

A PRELIMINARY STUDY OF NEST-SITE
COMPETITION IN A GROUP OF HOLE-NESTING BIRDS

by

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ABSTRACT

This study was restricted to birds using tree-holes as nest-sites. Of a total of 20 species in the study area, only 13 were sufficiently abundant to merit consideration. These fell into three natural groups on the basis of hole size, with only one euryoecious species (Iridoprocne bicolor) nesting in all three groups. Only the group based on holes made by the Colaptes woodpeckers (Flickers) can presently be construed as showing evidence of nest-site competition. Physical and ecological characteristics of nest-sites are analyzed in terms of intensification or amelioration of nest-site competition. The competing species, all using holes made by Colaptes cafer, are Sturnus vulgaris, Sialia currucoides, Bucephala albeola, Iridoprocne bicolor and Falco sparverius.

The data suggest that although competition is now present in this group, it may have been absent before the advent of Sturnus in the avifauna. Neither selection for different sites nor competitive exclusion seem to have occurred before the appearance of Sturnus, which now occupies roughly 25% of all available nests, but one or both of these may now be going on.

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INTRODUCTION

Objects of the Study

The type of ecological relationship commonly designated as competition has long been a subject of both interest and controversy. Ample documentation is found in the ecological literature of the fact that this term has been widely and variously used to refer to a broad spectrum of ecological relationships, although attempts are now being made to restrict its use to one well-defined phenomenon or class of phenomena (cf. Birch, 1957; Milne, 1961).

Birds utilizing tree-holes as nest-sites are frequently referred to as typical cases of inter- or intra-specific competition for the use of a limited number of available nest-sites, although opportunities are rarely utilized for careful evaluation of this situation under natural conditions. The present work represents the first stage of a series of studies designed to explore the nature and extent of such competition in local avifaunas, and consists basically of an attempt to define, on as quantitative a basis as possible, the extent and nature of nest-site competition among the tree-hole-nesting birds of the Cariboo region of the interior of British Columbia.

Terminology

Frequently, considerable misunderstanding and controversy arise as a result of poor or incomplete exposition of the exact meanings attributed to crucial terms and concepts used in the development of scientific arguments. The following definitions are thus offered for terms used in the present paper:

Competition - the demand by more than one individual organism during a given period of time for an environmental resource which is present in insufficient amounts to supply the total demand.

It is important to note that this definition stresses both spatial and temporal contiguity of the competitors, as well as availability of sites. An expanded discussion of this problem of the definition of competition is included in the discussion section below.

"Hole-nesting bird"- those species of birds which normally, or occasionally, utilize tree-cavities as nest sites, whether able or not to construct such cavities. Although many other species, such as various Swallows (Hirundinidae), Kingfishers (Alcedinidae), Petrels (Hydrobatidae), and Shearwaters (Procellariidae), to name but a few examples, also nest in holes, this study was restricted to tree hole breeders for the obvious reason of ecological continuity.

Primary hole-nester - a hole-nesting species capable of excavating the nest cavity.

Secondary hole-nester - a hole-nesting species requiring a cavity as a nest-site, but incapable of carrying out the necessary excavation.

Ecological niche - the ecological niche is a particular combination of physical factors and biotic relations required by a species for the normal course of its life (Kendeigh, 1961).

Diameter at breast height (dbh) - the diameter of any tree as measured at a standard height of four and one-half feet above ground level. This is a standard forester's measure, and was made with a standard diameter tape (see below).

Hole height - height above ground of the bottom of the entrance of any given nest.

Hole size - this parameter was always recorded with the horizontal value before the vertical value, as, 2.5 X 2.7 cm.

Sill size - thickness of the base of the entrance hole of any cavity.

Cavity - horizontal distance from inside edge of sill to opposite wall of the cavity.

Depth - vertical distance from sill to bottom of cavity. In the case of species which place extraneous material in the cavity, both level of nest and actual depth of cavity were measured wherever possible.

Hole direction - direction toward which entrance hole is oriented. This parameter was determined with a standard forester's compass.

Figure 1 is a diagrammatic representation of the relationship between various nest-site parameters.

Equipment and Methods

Little was required in terms of special equipment for the field work phases of this study; particular items used are discussed below.

Nest sites were located by searching of selected areas on foot, and other sites were located incidentally by sightings from vehicles, reports from interested persons, etc.

All measurements made in 1958 were in feet and inches, and were later converted to metric equivalents. In 1959, all measurements were made directly in metric units, except tree diameters and tree heights, and a few extremely high nest heights. All measurements of tree diameters were made with a standard forester's diameter tape which was graduated in diameter-equivalents of circumference, expressed in inches and tenths of inches. Tree heights and extreme nest heights were measured with a standard Abney level or were roughly triangulated when characteristics of terrain or vegetation precluded the use of this instrument.

Nest-holes were opened when necessary by a procedure described by Erskine (1959 (b)).

Various means were utilized to reach nest-sites at different heights, including lineman's climbing spurs, a collapsible aluminum utility ladder, and improvisation from natural materials at hand.

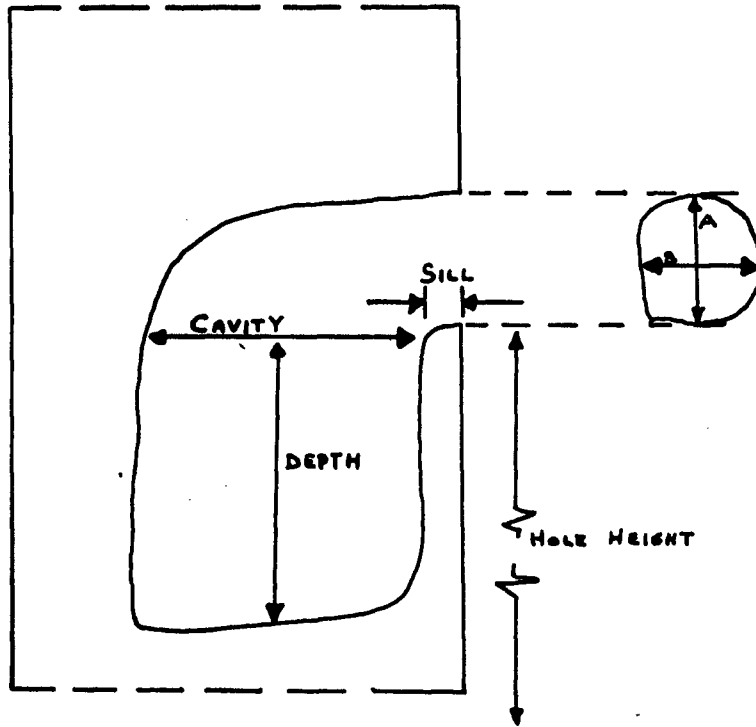


FIG. 1 SITE MEASUREMENTS

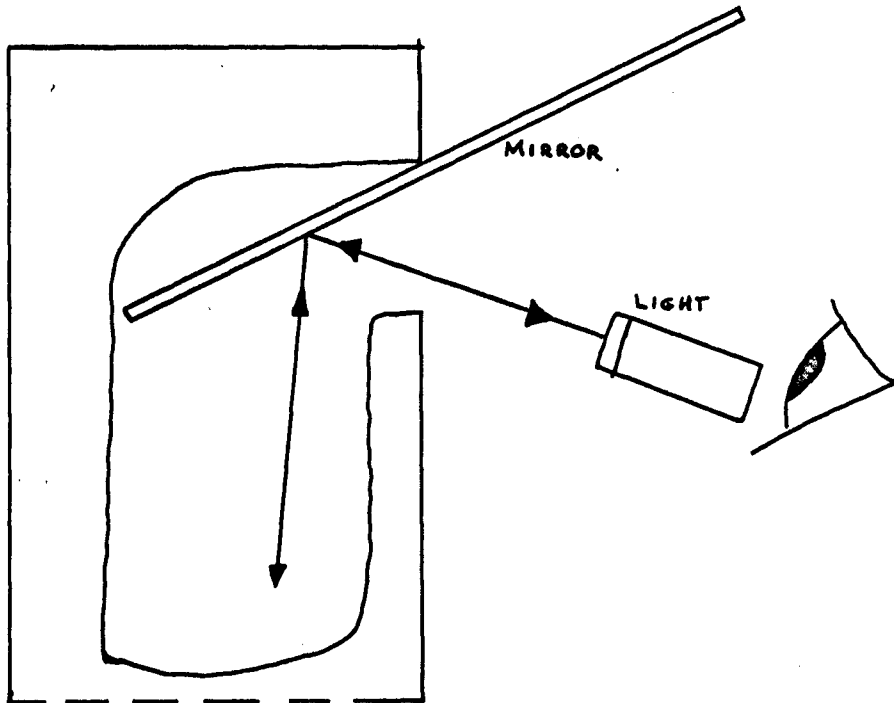


FIG. 2 INSPECTION METHOD

In collaboration with L.G. Sugden, then Regional Game Biologist, B.C. Fish and Game Branch, Williams Lake, B.C., and Dr. A.J. Erskine, a special technique was devised to permit examination of the interiors of nest holes without opening as in the technique mentioned above. Long slips of mirror glass were used in conjunction with a pocket flashlight in the manner indicated in Figure 2, and judicious manipulation of both elements in the system provided a lighted view of the interior of a cavity which was sufficiently good in most cases to permit accurate identification of the contents of the cavity. A notable exception occurred in the cavities excavated by the sapsucker, Sphyrapicus varius, in which the width of sill was in most cases so great as to preclude the use of this technique.

In the analysis of data, all techniques used were drawn from the standard repertoire of graphic and statistical methods available in most standard books (e.g., Snedecor, 1956; Bailey, 1959; etc.). Calculations and computations were made to an accuracy of three significant figures; under field conditions it was rarely possible to achieve measurements of greater refinement than this.

Location of Study Areas

Munro and Cowan (1947) described thirteen terrestrial biotic areas in British Columbia, using the criteria of presence of distinctive plant species, presence of distinctive animal species, and absence of plant and animal species of other zones. The study area used in the present investigation was that named by Munro and Cowan as the Cariboo Parklands Biotic Region. Recent botanical studies tend to indicate that this area is more properly a part of the Interior Douglas Fir bioclimatic zone. This matter is discussed at greater length below.

