breakdown of territorial behavior at the termination of the breeding season is adaptive in that it permits the aggregation of woodpeckers at localities with abundant prey. That territorial behavior does break down is evidenced by the aggregations of woodpeckers previously observed (Blackford, 1955; Yeager, 1955; and this study). That the breakdown of territorial behavior is fairly complete is evidenced by Baldwin's (1960) observations of up to 12 woodpeckers feeding together in adjacent snags at Wolf Creek Pass and by several observations of from three to five woodpeckers feeding together in the same or adjacent snags at Deadman. The birds at Deadman fed fairly closely together but maintained individual distances of at least two feet; a woodpecker approaching a second woodpecker any closer than two feet was quickly repelled by the second bird.

Differential Selections of Prey

As previously mentioned, spruce beetles represented 99 per cent of the items in the stomachs of the woodpeckers collected by Hutchison (1951); consequently, differential selection of prey by

the woodpeckers at Rabbit Ears Pass was essentially non-existent. At the lower densities of the Engelmann spruce beetle at Wolf Creek Pass and Deadman, however, not only were more alternative prey taken in lieu of the spruce beetle, but, as shown in Tables 26 through 31, the different species of woodpeckers took different proportions of the alternative prey available. The interpretation of these results is that the effect of character displacement, a product of the process of competitive exclusion (Brown and Wilson, 1956; Mayr, 1963; Hutchinson, 1965) and an adaptation responsible for differential utilization of resources (MacArthur and Levins, 1964), becomes progressively less important at progressively higher densities of prey, until at or above a certain level the effect disappears altogether, especially when alternative prey are in limited supply.

A general discussion of character displacement has been dealt with (pp. 116 to 144); a manifestation of character displacement as it affects differential selection of prey by the three species of woodpeckers will now be considered. The study of feeding behavior conducted at Deadman can be used as the basis for the consideration; thus, the foraging behavior of adult, non-nesting woodpeckers exposed to declining populations of prey in a spruce-fir forest is involved. It would be desirable to have had estimates of the densities of insect prey; however, the absence of this data does not prevent the consideration, because it is axiomatic that insects in temperate climates are most abundant during the summer and early fall and least abundant during the late fall, winter, and early spring. Accordingly, a comparison of the data on foraging behavior in Tables 8 and 12--covering the period of time when prey

were most numerous--with the data in Tables 9, 10, 11, 13, 14, and 15--covering the period of time when prey were least numerous--provides the basis for the consideration.

Presumably, predation by the Northern Three-toed and Hairy Woodpeckers reduced the densities of insect prey in the stems of the snags at Deadman to the point that by mid-October the birds began feeding on insects in the higher positions of the stems and the larger branches. As prey continued to decline the woodpeckers foraged at progressively higher positions on the stems and further out on the branches. The Hairy Woodpecker decreased its feeding activities on the older snags--probably because the insects in them were depleted or nearly depleted--and increased its feeding attention upon freshly killed Engelmann spruce snags, the same species of snag the Northern Three-toed Woodpecker was devoting the majority of its feeding attention upon. This implies that there was more overlap in the food resources of these two woodpeckers when food was scarce than when it was more abundant. Averages of the indices of difference in Table 24 show that the overall difference in foraging behavior between the Northern Three-toed and Hairy Woodpeckers for the period of high densities of prey was greater $\frac{39 + 58}{2} = 48.5$ than for the period of low densities of prey, $\frac{13 + 68}{2} = 40.5$; conversely, the overlap in foraging behavior for the period of high densities of prey was less $(200 - 48.5 = 151.5)$ than for the period of low densities $(200 - 40.5 = 159.5)$.

The overlap in foraging behavior between the Northern Three-toed and Hairy Woodpeckers did not persist, however, because, as shown in Figure 7, a decrease in the densities of both woodpeckers

accompanied the shifts in feeding behavior. The downward trend in numbers of the Hairy Woodpecker continued until the birds disappeared during the winter--between October and November--of 1963-1964 and during the winter--between December and April--of 1964-1965, the later disappearance of the bird during the latter winter is attributed to higher densities of insects at Deadman during the fall of 1964 than during the fall of 1963.

The Downy Woodpecker was regularly observed at Deadman only during the interval October 16, 1964 to May 10, 1965 (Figures 7-9). During this time the birds fed upon insects attracted to the smaller branches and twigs of Engelmann spruce killed by the 1962 fire, while the foraging behavior of the Northern Three-toed and Hairy Woodpeckers remained essentially unchanged (Tables 9, 10, 11, 13, 14 and 15).