Geographic limits of the Cariboo area are as follows: to the east and west, the area meets relatively definite limits on the slopes of the coast mountains, and along the North Thompson River; to the south, in the vicinity of

Clinton, there is a gradual merging with the dry forests of the Ponderosa Pine Zone, and to the north, in the area just south of Quesnel, is a broad region of intergrading with the Boreal Forest. Clearly, the limits of this area are not well defined, particularly along the north and south boundaries. More exact definition of these boundaries awaits more detailed ecological study of these ecotone areas.

ECOLOGICAL CONTEXT OF THE PROBLEM

Systematic and Ecological Classification of the "Competitors"

Included in the avifauna of the study area are 17 species which satisfy the above definition of "hole-nesting" species. In Table I these are summarized and classified according to families, status as secondary or primary hole-nester, and relative abundance. These 17 species occupy an equal number of ecological niches within the ecosystems, and as is shown below for members of one of the three ecological groupings, these niches show little overlap except in terms of nest sites. Heretofore, it has been widely assumed that as a result of this apparent overlap in one aspect of their respective niches, hole-nesting birds must "compete" for nest-sites. As noted above, this study was designed as a preliminary step in the careful evaluation of that assumption.

In Table I, order of occurrence, common names and scientific names follow the Fifth Edition of the A.O.U. Checklist of North American Birds (1957). As can readily be seen, the bird species using tree-holes as nest sites in the study area are drawn from a wide variety of taxa, and as might be expected, the variety of their ecological niches is equally broad. Clearly, then, the ecological relationships pertaining to nest-site competition within this group are unlikely to be represented by their taxonomic affinities. Therefore it was essential for the purposes of this study to devise an ecologically-oriented classification in the context of which these relationships could be appreciated.

Several factors are relevant to the elaboration of such a classification. Perhaps the most obvious of these is relative population densities of the species involved: clearly, a very rare species cannot exert an appreciable effect upon large numbers of competing individuals or pairs. The following species, although represented in faunal lists for the area were not found nesting during the study

TABLE I. HOLE-NESTING SPECIES IN THE STUDY AREA.

SPECIES	FAMILY	STATUS	RELATIVE \pm ABUNDANCE
Barrow's Goldeneye (<u>Bucephala islandica</u>)	Anatidae	Secondary	Common
Bufflehead (<u>Bucephala albeola</u>)	Anatidae	Secondary	Common
Sparrowhawk (Kestrel) (<u>Falco sparverius</u>)	Falconidae	Secondary	Uncommon
Screech Owl (<u>Otus asio</u>)	Strigidae	Secondary	Rare
Great Horned Owl (<u>Bubo virginianus</u>)	Strigidae	Secondary	Relatively Common
Saw-whet Owl (<u>Aegolius acadicus</u>)	Strigidae	Secondary	Rare
Flicker (<u>Colaptes cafer</u>)	Picidae	Primary	Common
Pileated Woodpecker (<u>Dryocopus pileatus</u>)	Picidae	Primary	Rare
Yellow-bellied Sapsucker (<u>Sphyrapicus varius</u>)	Picidae	Primary	Common
Hairy Woodpecker (<u>Dendrocopos villosus</u>)	Picidae	Primary	Rare
Downy Woodpecker (<u>Dendrocopos pubescens</u>)	Picidae	Primary	Rare
Tree Swallow (<u>Iridoprocne bicolor</u>)	Hirundinidae	Secondary	Common
Black-capped Chickadee (<u>Parus atricapillus</u>)	Paridae	Primary	Rare
Mountain Chickadee (<u>Parus gambeli</u>)	Paridae	Primary	Relatively Common
Red-breasted Nuthatch (<u>Sitta canadensis</u>)	Sittidae	Primary	Common
Mountain Bluebird (<u>Sialia currucoides</u>)	Turdidae	Secondary	Relatively Common
European Starling (<u>Sturnus vulgaris</u>)	Sturnidae	Secondary	Common

\pm The terms used to refer to relative abundance are extremely general and open to criticism. However, no more suitable expression is available in the absence of extensive census data.

and were seen only rarely, if at all: Screech Owl, Saw-whet Owl, Hairy Woodpecker, and Downy Woodpecker. In addition to these species, the Hooded Merganser (Lophodytes cucullatus) was represented by one brood at Philillo Lake, and the Black-backed Three-toed Woodpecker (Picoides arcticus) by one nest, also at Phililoo Lake. These species were ignored in the analysis of data since for all practical purposes they were absent from the area (c.f. Andrewartha and Birch, 1954).

The remaining species are immediately divisible into three groups on the basis of size both of the birds themselves and of the cavities in which they nest. Only the Tree Swallow (Iridoprocne bicolor) occurs in all three groups, and only one other, the Sparrow Hawk (Falco sparverius) in more than one. In addition to the three types of bird-excavated holes, the Tree Swallow utilizes other natural holes and a wide variety of niches, and is generally highly euryoecious in terms of its nest-site. The overall species-site relationships as they were found to exist on the study area are represented in Figure 3.

Table II gives the effective species composition of the three groups: the values given for size represent length measurements as given in inches by Peterson (1961) and are included to emphasize size relationships.

Further details on the three groups are provided below in the section on analysis of nest-site competition.

To recapitulate, it has been shown that the taxonomic classification of these hole-nesting bird species is unsuitable for ecological purposes, and they have been classified in terms of the sizes of holes utilized for nest sites.

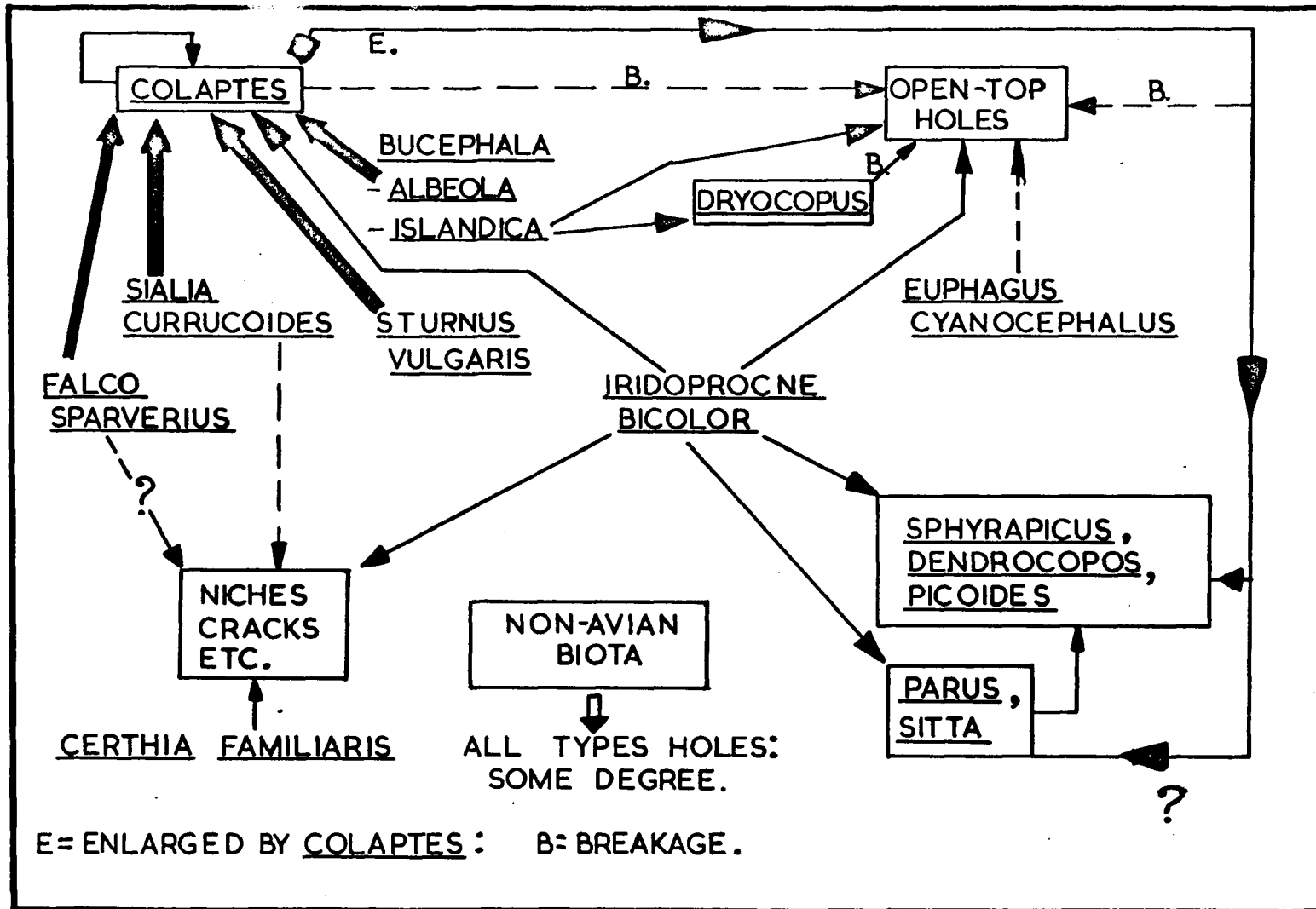


FIG. 3 : SPECIES-SITE RELATIONSHIPS

TABLE II. SPECIES COMPOSITION OF SUB-GROUPS OF HOLE-NESTING BIRDS IN THE STUDY AREA.

GROUP	SPECIES	SIZE *
Small-Hole	Tree Swallow (<u>Iridoprocne bicolor</u>)	5-6 $\frac{1}{4}$
	Mountain Chickadee (<u>Parus gambeli</u>)	5-5 $\frac{3}{4}$
	Black-Capped Chickadee (<u>Parus atricapillus</u>)	4 $\frac{3}{4}$ -5 $\frac{3}{4}$
	Red-breasted Nuthatch (<u>Sitta canadensis</u>)	4 $\frac{1}{2}$ -4 $\frac{3}{4}$
	Yellow-bellied Sapsucker (<u>Sphyrapicus varius</u>)	8-9
Medium-Hole	Red-shafted Flicker (<u>Colaptes cafer</u>)	12 $\frac{1}{2}$ -14
	Bufflehead (<u>Bucephala albeola</u>)	13-15 $\frac{1}{2}$
	European Starling (<u>Sturnus vulgaris</u>)	7 $\frac{1}{2}$ -8 $\frac{1}{2}$
	Mountain Bluebird (<u>Sialia currucoides</u>)	6 $\frac{1}{2}$ -7 $\frac{3}{4}$
	Sparrow Hawk (<u>Falco sparverius</u>)	9-12
	Tree Swallow (<u>Iridoprocne bicolor</u>)	5-6 $\frac{1}{4}$
Large-Hole	Pileated Woodpecker (<u>Dryocopus pileatus</u>)	16-19 $\frac{1}{2}$
	Barrow's Goldeneye (<u>Bucephala islandica</u>)	16 $\frac{1}{2}$ -20
	Sparrow Hawk (<u>Falco sparverius</u>)	9-12
	Great Horned Owl (<u>Bubo virginianus</u>)	18-25
	Tree Swallow (<u>Iridoprocne bicolor</u>)	5-6 $\frac{1}{4}$

General Plant Ecology of the Study Area

The ecology of any terrestrial animal is intimately related to the ecology of the plant components of the ecosystem in which it occurs. This is particularly true of many groups of terrestrial birds whose ecological niches involve, among many other factors, gestalt-type behavioural responses to the overall physical aspect of the environment. It is therefore necessary, in considering the ecological context of the present problem, to review briefly the factors which affect the distribution of the various habitat-types. The following section is thus presented as an attempt to summarize the results of some relevant studies and to apply these results to a brief consideration of the habitats in the study area.

* Sizes are given in inches as taken from Peterson (1961).

According to Tisdale and McLean (1957), the entire Cariboo region is located well within the limits of the interior *Pseudotsuga* Zone. They define this zone as being, in British Columbia, in the southern interior between the Rocky Mountains and the Coast Range on the East and West, ending at about Latitude 53 degrees to the north, and composing the northern extremity of the Rocky Mountain Douglas fir forest.

The climate of the area is rather complicated, with topography having pronounced effects upon local conditions, and exposure causing further complications. Splisbury and Tisdale (1944) described vertical zonation of soils, climate and vegetation. On south and west slopes, the boundaries of main vegetation zones show differences in elevation of as much as 800 feet from those of north and east exposures (Tisdale and McLean, 1957). The same authors also point out that regular meteorological data fail to illustrate variation in climate within the region, as weather stations are largely located in the major valleys where settlement is concentrated. They furnish data to illustrate the changes in climate encountered in passing from the dry grassland areas in the Kamloops area to the northern Spruce-Fir zone, at McCulloch. As Tisdale and McLean indicate, many large gaps exist in our knowledge with regard to the climatology of this region, but in a general way, it can be stated that the *Pseudotsuga* zone is cooler and moister than the grasslands-Yellow Pine (*Pinus ponderosa*) areas, and drier and warmer (in summer at least) than the *Picea-Abies* zone. No data are available for zonal ecotones.

Tisdale and McLean (op. cit.) indicate that the major portion of the zone is now, as a result of the effects of fire, dominated by seral tree species, particularly *Pinus contorta* and *Populus tremuloides*. They further state that although present conditions favour the establishment of the climax tree species over the region, there are large areas in which the process will be very slow due to lack of *Pseudotsuga* seed sources.

Soils in the Cariboo have been little studied. Beaton (1953) classified the soil of the upper Douglas fir zone near Kamloops as "Brown Podsollic Soil". In general, the area is a large lava flow covered by glacial till of varying coarseness.

The role of fire in forest succession has been widely studied and the relationship of aspen (Populus tremuloides) to fire is well established (see Baker, 1925; Moss, 1932). Aspen reproduction after fire seems mainly to occur by means of adventitious shoots arising from the roots. Among reasons put forward for the scarcity of cases of aspen reproduction by seed are the shortness of the period of seed viability and slow initial root growth (Moss, 1932), and a frequent lack of seed trees after fire (Tisdale and McLean, 1957). In the region of Kamloops, however, Tisdale and McLean observed "considerable numbers" of aspen seedlings in burned areas of the Douglas fir zone during the summer of 1952.

In the grassland openings of the Cariboo Parklands, aspen groves can be found on level ground either in small, isolated, fairly discrete groups, frequently clonal in nature, or in large semi-open stands in such locations as are well supplied with soil or surface water. Grassy areas of uneven topography have small groves in gullies and other drainage routes, while low-lying wetlands are frequently covered with thick growths of willow thickets, etc.

Past use by man has had a profound effect upon the entire Douglas fir zone, and the Cariboo Parklands portion is not excepted. Both Macoun (1876) and Dawson (1894) remarked on the replacement by poplar (or aspen) and Pinus contorta of the original vegetation, and Dawson refers to the abundance of fires caused by both Indians and whites. Suppression of fire in recent years in the grazing areas has resulted in the occupation of many acres by Douglas fir regeneration as a result of the lack of fire destruction of young trees, (L.G. Sugden, pers. comm.).

Grazing also is effective in restricting or preventing aspen regeneration. Logging, although carried out in the Douglas Fir zone since the 1860's, has only

recently become important in the Cariboo area. As yet, only Douglas fir is exploited in quantity, but continually greater use is being made of Pinus contorta and Spruce, Picea engelmanni, as well. Aspen, as a result of its small size, usually rather gnarled growth habit and almost universal susceptibility to attack by Fomes igniarius, a heart-rot, is not likely to become a commercially important species in the foreseeable future. Industrialization on a large scale has not yet appeared in the Cariboo. Small sawmills are scattered throughout the area, and usually are present in a given location for only a relatively short period, leaving behind sawdust piles and large heaps of slab, scrap and reject material. These refuse deposits constitute serious fire hazards, and their decomposition also is extremely slow.

Insect outbreaks of major proportions have occurred in recent decades. The most destructive of these have been the infestations of Lodgepole Pine (Pinus contorta) by the bark beetles, Dendroctonus and Ips. Parts of the Douglas Fir zone other than the Cariboo were hardest hit. The Aspen Leaf Miner, Phyllocnistis populiella, a lepidopteran, has caused widespread heavy attacks of aspen from Golden, in the Interior Wet Belt, through the Cariboo and north at least to the vicinity of Quesnel (c.f. Tisdale and McLean). Infestation by this insect seems to cause no particular damage, and some trees at least were seen during the present study to produce new leaves in midsummer when infestation was particularly high.

Lynch (1955) discusses the role of the wood rotting fungus, Fomes igniarius, in the aspen groveland of Glacier County, Montana. He states that this fungus causes widespread damage and that it is exceptional for aspen not to have discolored heartwood. Schmitz and Jackson (1927) also found this to hold for Minnesota. Moss (1932) and Bird (1930) found F. igniarius to be abundant in Alberta and Manitoba respectively, and Bird states that it causes the "premature" death of many trees. Moss found sporophores rare on 35-year-old aspens, but not uncommon

on 50 year-old trees. The decay of heartwood caused by this fungus, which starts while the tree is still rather small, may have considerable significance to the Flicker populations of the aspen groveland areas: the much softer heartwood is attacked for nest-hole excavations much more frequently than are healthier trees; and frequently the birds commence excavation in a scar or broken branch stub in which decay has softened the wood. Sapsuckers, on the other hand, rarely if ever excavate a hole in previously injured wood on the outside of the tree. Even in these cases, however, they usually do not begin to enlarge the nest-cavity itself until the excavation reaches the softer, decayed heartwood.

Lynch (1955) believes that the exhaustion of water available for plant growth is a critical factor in the stabilization of grove boundaries for aspen. This, he feels, is due to the fact that while the main root zone of aspen rarely goes below 2', the roots functioning in shoot production are usually at depths less than 1', and the reduction of soil water past the permanent wilting percentage results in the failure of shoots to develop in the dry soil. He feels also that lack of seed accounts for the failure of aspen to establish in lowland spots where the understory vegetation implies suitable moisture conditions. Lynch again points out the effect of grazing in preventing aspen regeneration.

McMinn (1952) studied the effects of soil drought on the distribution of vegetation in the Rocky Mountains of the northern U.S.A., and concluded that in areas where precipitation is mostly in the winter and summer drought is normal, different plant associations are correlated with different extents of soil drought.

To summarize the plant ecology of the study area, the following points are relevant. It seems now to be generally agreed that the Cariboo region is characterized by the climatic climax forest type known as the Interior Douglas Fir (or Pseudotsuga) Zone (c.f. Krajina, 1959) which has, however, been extensively altered so that very large areas now support a seral association in which Lodgepole

Pine, Pinus contorta, is the dominant and frequently only tree. Some extensive grassland areas also exist; the permanence of these areas is doubtful, however, except in the southerly ecotone with the Ponderosa Pine-Grassland Zone, and along the great trench of the Fraser River. The latter area virtually splits the Cariboo-Chilcotin plateau into two separate areas, and requires special study from an ecological and biogeographical viewpoint. Trembling Aspen (Populus tremuloides), the presence of which is a dominant factor in the ecologies of hole-nesting birds in the area, occurs in stands of several different types. "Fringe" stands frequently occur along edges between grasslands and coniferous stands, large pure stands are found occasionally, and scattered "groves" are found in grassland areas around lakes, in low moist-soil areas and in gullies and other natural drainage courses. Although much more work is needed, the hypothesis seems favoured that not only the Lodgepole Pine, but also Grassland and Aspen habitats are seral stages resulting from the effects of fire. Various types of edaphic wetland communities occur also, but these are very little used by the bird species under study.

Aspen and Douglas Fir trees contained more than 90% of all nests studied, which indicates clearly the importance of these two species. The distribution and abundance of both appears to have been profoundly affected by fire, and that of Aspen also by soil-water considerations. It might be suggested also that extensive range-use studies would be of great value in assessing the effect of grazing by domestic livestock upon tree regeneration, particularly of Aspen. The overall effects of these considerations of plant ecology upon distribution and abundance of hole-nesting birds are discussed in a later section.

Further descriptions of habitat-types and plant communities are to be found in Krajina (1959), Tisdale and McLean (1957), Munro and Cowan (1947), and Erskine (1960), and further elaboration is not needed here.