Tables 16, 17, 20 and 21 show that the shift in feeding positions of the Northern Three-toed Woodpecker was accomplished by differential feeding behavior of the sexes. There were only slight differences in the feeding behavior of the sexes of the Hairy Woodpecker as summarized in Tables 18, 19, 22 and 23; the differences between Tables 18 and 19, and between 22 and 23, were accumulated during the October 16 to May 10 periods. It is interesting to note that the trend of the differences--which were actually statistically non-significant--is in the same general direction as the trend of differences seen in the feeding behavior of the sexes of the Northern Three-toed Woodpecker. Thus, as prey numbers in the stems of the snags declined, the females of the Northern Three-toed Woodpecker and possibly the females of the Hairy Woodpecker devoted more of

their feeding attention to the prey in the smaller branches and twigs of the freshly killed snags, while the males continued feeding on insects in the stems of these snags.

Reference to Tables 26 through 31 shows that there is good correlation between the foraging positions just described and the kinds of insect prey obtained at these positions. Thus, scolytids and cerambycids inhabiting the stems of freshly killed snags formed the majority of the prey in the diet of the Northern Three-toed Woodpecker; while scolytids and cerambycids inhabiting the stems of freshly killed snags, and formicids, mainly carpenter ants (Camponotus sp.) inhabiting the stems of older snags, formed the majority of the prey in the diet of the Hairy Woodpecker; Pityophthorous, a genus of scolytid inhabiting the twigs of freshly killed snags, and other small scolytids inhabiting branches and twigs of freshly killed snags formed the majority of the prey in the diet of the Downy Woodpecker.

CONCLUSIONS

According to a general theory developed in this dissertation, two species predator-prey systems are inherently unstable; in the absence of complicating factors the predators inevitably exterminate the prey and then themselves starve to extinction. The introduction of prey refuges prevents extermination of the prey, but populations of both predators and prey fluctuate wildly and periodically. The addition of alternative prey further complicates the system and depresses the amplitude of the population fluctuations. The addition of a ceiling to the predator population is a third complication which depresses even further the amplitude of the population fluctuations. The presence of additional species of predators complicates the system even more and should also, therefore, exert a dampening influence on the population fluctuations.

The numerical and functional responses of woodpeckers to numerical changes in populations of the Engelmann spruce beetle are manifestations of the instability of this predator-prey system; but prey refuges in logs and basal portions of snags buried in snow, the influence of alternate prey in diverting the feeding attention of the woodpeckers away from the spruce beetle, the ceiling imposed on population density of the woodpeckers by nesting territoriality, and the presence of three species of woodpeckers each contribute a stabilizing influence on the predator-prey system. Thus, the aforementioned characteristics of the predator-prey system between

woodpeckers and the spruce beetle are in concordance with the general theory.

General theory also suggests that maximum yield to predators results when approximately 10 per cent of the total food energy consumed by the prey is harvested in the form of prey animals. The ecological efficiency of the predator-prey system between woodpeckers and the spruce beetle cannot be calculated because an estimate of one of the variables needed for the calculation--caloric content of the total amount of food consumed by the prey--is lacking.

Finally, general theory suggests that when a given species of prey, limited in supply, is a significant constituent in the diets of two or more species of predators (i.e., when the prey represents five per cent or more of the diet of each predator), the predators must be exploiting the commonly utilized prey in entirely different ways. Because nesting territoriality imposes a ceiling on numbers of woodpeckers, epidemic populations of spruce beetles, initially at least, represent an unlimited food supply for the birds. Consequently, all three species of woodpeckers prey upon epidemic populations of the spruce beetle but only the Northern Three-toed and Hairy Woodpeckers prey upon endemic populations of the beetle, and then the insect is a significant dietary constituent of only the Northern Three-toed Woodpecker. Thus, again, this predator-prey system between woodpeckers and the spruce beetle conforms to general theory.

Behavioral and morphological adaptations affecting spatial, temporal, and dietary differences among the three species of woodpeckers account for the decreased attentiveness of Hairy and Downy Woodpeckers to endemic populations of the spruce beetle; similar

adaptations are responsible for diverting the feeding attention of female Northern Three-toed Woodpeckers and possibly female Hairy Woodpeckers away from insects inhabiting stems of snags and logs (including the Engelmann spruce beetle) to insects inhabiting branches and twigs.