Finally, then, it is clear that although the ecology of this complex and much-changed phytocoenosis can be understood in very general terms, there remains much botanical work to be done before the overall ecological context of the present investigation can be fully appreciated.

Non-Avian Hole-Using Biota

Tree-holes are utilized for various purposes by many members of the fauna other than birds. The most numerous of those encountered during this study were two species of sciurid rodents, the Flying Squirrel (Glaucomys sabrinus) and the Red Squirrel (Tamiasciurus hudsonicus), both of which were found in a few cases to be nesting in holes of the medium-hole, (see p. 24), cycle. Numbers of cases, however, were very small, and it is speculated that Glaucomys may tend to use niches, cracks, etc. to a considerable extent, and Tamiasciurus is also known to build large nests of twigs, leaves, etc., as well as to use woodpecker holes. Only six nests of both Squirrel species were in Flicker-source holes, and these were disregarded in the analysis for competition for the same reasons as were the rare bird species discussed above.

A note of caution is advisable in this regard. Local opinion was that Red Squirrel populations were "low" during the period of the study, and the possibility must be introduced that during population peaks of this species, a demand upon flicker-cycle holes could develop which might assume significant proportions in the overall competitive situation. Such a situation could conceivably result also in an increased rate of non-specific predation by squirrels on both eggs and young of the hole-nesting birds as well as those of other nesting habits. These factors were apparently not operative to a significant degree during the present study, but they remain nevertheless as potentially significant ecological parameters.

Very little is known of the natural history of Flying Squirrels in this area. In fact, many local persons were unaware that this species existed in the region.

Nothing is known of population levels, amplitude of fluctuations, or any other aspect of the population dynamics of this species, nor is it known what proportion of nests fall within the flicker-cycle. In short, essentially nothing is known of this species except that it occurs in the area, and that occasional individuals were flushed from flicker-source holes during the investigation.

Other workers and casual informants have reported verbally the occasional finding of Bats (family Vespertilionidae), Deer Mice (Peromyscus maniculatus: family Cricetidae), Bushy-tailed Woodrats (Neotoma cinerea: family Cricetidae) and assorted insects, largely Hymenoptera. Again, only scattered evidence of such use was encountered in this study. No bats were encountered during the two summers, and only one mouse was discovered in an empty, incomplete nest-hole. Several holes were found to be completely filled with assorted debris, and it is widely held locally that this filling of holes is done by the Bushy-tailed Woodrat (Neotoma cinerea), usually called the "Pack Rat". At no time during the two year period of field work was any such debris deposited in nest sites under study.

The "Life History" of Nest Sites

For most bird species, nest-sites are probably a measurable ecological parameter. This is perhaps most obvious for secondary hole-nesting species, but Stein (1958) and Mayfield (1960), to mention but two, have shown the measurable and relatively clearly defined nature of nest-sites for species of other ecological characteristics.

Among the hole-nesting birds of this study, perhaps more than in most other cases, the "life-history" of the sites themselves can clearly be seen to have an important relationship to the population ecologies of the species involved.

It has already been noted (c.f. above) that the durability of stumps and "snags" of Douglas Fir (Pseudotsuga menziesii) appears to be an important factor

in the functioning of the Large-Hole Cycle, and may well be a key factor in determining the population density of the Barrow's Goldeneye (Bucephala islandica).

Equally clear is the differential role of Aspen (Populus tremuloides) trees in the Small- and Medium-Hole cycles, at least in terms of the Yellow-bellied Sapsucker (Sphyrapicus varius) in the former cycle. As noted above, essentially all trees of Aspen of a diameter at breast height of about five inches or greater are infected by the heart-rot fungus, Fomes igniarius. This may be regarded as a conditioning factor, and it is clearly of great significance that the areas supporting this combination of Populus and Fomes are also the areas in which hole-nesting birds are known to be vastly more abundant than elsewhere. It is concurrently true that other features of the phytocoenosis which includes Populus tremuloides are no doubt also essential to the hole-nesting species under study, but it is suggested that this conditioning of trees, in the sense that heartwood is rendered softer and more readily excavated, is of considerable significance. The Sapsucker (Sphyrapicus) normally commences nest-site excavation in sound sapwood, but always at a sufficiently great diameter (in 40 nests, never less than 7.0", except one of 6.5") that decayed heartwood is present, and in all nests studied, did not commence to enlarge the cavity until this decayed wood had been reached. The Flicker (Colaptes), on the other hand, rarely began excavation in sound wood, but usually utilized branch stubs, cracks, checks, "cats-paws" and other types of scars in which to commence excavation. The predominant feature seemed to be that holes were begun in locations at which decay had occurred in sapwood, thus providing softer wood with which to work. It is clearly significant that Sphyrapicus is a "generalized" woodpecker, while Colaptes shows various adaptations for ground-foraging, including a well-marked curvature of the bill (Burt, 1930). It may be presumed that such a bill, primarily adapted for foraging, is less suitable for excavating sound wood.

As noted below, there seems to be little evidence for the existence of competition among members of the small-hole cycle, and little is known of the large-hole group, except that the durability of Douglas fir stumps could be an important factor. With respect to the medium, or Flicker cycle, however, it is essential to examine very carefully all factors related to the characteristics and availability of holes. Thus, it is necessary to review the "life histories" of Flicker nests after they are excavated. It was not possible during the time allotted to this study to gather many relevant data, and the need is very clear for a long-term study of a series of fixed plots in order properly to appreciate such factors as rate of production of holes, longevity of individual sites, and the ways in which and rate at which sites become unavailable, as well as to detect any differences which may exist between habitat types. However, personal observations over two years, together with some data from other sources, do permit a qualitative description of the situation, as rather a sideline to the central purpose of this study.

The rate of production of holes is naturally of considerable interest. The Sapsucker (Sphyrapicus) excavates a new hole each year,^{*} and many trees may be found to contain a series of nests. Among the other small-hole species, the Red-breasted Nuthatch (Sitta canadensis), the Black-capped Chickadee (Parus atricapillus) and the Mountain Chickadee (Parus gambeli) are all known to be capable of excavating holes in soft, well decayed wood, although they do not always do so. Flickers (Colaptes) usually excavate a new hole each year, and were observed in five separate cases to excavate a second hole after expulsion from the original hole by Starlings (Sturnus vulgaris). The Pileated Woodpecker (Dryocopus pileatus) is said to excavate a new hole each year, as well as individual roost holes during winter (Hoyt, 1957).

An important consideration is the durability of trees. Many aspen trees

* Possibly of several species.

are in an advanced state of decadence when they become suitable for excavation by Colaptes, and are highly susceptible to breakage, windthrow, etc. This is in marked contrast to Douglas Fir "snags", which, even when dead, tend to remain standing for long periods. Thus a difference might be expected between climatic climax Douglas Fir stands and seral Aspen stands, in terms of hole longevity.

In addition to breakage and windthrow, as mentioned above, holes tend to become unavailable in a number of ways. As previously noted, filling of cavities by Bluebird (Sialia) and Tree Swallow (Iridoprocne) has the effective result of rendering holes unavailable for other species. In decadent and dead trees, tunneling by Carpenter Ants (Camponotus sp.) tends to fill holes with a sawdust-like material which results from the tunneling activity of the ants. In a single instance, an old hole in a dead aspen tree was observed over a six hour period to be filled at a rate of nearly 1 cm. per 2 hours. This was almost certainly an exceptional case, but it does serve to emphasize the role of this phenomenon as a "hole mortality" factor. Various persons have also informed me that filling of holes is carried out by Wood Rats (Neotoma), Deer Mice (Peromyscus), Flying Squirrels (Glaucomys) and Red Squirrels (Tamiasciurus), (c.f. above). Nests of the latter two species encountered in this study were composed largely of lichens and mosses, and nearly filled the holes which they occupied. This again, once the filling of the holes is done, would act as a factor conditioning the environment, although it is possible that actual strife could occur early in the season, when nest sites are being sought. Even this "conditioning", however, since it is done by hole-using animals, may be regarded as an aspect of competition.

In summary, the "life history" of the holes themselves is a factor which should be considered in reviewing the ecological context of the present study.

Aspects to be considered include rate of production, longevity, and rate at which holes become unavailable. Factors affecting these are also important, and they have been reviewed qualitatively at least, pending a detailed study for the purpose of establishing more specific values.

Recapitulation: Ecological Context

Hole-nesting birds in the study area include 17 species of seven different families, divisible into three natural groups. The group based upon holes of medium size includes 6 common species, none of whose ecological niches are particularly similar except in terms of nest sites.

The importance of habitat is recognized with a brief review of the plant ecology of the study area, with particular attention to factors thought to influence the distribution of various plant communities. Of these, the climatic climax Douglas Fir Zone supports considerable hole-nester populations, as do the Aspen groves of the seral Aspen-Grassland "parkland" regions. The seral Lodgepole Pine association supports few birds of this nesting habitus.

Non-avian hole-using biota are reviewed briefly, and comments are offered on their role in the ecosystem, with respect to nest-site competition.

Factors affecting the "life history" of nest sites themselves are discussed, and the need is pointed out for a definitive study of this aspect of the problem. The matters of rate of production, longevity and rate of loss of holes are reviewed in general, in terms of factors influencing them.

ANALYSIS OF NEST-SITE COMPETITION

The "Cycles"

As noted above, the 13 common hole-nesting species in the study area may be placed in three natural ecological groupings in terms of nest-sites. These may, for convenience, be termed the Large-, Medium- and Small-Hole Cycles. It will be clear from the following passages that of these three groups, only the Medium-Hole Cycle may presently be construed as showing evidence that competition could be occurring for nest-sites. Each group is discussed separately below.