Of the three species, the Northern Three-toed Woodpecker is the most effective predator and the Downy Woodpecker the least effective predator in controlling numbers of the spruce beetle. The combined predator pressure of the three species of woodpeckers kills 20-50 per cent of the individuals in endemic populations of the beetle and 55-85 per cent of the individuals in epidemic populations of the beetle. This aspect of the predator-prey system between woodpeckers and spruce beetles is unique because few, if any, other prey populations are known to experience mortalities of this magnitude as a result of predation by vertebrates.

SUMMARY

A general theory concerning the population dynamics of predator-prey systems was developed from a survey of the pertinent literature. According to the theory, populations of simplified predator-prey systems fluctuate wildly and periodically. Complicating factors dampen the amplitude of the population fluctuations and thus exert a stabilizing influence on the systems.

The biological characteristics of woodpeckers and bark beetles overcome many of the difficulties previously encountered in studies on natural predator-prey systems; consequently, the system between the Northern Three-toed, Hairy and Downy Woodpeckers, and the Engelmann spruce beetle was chosen for an investigation of the population dynamics of a natural predator-prey system.

The field portion of the study was conducted in a subalpine forest in northern Colorado between 1962 and 1965.

The population densities of several species of bark beetles attracted to trees killed and damaged by a fire on the study area, increased to levels that attracted the feeding attention of the woodpeckers.

The numerical response of the woodpeckers to prey density was graded, that of the Northern Three-toed Woodpecker was the most pronounced and that of the Downy Woodpecker was the least pronounced.

Apparent spatial and temporal differences were noted in the foraging behavior of the three species of woodpeckers; similar but

less apparent differences were also noted in the foraging behavior between the sexes of the Northern Three-toed and Hairy Woodpeckers.

Both the interspecific and intersexual differences in foraging behavior were correlated with morphological (body size and culmen length) and dietary differences.

The metabolic demands of free-living woodpeckers were estimated by feeding diets of known caloric content to caged woodpeckers at several different ambient temperatures. The birds were provided with small bolts of spruce which they pecked upon for long periods of time and in so doing maintained levels of activity comparable to those in the free-living state.

Estimates were also made of the caloric content of Engelmann spruce beetle larvae and the rate at which they are digested by woodpeckers. Combining these two estimates with the estimates of metabolic demand, the estimates of the relative densities of woodpeckers, and the average number of spruce beetle larvae found per woodpecker stomach made it possible to estimate the number of larvae consumed by each species of woodpecker. This method gave results very similar to the usual method whereby the number of larvae surviving in bark protected from woodpeckers is compared with the number surviving in bark exposed to woodpeckers.

Every aspect of the predator-prey system between woodpeckers and the Engelmann spruce beetle, except the number of larvae destroyed, conforms to general theory. The number of prey destroyed in this predator-prey system is higher than that known for any other system involving vertebrate predators and invertebrate prey.

LITERATURE CITED

- Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders Company, Philadelphia. xii + 837 p.
- Anman, G. D. 1958. A comparative study of methods for censusing woodpeckers in spruce-fir forests of Colorado. Master's Thesis. Colorado State University. 125 p.
- Anman, G. D. and P. H. Baldwin. 1960. A comparison of methods for censusing woodpeckers in spruce-fir forests of Colorado. Ecology, 41:699-706.
- Andrewartha, H. G. and L. C. Birch. 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago. xv + 782 p.
- Armstrong, J. T. 1960. The dynamics of Daphnia pulex populations and of Dugesia tigrina populations as modified by immigration. Ph.D. Dissertation. University of Michigan. 102 p.
- Baldwin, P. H. 1960. Overwintering of woodpeckers in bark beetle-infested spruce-fir forests of Colorado. Proceedings of the International Ornithological Congress, Helsinki. 12:71-84.
- Birch, L. C. 1957. 'The meanings of competition.' The American Naturalist, 91:5-18.
- Blackford, J. L. 1955. Woodpecker concentration in a burned forest. The Condor, 57:28-30.
- Brewer, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina Chickadees. The Auk, 80:9-47.
- Brown, W. L. and O. E. Wilson. 1956. Character displacement. Journal of Systematic Zoology, 5:49-64.
- Buckner, C. H. 1966. The role of vertebrate predators in the biological control of forest insects. Annual review of Entomology, 11:449-470.
- Carson, Rachel. 1962. Silent Spring. Houghton Mifflin Company, Boston. 368 p.