The Large-Hole Cycle

This is the least well-known of the three groups, despite extensive efforts in terms of field work by several workers representing the University of British Columbia, as well as field representatives of both Provincial and Federal wildlife agencies. The producer species, the Pileated Woodpecker (Dryocopus pileatus), is comparatively rarely seen, and even less often found nesting. Munro and Cowan (1947) list only two nesting records for British Columbia, and the B.C. Nest Records Scheme contains only 5 further entries for the Province. During the two seasons of field work in this study, only one nest was encountered, and even in that case, excavation was not completed. Another species, the Great Horned Owl (Bubo virginianus) is quite commonly encountered in the study area, but few nests have been found. The files of the B.C. Nest Records Scheme to date contain 8 records of the latter species, only one of which was in a hole; this was a natural cavity from a broken branch in a Cottonwood (Populus trichocarpa) tree near Fraser Lake, B.C. Of the remaining 7 records, 4 were platform-type stick nests, and three were records of fledged young.

In view of the degree of effort expended in studies involving the Barrow's Goldeneye, remarkably few data are available regarding its nest-sites.* Available

* M.F. Jackson, the University of British Columbia, has data on a number of natural sites of Barrow's Goldeneye. It is virtually impossible to estimate the time spent searching for these nests, as many records resulted from casual encounters, but the efforts of many people over many years are involved (oral comm.).

data do suggest very strongly, however, that the "typical" nest-site is an old Pileated Woodpecker hole. The Goldeneye, however, is one of the more abundant ducks of the study area, and its populations are exceedingly dense in comparison with populations of the Pileated Woodpecker. This fact, on first examination, might well be thought to militate against the above-mentioned "typical" site. Two factors in the nesting ecology of the Pileated Woodpecker, however, tend to explain this apparent anomaly. Firstly, each pair of Pileated Woodpeckers excavates a new cavity each year, as well as individual roost-holes each winter (c.f. Hoyt, 1957); secondly, in the study area, few trees except Douglas Fir (Pseudotsuga menziesii), are large enough to contain a Pileated Woodpecker nest, and this tree is extremely long-lived. Thus, the supply of available holes is far greater than might be directly indicated by the Dryocopus population at any given time. Additionally, Dryocopus pileatus is a large bird, and might be expected to live several years. J.S.Y. Hoyt (1950) gives an age of 9 years for a captive specimen. No age records are given in Bent (1939). Jackson (pers. comm.) also feels that since 1952, populations of both Pileated Woodpeckers and Barrow's Goldeneye have declined in the study area. As pointed out earlier, logging, which was just gaining momentum by 1952, has been concentrated on Douglas Fir, and a strong possibility exists that removal of large trees of this species may be a primary reason for these population reductions.

Jackson also feels that, although her data cover a wide range of site characteristics, there is a considerable possibility that many sites may be missed, particularly those high in stubs of Douglas Fir, and those at great distances from water.

During recent years, the British Columbia Fish & Game Branch has been conducting a programme providing nest boxes for Barrow's Goldeneye over much of the study area.

Up to 20% of these boxes have been used in the first year after placement (verbal communication, L.G. Sugden). Such heavy use may be interpreted as indirect evidence that natural nest-sites must be in short supply: however, it could equally well be argued that boxes are used merely by virtue of being close to the lakes on which Goldeneye broods are raised, and are thus more "desirable" than distant natural sites. This could be advantageous to Goldeneye populations in that brood mortality in transit from remote nests to brood lakes, might well be reduced to a significant extent.

It is clearly indicated in the foregoing that the Large-Hole Cycle, although clearly defined in general terms, is too poorly known in detail to be considered here. Further studies are needed to elucidate possible competitive relationships. Present knowledge by no means precludes the occurrence of nest-site competition within this group, but data now in hand do not permit any great degree of generalization on this matter.

The Small-Hole Cycle

This group is composed of 5 species, of which the Tree Swallow (Iridoprocne bicolor), is the only form incapable of excavating its own cavity. Thus it is difficult to envision nest-site competition in this group. This situation is in direct contrast with the equivalent group in Europe, which contains many species of Paridae, Turdidae, Muscicapidae, etc., few if any of which have this ability. The hole-nesting avifauna of Europe is much richer in all three groups, although greater attention has been paid to the smaller passerines. No doubt it is from this situation that the current widely-held views have arisen on nest-site competition among hole-nesting birds (c.f. Udvardy, 1951). This situation in the study area is, then, quite different from that found in Europe, and widely studied there.

The Medium-Hole, or "Flicker" Cycle

For purposes of brevity, the medium-hole group will be referred to hereafter as the "Flicker" cycle, to emphasize that this species is the hole-producer for the group.

Figures 3 and 4 show rather clearly the separation of the three cycles in terms of hole sizes and observed species-site affinities. The group now under discussion includes 6 regular component species in the study area, among which only the Flicker (Colaptes) produces holes. The remaining 5 species are, as defined above, secondary hole-nesters. Figure 3 includes a diagrammatic representation of the species-site relationships within the Flicker cycle, and of this cycle to the other two groups. Figure 5 is an attempt to describe the ecological niches of the component species of the Flicker cycle, and to show how these niches combine with other environmental factors to produce an overall "ecological demand" upon the supply of tree-holes excavated by the Woodpecker, Colaptes. Mensurational data were collected concerning ecological and physical characteristics of these holes and were analyzed in terms of the question, "which factors tend to mitigate, and which to intensify, nest-site competition in this group of birds, all of which seem to share a single environmental resource?" Ideally, each species would be considered in terms of all parameters so as to synthesize a "theoretical ideal nest-site" for that species, and these statistical entities compared. However, as will be seen in the following treatment, actual field conditions rendered such idealized treatment unrealistic. Additional complications are introduced by the combination of differing sample sizes and widely divergent degrees of variability in nest-site characteristics from species to species. The alternative method of analysis, consideration of all species together, parameter by parameter, was undertaken, and the analysis is given below. Sample sizes vary from one parameter to another, as it was not possible in many cases to secure values for all Parameters.