- Chitty, D. 1960. Population processes in the vole and their relevance to general theory. *Canadian Journal of Zoology*, 38:99-113.
- Chitty, Helen. 1950. Canadian arctic Wildlife, 1943-49, with a summary of results since 1933. *The Journal of Animal Ecology*, 19:180-193.
- Clausen, C. P. 1951. The time factor in biological control. *The Journal of Economic Entomology*, 44:1-9.
- Cole, L. C. 1954. Some features of random cycles. *The Journal of Wildlife Management*, 18:107-109.
- Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology*, 37:451-460.
- Craighead, J. J. 1962. Predation by hawks, owls and gulls, pp., 35-42. In *The Oregon meadow mouse irruption of 1957-1958. A collection of reports published by the Federal Cooperative Extension Service, Oregon State University.* 88 p.
- Craighead, J. J. and F. C. Craighead Jr. 1956. *Hawks, Owls and Wildlife.* Stackpole Company, Harrisburg, Pennsylvania. xix + 443 p.
- Crombie, A. C. 1945. On competition between different species of graminivorous insects. *Proceedings of the Royal Society, London, (B)* 132:362-365.
- . 1947. Interspecific competition. *The Journal of Animal Ecology* 16:44-73.
- Darwin, C. 1859. *The origin of species by means of natural selection or the preservation of favored races in the struggle for life.* The Modern Library, New York. x + 386 p.
- Davis, J. 1965. Natural history, variation, and distribution of the Strickland's Woodpecker. *The Auk*, 82:537-590.
- Dixon, W. J. and F. J. Massey, Jr. 1957. *Introduction to Statistical Analysis.* McGraw-Hill, New York, New York. xiii + 488 p.
- Egler, F. E. 1964a. Pesticides--in our ecosystem. *American Scientist*, 52:110-136.
- Egler, F. E. 1964b. Pesticides in our ecosystem: communication II. *Bioscience*, 14 (11):29-36.
- Elton, C. 1927. *Animal Ecology.* Sidgwick and Jackson Limited, London, England. xx + 209 p.

- _____. 1942. Voles, Mice and Lemmings. Clarendon Press, Oxford, England. 496 p.
- Errington, P. L. 1946. Predation and vertebrate populations. The Quarterly Review of Biology, 21:145-177, 221-245.
- _____. 1963. The phenomenon of predation. American Scientist, 51:180-192.
- Frank, P. W. 1952. A laboratory study of intraspecies and interspecies competition in Daphnia pulicaria and Simocephalus vetulus. Physiological Zoology, 25:178-204
- _____. 1957. Coaction in laboratory populations of two species of Daphnia. Ecology, 38:510-519.
- Gause, G. F. 1934. The Struggle for Existence. Williams and Wilkins. vii + 163 p.
- Gause, G. F. and A. A. Witt. 1935. Behavior of mixed populations and the problem of natural selection. The American Naturalist, 69:596-609.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. The Auk, 34:427-433.
- _____. 1924. Geography and evolution. Ecology, 5:225-229.
- _____. 1928. Presence and absence of animals. The University of California Chronicle, 30:429-450.
- Hardin, G. 1960. The competitive exclusion principle. Science, 131:1292-1297.
- Hoffmann, R. S. 1958. The role of predators in "cyclic" declines of grouse populations. The Journal of Wildlife Management, 22:317-319.
- Holling, C. S. 1959b. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist 91: 385-398.
- _____. 1959a. The components of predation as revealed by a study of small mammal predators of the European pine sawfly. The Canadian Entomologist, 91:293-320.
- _____. 1961. Principles of insect predation. Annual Review of Entomology, 6:163-182.
- _____. 1963. An experimental component analysis of population processes. Memoirs of the Entomological Society of Canada, 32:22-32.