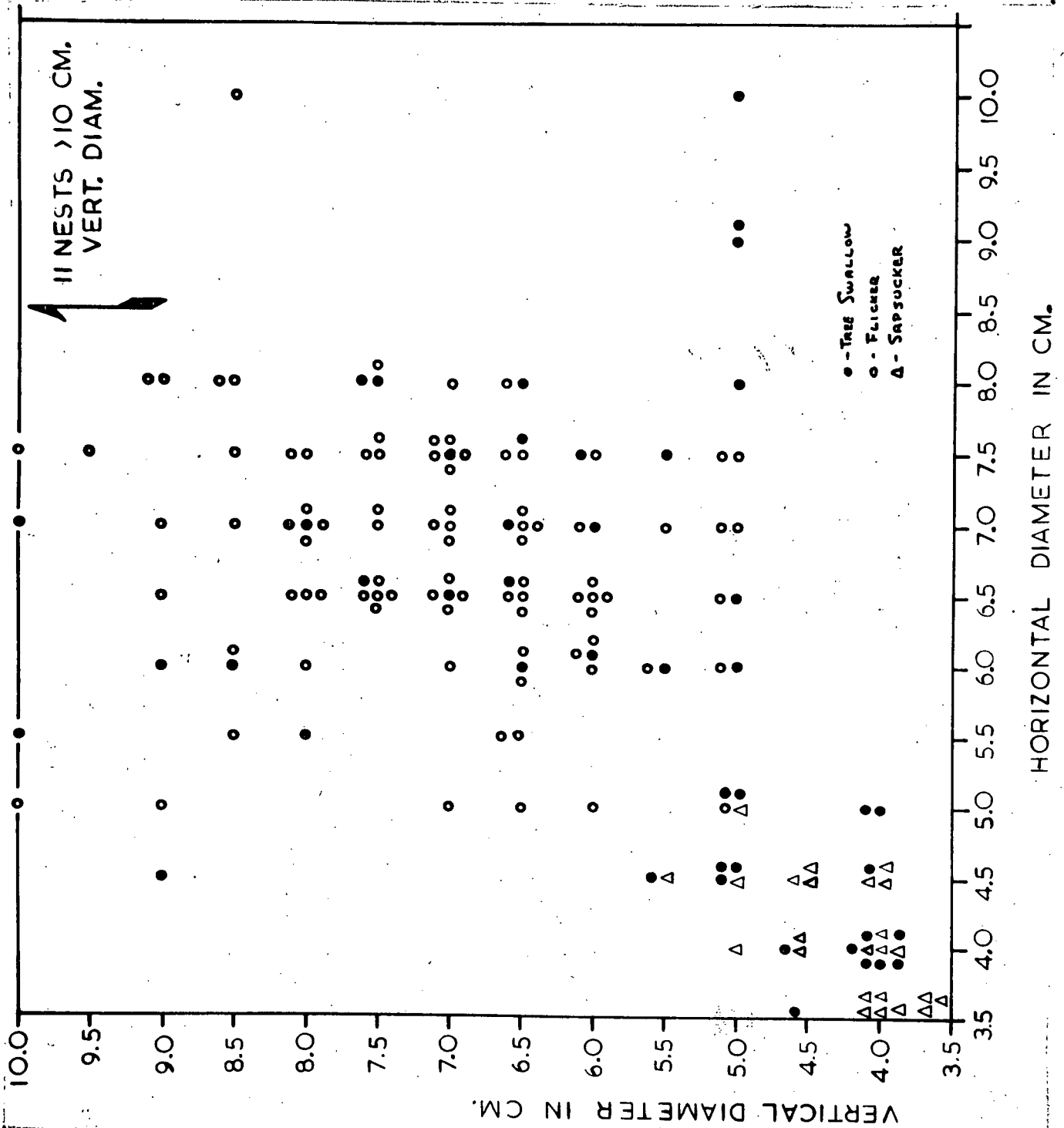


FIG 4:
HOLE-SIZE RELATIONSHIPS

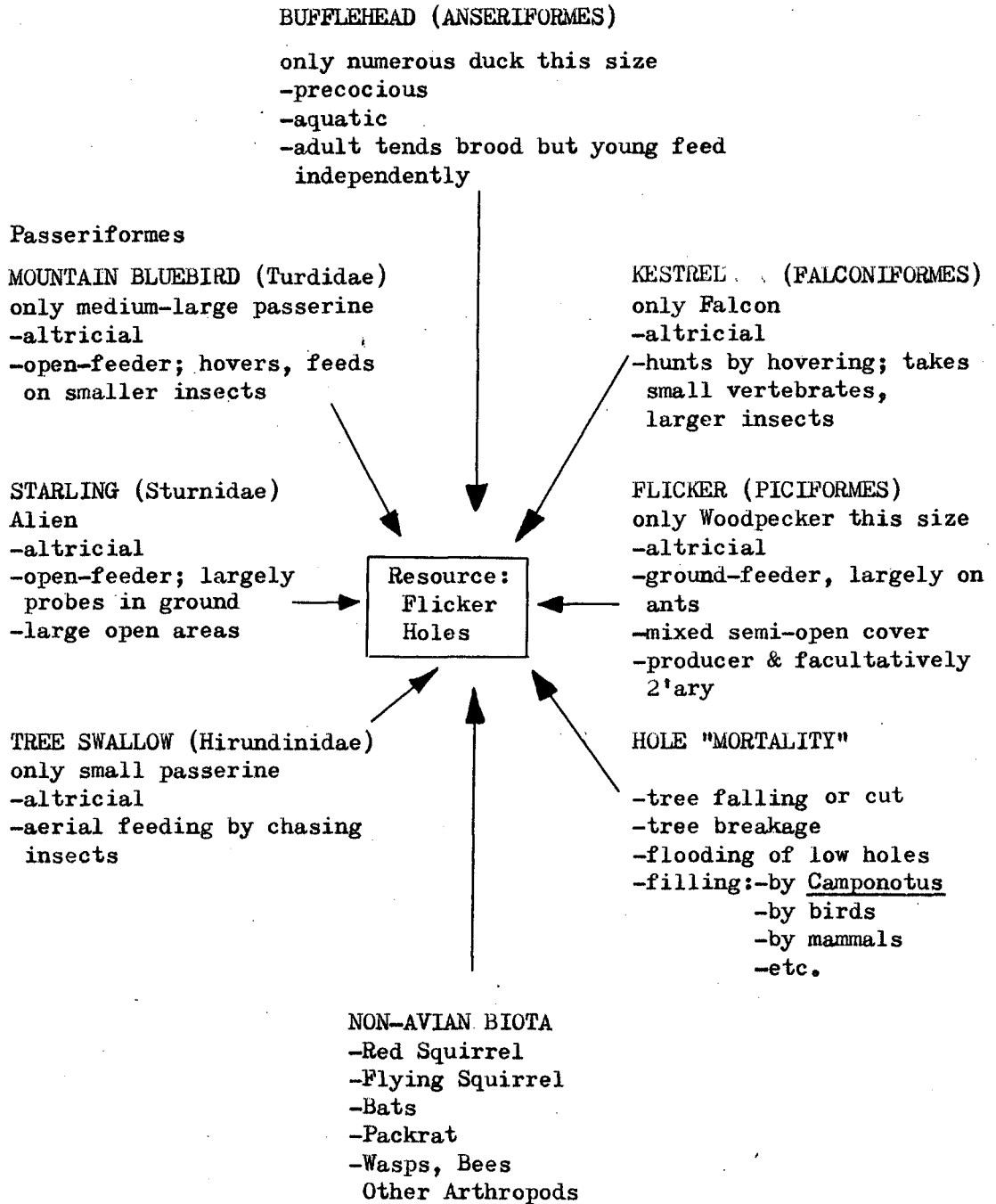


Figure 5. The Flicker Cycle: Demands Upon Hole Supply.

Hole Direction

One of the first considerations to arise is usually the suggestion that certain species might favor a particular directional orientation of the nest entrance, or that primary hole-nesters would show a preponderance of holes facing so as to utilize warming by the sun. In the study area, this would encompass the bearings between 090° (East) and 180° (West). In Table III are presented the actual data recorded.

Pymmonen (1939) found that the majority of woodpecker nests which he studied in Finland showed a northward orientation, but attributed this to the fact that prevailing winds in the area were from that direction, and that the bark of trees was thereby roughened, permitting the birds to cling more easily while the nest was being constructed.

In the present study, nests of Flicker cycle species in solitary trees showed no particular orientation (see Table III) and trees in groves were characterized by two attributes of holes: 1) all holes faced toward an open space; 2) holes tended to be at or near grove-edges, except in very sparse groupings of trees. This is readily explained by the characteristics of the flight of the hole producer, the Flicker (Colaptes). This species flies heavily in bounding swoops, and carries the wings nearly closed during a great proportion of the time spent in flight. Such a mode of flight imposes considerable restrictions on lateral manoeuvrability, with the result that a "clear run" is required by a Flicker flying toward or from a nest entrance.

Burns (1900) gives values of one to two metres for depth of swoops and three to five metres for length in the Yellow-shafted Flicker (Colaptes auratus): these values may be taken as quite acceptable for the Flickers of the study area. Thus the entrance to the nest must leave a flight path of at least these dimensions. All secondary species of this cycle in the study area are more manoeuvrable than

TABLE III. HOLE DIRECTIONS OF NESTS MEASURED WITHIN STUDY AREA.

Species	Directions																Species Total
	N		NE		E		SE		S		SW		W		NW		
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Flicker	5	5.3	11	11.4	10	10.4	8	8.3	27	28.1	17	17.6	12	12.4	6	6.2	96
Starling	13	7.7	21	12.6	11	6.5	29	17.2	30	17.8	30	17.8	17	10.1	17	10.1	168
Bufflehead	14	13.5	11	10.6	14	13.5	11	10.6	17	16.5	15	14.5	11	10.6	10	9.5	103
Bluebird	5	11.1	4	9.1	2	4.5	3	6.8	5	11.1	13	29.5	5	11.1	7	15.9	44
Tree Swallow	2	5.9	6	17.7	2	5.9	5	14.7	5	14.7	7	20.5	1	3.0	6	17.7	34
Fl. Source (Excl. Kestrel)	39	3.8	53	14.5	39	8.8	56	12.6	84	18.4	82	18.4	46	11.8	46	11.8	445

No. = nests measured

% = % of nests for that species.

Fl. source = holes made by Flicker.

the Flicker and thus have less exacting flightway requirements. However, in terms of compass direction, the choice available is that found in old Flicker sites. Table III shows hole directions measured for each species.

Figure 6, a graphic representation of the data in Table III, shows that a tendency exists for hole directions to face the arc between 90° and 180° . However, as can be seen from the data in both Table III and Figure 6, there is little deviation within the medium-hole group from the overall pattern of holes produced by the Flicker.

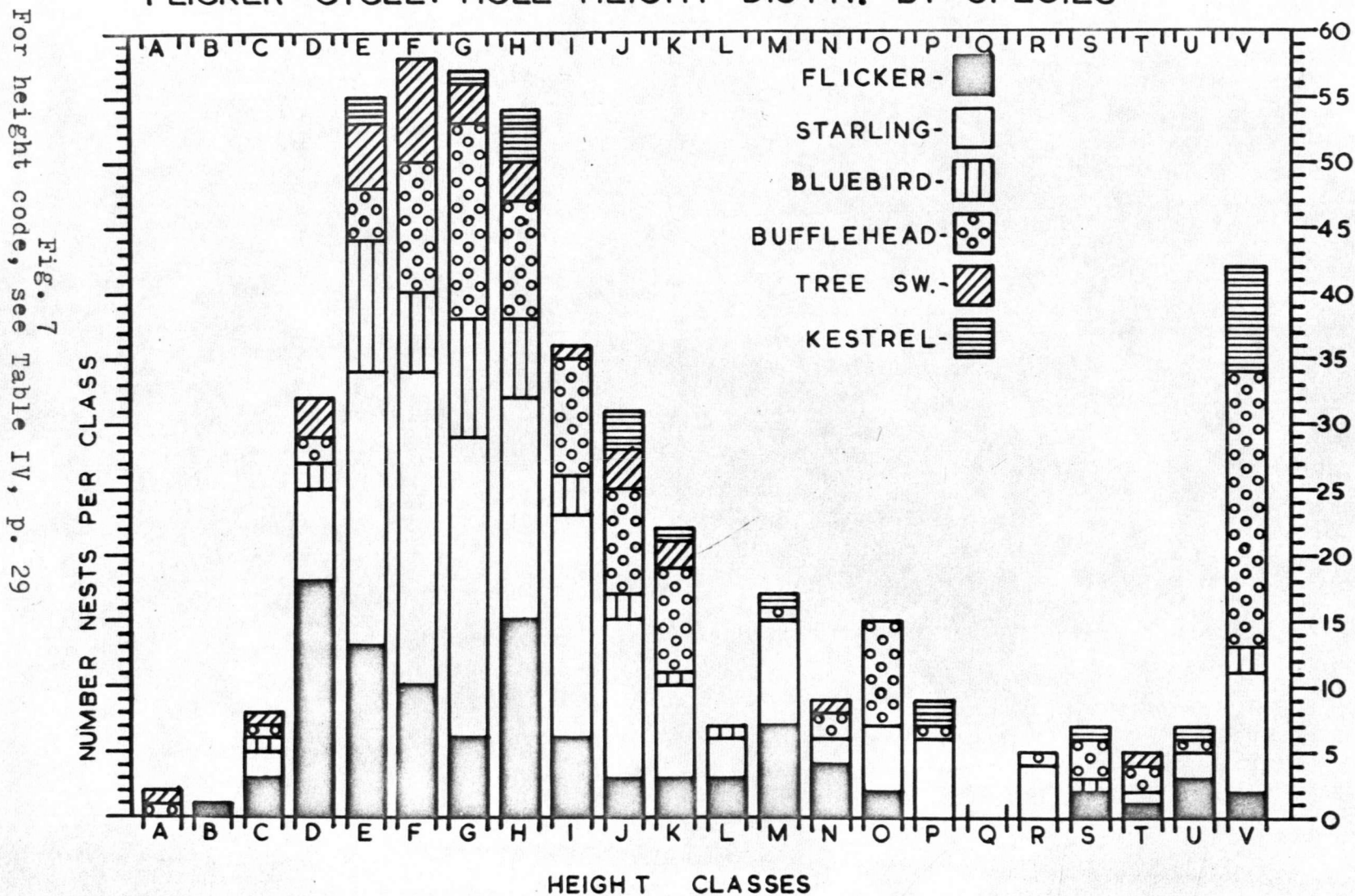
When hole directions of all species were tested by chi-square for goodness-of-fit against the overall pattern of Flicker holes, only the Bluebird showed a significant deviation, ($\chi^2 = 23.81$ at probl. level of 5%, 7 degree of freedom), and then only in one direction (SW). Since there is no depression in that direction in any other species, nor, in any other direction, any marked depression in Bluebirds accompanied by a "bulge" in another species, this deviation in Bluebirds seems more likely to be an artifact of sample size than an indication of competitive exclusion.