- _____. 1964. The analysis of complex population processes. The Canadian Entomologist, 96:335-347.
- _____. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada, 45:1-60.
- _____. 1966. The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada, 48:1-86.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. The American Naturalist, 100:419-424.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia, 27:343-383.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology, 32:571-577.
- _____. 1957. Concluding remarks. Cold Springs Harbor Symposia on Quantitative Biology, 22:415-427.
- _____. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? The American Naturalist, 93:145-159.
- _____. 1965. The Ecological Theater and the Evolutionary Play. Yale University Press, New Haven, Connecticut. xii + 139 p.
- Hutchison, R. T. 1951. The effects of woodpeckers on the Engelmann spruce beetle, Dendroctonus engelmanni Hopk. Master's Thesis. Colorado State University. 73 p.
- Istock, C. A. 1966. Distribution, coexistence, and competition of whirligig beetles. Evolution, 20:211-234.
- Kendeigh, S. C. 1949. Effect of temperature and season on energy resources of the English Sparrow. The Auk, 66:113-127.
- _____. 1961. Animal Ecology. Prentice-Hall Incorporated, Engelwood Cliffs, New Jersey. x + 468 p.
- _____. 1963. Relation of existence energy requirements to size of bird. American Zoologist, 3:77.
- Kilham, L. 1965. Differences in feeding behavior of male and female Hairy Woodpeckers. The Wilson Bulletin, 77:134-145.
- King, J. R. and D. S. Farner. 1961. Energy metabolism, thermoregulation and body temperature. In Biology and comparative physiology of birds, Volume II, edited by A. J. Marshall. Academic Press, New York, New York, pp. 215-288.

- Knight, F. B. 1958. The effects of woodpeckers on populations of the Engelmann spruce beetle. The Journal of Economic Entomology, 51:603-607.
- Koplin, J. R. 1963. Experimental predation on Microtus pennsylvanicus. The Journal of the Colorado-Wyoming Academy of Sciences, 5(4):50.
- Lack, D. 1945. The ecology of related species with special reference to cormorant (Phalacrocorax carbo) and shag (P. aristotelis). The Journal of Animal Ecology, 14:12-16.
- _____. 1946. Competition for food by birds of prey. The Journal of Animal Ecology, 15:123-129.
- _____. 1947. Darwin's Finches. Cambridge University Press, Cambridge, England. x + 208 p.
- _____. 1954a. Cyclic mortality. The Journal of Wildlife Management, 18:25-37.
- _____. 1954b. The natural regulation of animal numbers. Clarendon Press, Oxford, England. viii + 343 p.
- Lasiewski, R. C. 1963. Oxygen consumption of torpid, resting, active, and flying hummingbirds. Physiological Zoology, 36:122-140.
- Lasiewski, R. C. and W. R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor, 69:13-23.
- Leopold, A. 1933. Game Management. Charles Scribner's Sons, New York, New York. xxi + 481 p.
- _____. 1943. Deer irruptions. Wisconsin Conservation Publication, 321:1-11.
- Leopold, A. S., S. A. Cain, C. M. Cottam, I. N. Gabrielson, and T. L. Kimball. 1964. Predator and rodent control in the United States. Report to Stewart Udall, Secretary of the Interior. March 9, 1964. Mimeographed, 28 p.
- Linsdale, J. M. 1957. Ecological niches for warm-blooded vertebrate animals. The Wasmann Journal of Biology, 15:107-122.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology, 39:599-619.
- MacArthur, R. H. and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. The Proceedings of the National Academy of Sciences, 51:1207-1210.

- MacLulich, D. A. 1937. Fluctuations in the numbers of the varying hare (Lepus americanus). University of Toronto Studies in Biology Series, Number 43:1-136.
- Margalef, R. 1963. On certain unifying principles in biology. The American Naturalist, 97:357-374.
- Massey, C. L. and N. D. Wygant. 1954. Biology and control of the Engelmann spruce beetle in Colorado. U. S. Department of Agriculture Circular Number 944. i + 35 p.
- Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts. xiv + 797 p.
- Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. Methods and Principles of Systematic Zoology. McGraw-Hill, New York, New York. ix + 328 p.
- Miller, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. Ecology, 45:256-272.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University, Series E (Biology) 3:65-80.
- Morris, R. F. 1957. The interpretation of mortality data in studies on population dynamics. The Canadian Entomologist, 89:49-69.
- Nagel, R. H., D. CcComb and F. B. Knight. 1957. Trap tree method for controlling the Engelmann spruce beetle in Colorado. The Journal of Forestry, 55:894-898.
- Neyman, J., T. Park, and E. L. Scott. 1959. Struggle for existence: the Tribolium model: biological and statistical aspects. Proceedings of the third Berkeley Symposium on Mathematical Statistics and Probability, 4:41-79.
- Nicholson, A. J. 1947. Fluctuation of animal populations. Presidential Address, Section D of the Australian and New Zealand Association for the Advancement of Science, 26:1-14.
- Nicholson, A. J. and V. A. Bailey. 1935. The balance of animal populations. Proceedings of the Zoological Society of London, 1935:551-598.
- Odum, E. P. 1959. Fundamentals of Ecology. Second Edition. W. B. Saunders Company, Philadelphia, Pennsylvania. xvii + 546 p.
- Oosting, H. J. and W. D. Reed. 1952. Virgin spruce-fir forest in the Medicine Bow Mountains, Wyoming. Ecological Monographs, 22:69-91.