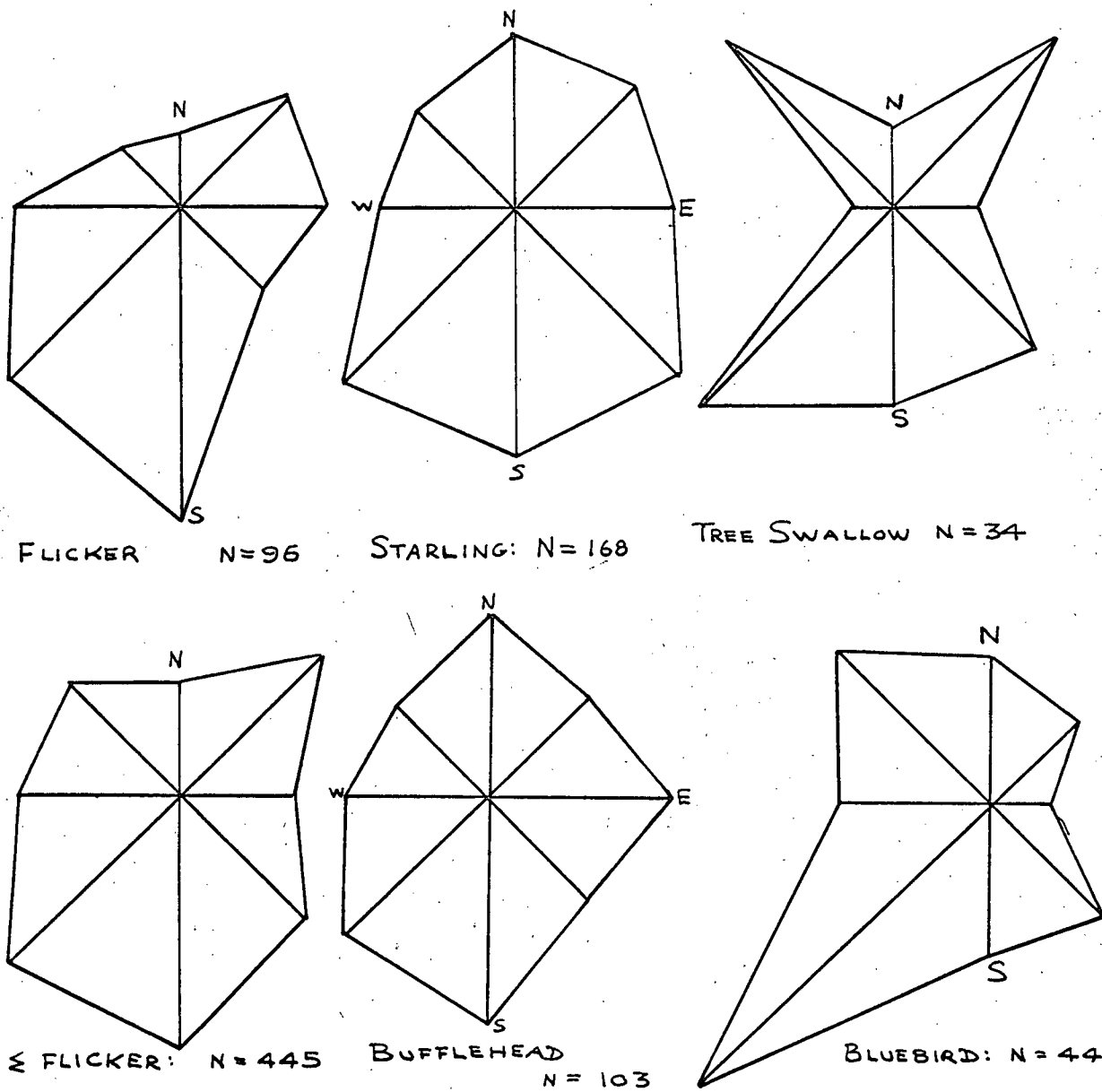
In any event, it is clear that differences in hole directions are hardly of such magnitude as to be of sweeping biological significance. The importance of these data rests in the fact that hole directions are essentially similar in all species.

Hole Height

The distribution of hole heights is subject to a greater degree than other physical characteristics of the cavity to alteration in response to the species and growth forms of the trees in which cavities are excavated. In Table IV and Figure 7, the overall height distribution is given in 25 cm. height classes for

FLICKER CYCLE: HOLE HEIGHT DIST'N. BY SPECIES





(DATA: TABLE III)

FIG. 6-

FLICKER CYCLE: FREQUENCY DISTN.
OF HOLE DIRECTIONS (two mm=1%)

479 nests constructed by Flickers (Colaptes) and measured while being used by species of the Flicker cycle. In both Table IV and Figure 7, the only Tree Swallow (Iridoprocne bicolor) nests considered were those in holes originally made by Flickers. In the height range between 0 to 4 metres, most nests were in Aspen (Populus tremuloides) trunks and stubs, and in the range over approximately 4.5 metres were a greater proportion of Douglas fir (Pseudotsuga menziesi) trees. It can be seen from both Table IV and Figure 7 that two "humps" occur in the height distribution of holes excavated by Flickers, the second being much more diffuse, and covering a wide range; the first is around the level of 1.75 metres, with a drop to fairly low values in the 4 to 5 metre range, followed by about 10% of all nests at scattered heights over 5 metres. For two reasons, it is almost certain that these higher height classes are under-represented: 1) vastly greater difficulty in locating under field conditions, 2) many high holes, even though located, could not be reached safely. In the latter cases, however, it was usually possible to establish occupancy and determine height by use of an Abney level. Other measurements were not always obtained for such sites.

The form of the height distribution curve can thus be seen to be related to growth-form and thus species of trees used, rather than to an innate height preference of Colaptes. Although no quantitative data are available, it can be stated on a basis of common sense and experience that the ratio of high (over 5 m) to low (under 4 m) nests appears to parallel the ratio of tall to low trees in the study area. Again, detailed census and survey data are badly needed, despite the very great efforts necessary to secure them. In short, the form of the height distribution of holes made by Colaptes is a function of the availability of tree-trunk surface with appropriate decay conditions and facing a suitable flight corridor. It was realized nearly at the conclusion of the study that this would have been shown clearly by the recording of the height of the bottom of the tree canopy over

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TABLE IV. HOLE HEIGHTS: SUMMARY FOR FLICKER CYCLE.

Ht. Class in Cm.	Flicker		Starling		Bluebird		Bufflehead		Tree Swallow *		Kestrel		Flicker Source		
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
A	0-25	-	-	-	-	-	1	0.9	1	3.1	-	-	2	0.4	
B	26-50	1	1.0	-	-	-	-	-	-	-	-	-	1	0.2	
C	51-75	3	3.0	2	1.2	1	2.3	1	0.9	1	3.1	-	-	8	3.7
D	76-100	18	18.0	7	4.1	2	4.5	2	1.8	3	9.4	-	-	32	6.6
E	101-125	13	13.0	21	12.3	10	22.7	4	3.7	5	15.6	2	8.3	55	11.5
F	126-150	10	10.0	24	14.1	6	13.6	10	9.3	8	25.0	-	-	58	12.1
G	151-175	6	6.0	23	13.5	9	20.4	15	14.0	3	9.4	1	4.2	57	11.9
H	176-200	15	15.0	17	10.0	6	13.6	9	8.4	3	9.4	4	16.6	54	11.3
I	201-225	6	6.0	17	10.0	3	6.8	9	8.4	1	3.1	-	-	36	7.5
J	226-250	3	3.0	12	7.0	2	4.5	8	7.5	3	9.4	3	12.5	31	6.5
K	251-275	3	3.0	7	4.1	1	2.3	8	7.5	2	6.2	1	4.2	22	4.6
L	276-300	3	3.0	3	1.8	1	2.3	-	-	-	-	-	-	7	1.5
M	301-325	7	7.0	8	4.7	-	-	1	0.9	-	-	1	4.2	17	3.5
N	326-350	4	4.0	2	1.2	-	-	2	1.8	1	3.1	-	-	9	1.2
O	351-375	2	2.0	5	2.9	-	-	8	7.5	-	-	-	-	15	3.1
P	376-400	-	-	6	3.5	-	-	1	0.9	-	-	2	8.3	9	1.9
Q	401-425	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R	426-450	-	-	4	2.4	-	-	1	0.9	-	-	-	-	5	1.1
S	451-475	2	2.0	-	-	1	2.3	3	2.8	-	-	1	4.2	7	1.5
T	476-500	1	1.0	1	0.5	-	-	2	1.8	1	1.31	-	-	5	1.1
U	501-525	3	3.0	2	1.2	-	-	1	0.9	-	-	1	4.2	7	1.5
V	>525	2	2.0	9	5.2	2	4.5	21	18.6	-	-	8	33.5	42	8.8
TOTALS		102 nests		170 nests		44 nests		107 nests		32 nests		24 nests		479 nests	

* Only Flicker-source Tree Swallow nests were used here.

+ % values are for total nests of each species and are calculated to three significant figures.

each nest. This measurement, however, was not taken for most nests, although its inclusion is recommended for future workers. Tree heights were recorded for all nests, but these seem to bear no relationship to hole height distribution. Along with all other data, tree height measurements are deposited in the archives of the Department of Zoology in the University of British Columbia, but for reasons of space economy, they are not presented here.

Several factors can be seen, however, which could be of significance in possible nest site competition: 1) virtually no Bluebird (Sialia) or Tree Swallow (Iridoprocne) nests were found above the 3 to 4 metre level; 2) only 3 of 24, or approximately 13%, of Sparrowhawk (Falco sparverius) nests occurred below 1.75 metres. Also, no Sparrowhawk nest below about 5 metres was known to be successful in fledging young; 3) other than these points, approximately 80% of all species (Fl.-81%, St.-78%, Bluebird-93%, Buff.-63%, T.S.-90%, Kes-45.8%) were in the 50-300 cm. height range: 77% of all nests in this cycle fell within the same range.