- Orians, G. H. and G. Collier. 1963. Competition and blackbird social systems. *Evolution*, 17:449-459.
- Otvos, I. S. 1964. Studies on avian predators of Dendroctonus brevicomis LeConte (Coleoptera: Scolytidae) with special reference to Picidae. Master's Thesis. University of California at Berkeley. 69 p.
- _____. 1965. Studies on avian predators of Dendroctonus brevicomis LeConte (Coleoptera: Scolytidae) with special reference to Picidae. *The Canadian Entomologist*, 97:1184-1199.
- Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetle, Tribolium confusum Duval and Tribolium castaneum Herbst. *Ecological Monographs*, 18:265-308.
- _____. 1954a. Competition: an experimental and statistical study. In *Statistics and mathematics in biology*, edited by O. Kempthorne. Iowa State University Press, Ames, Iowa. pp. 175-195.
- _____. 1954b. Experimental studies of interspecies competition. II. Temperature, humidity and competition in two species of Tribolium. *Physiological Zoology*, 27:177-238.
- _____. 1962. Beetles, competition, and populations. *Science*, 138:1369-1375.
- Pitelka, F. A., P. Q. Tomich, and G. W. Treichel. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecological Monographs*, 25:85-117.
- Pynnonen, A. 1943. Beitrage zur Kenntnis der Biologie finnischer Spechte. *Annales Zoologici Societatis Zoologicae--Botanicae Fennicae Vanamo*, 9:1-60.
- Richman, S. 1958. The transformation of energy by Daphnia pulex. *Ecological Monographs*, 28:273-291.
- Ridgway, R. 1914. The birds of North and Middle America. U. S. National Museum Bulletin, Number 50, Part 6.
- Rosenzweig, M. L. and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist*, 97:209-223.
- Russo, J. P. 1964. The Kaibab north deer herd. Its history, problems, and management. State of Arizona, Game and Fish Department, Wildlife Bulletin, Number 7. vi + 195 p.

- Schoener, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution*, 19:189-213.
- Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *The Condor*, 68:113-151.
- Selander, R. K. and D. R. Giller. 1963. Species limits in the woodpecker genus centurus (Aves). *Bulletin of the American Museum of Natural History*, 124:213-274.
- Shannon, C. E. and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, Illinois. 125 p.
- Simpson, E. H. 1949. Measurement of diversity. *Nature*, 163:688.
- Simpson, G. G., Anne Row, and R. C. Lewontin. 1960. Quantitative Zoology. Harcourt, Brace and Company, Incorporated, New York, New York. vii + 440 p.
- Slobodkin, L. B. 1959. Energetics in Daphnia pulex populations. *Ecology*, 40:232-243.
- _____. 1960. Ecological relationships at the population level. *The American Naturalist*, 94:213-236.
- _____. 1961. Growth and Regulation of Animal Populations. Holt, Rinehart and Winston, New York, New York. vii + 184 p.
- _____. 1965. On the present incompleteness of mathematical ecology. *American Scientist*, 53:347-357.
- Solomon, M. E. 1949. The natural control of animal populations. *The Journal of Animal Ecology*, 18:1-35.
- Spring, L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. *The Condor* 67:457-488.
- Staebler, A. E. 1949. The comparative life history study of the Downy and Hairy Woodpeckers (Dendrocopos pubescens and Dendrocopos villosus). Ph.D. Dissertation. University of Michigan. viii + 125 p.
- Stallcup, P. L. 1966. Spatio-temporal relationships of nuthatches and woodpeckers in northern Colorado. Ph.D. Dissertation. Colorado State University. iv + 111 p.
- Storer, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. *The Auk*, 83:423-436.
- Thimann, K. V. 1964. Pesticides and the P. S. A. C. *Bioscience*, 14:24-25.

- Wynne-Edwards, V. C. 1964. Population control in animals.
Scientific American, 211:68-74.
- Yeager, L. E. 1955. Two woodpecker population studies in relation
to environmental change. The Condor, 57:148-153.