Thus, except that Sialia and, to a much lesser extent, Iridoprocne, may tend to be restricted to lower nests, there appears not to be any significant separation of species in terms of hole height. The departure of hole height distribution in two aspects from normal distribution is referable to the influence of tree growth-form.

Entrance Size

Clearly, entrance size is quite important to secondary hole-nesting species. A minimum size is imposed by the body size of the species involved, and maximum limits, although largely a function of available sites so far as is now known, may also be set by behavioural responses.

The species of the three cycles are separable almost completely in this regard,

except for two regular exceptions. The Sparrowhawk (Falco sparverius) is known occasionally to use holes made by the Pileated Woodpecker, although no cases of this were found during the present study. The use by Falco of boxes designed for Wood Duck (Aix sponsa) and Barrow's Goldeneye (Bucephala islandica) has been reported in several instances in British Columbia (pers. comm: J. Mack, Enderby, B.C.; Game Biologists L.G. Sugden and P.W. Martin, B.C. Fish and Game Branch). Data obtained during this study included 4 cases of the use of Game Branch duck boxes, 10 nests in which entrance sizes could not be measured, and 10 for which complete measurements were obtained.

The Tree Swallow (Iridoprocne bicolor), nested not only in all three cycles, but in many other situations as well. Figure 4 shows the relationship of Tree Swallow nests to some sites occupied by Flicker and Sapsucker in terms of entrance sizes.

Purely as a space consideration, not all entrance-size data are plotted here. In Figures 8 and 9, absolute frequencies of 1959 data for Flicker and Starling are given in histogram form, and in Figures 10 to 14, horizontal diameters are plotted against vertical diameters for Flicker (Figure 10), Starling (Figure 11), Mountain Bluebird (Figure 12), and Bufflehead (Figure 13). Figure 4, should be referred to again for partial Tree Swallow data.

The major point to be made here is, again, that very little separation is evident from species to species, except that few Bufflehead nests were smaller than 6.0 X 6.0 cm., and none were smaller than 6.0 X 5.0 cm. (only one at this value). No Bufflehead nest showed a horizontal component of less than 6.0 cm., while many nests of the other species fell in the range from 5.0 to 6.0 cm. This is not unexpected, as the Bufflehead is somewhat larger, particularly in girth, than the other species of this group (see Table II for length measurements).

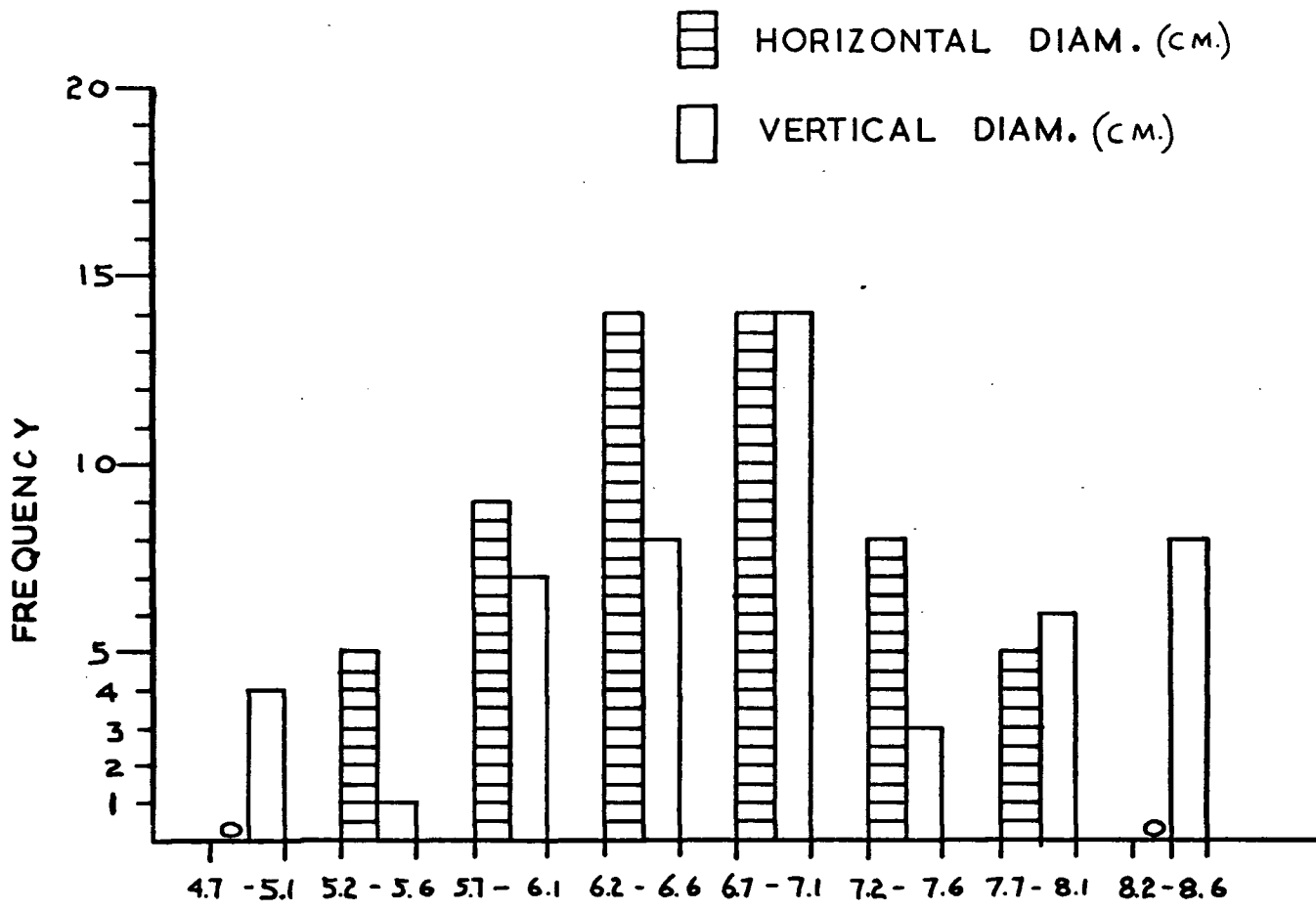


FIG. 8: FLICKER: HOLE SIZES, 1959

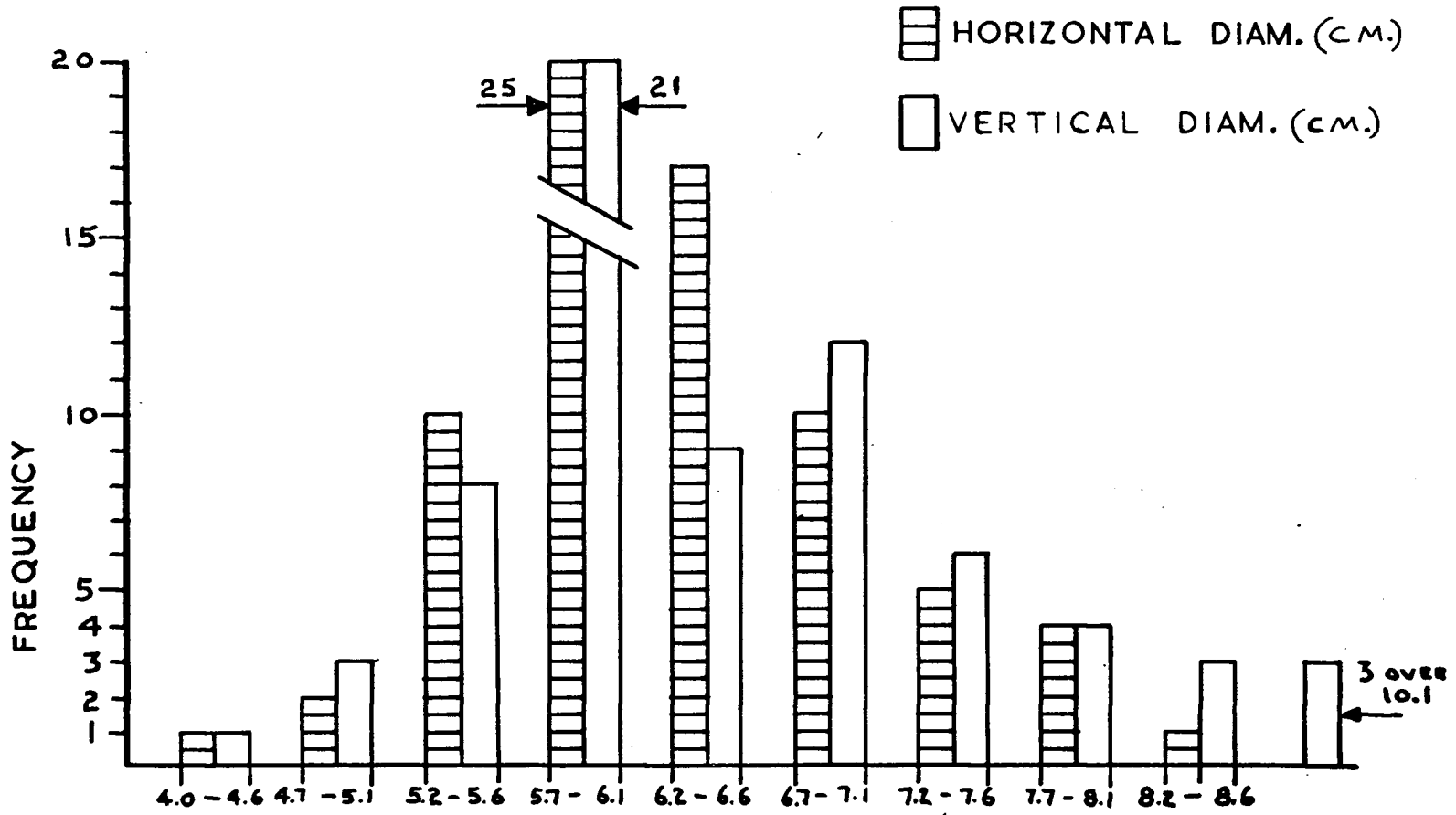


FIG 9: STARLING: HOLE SIZES, 1959

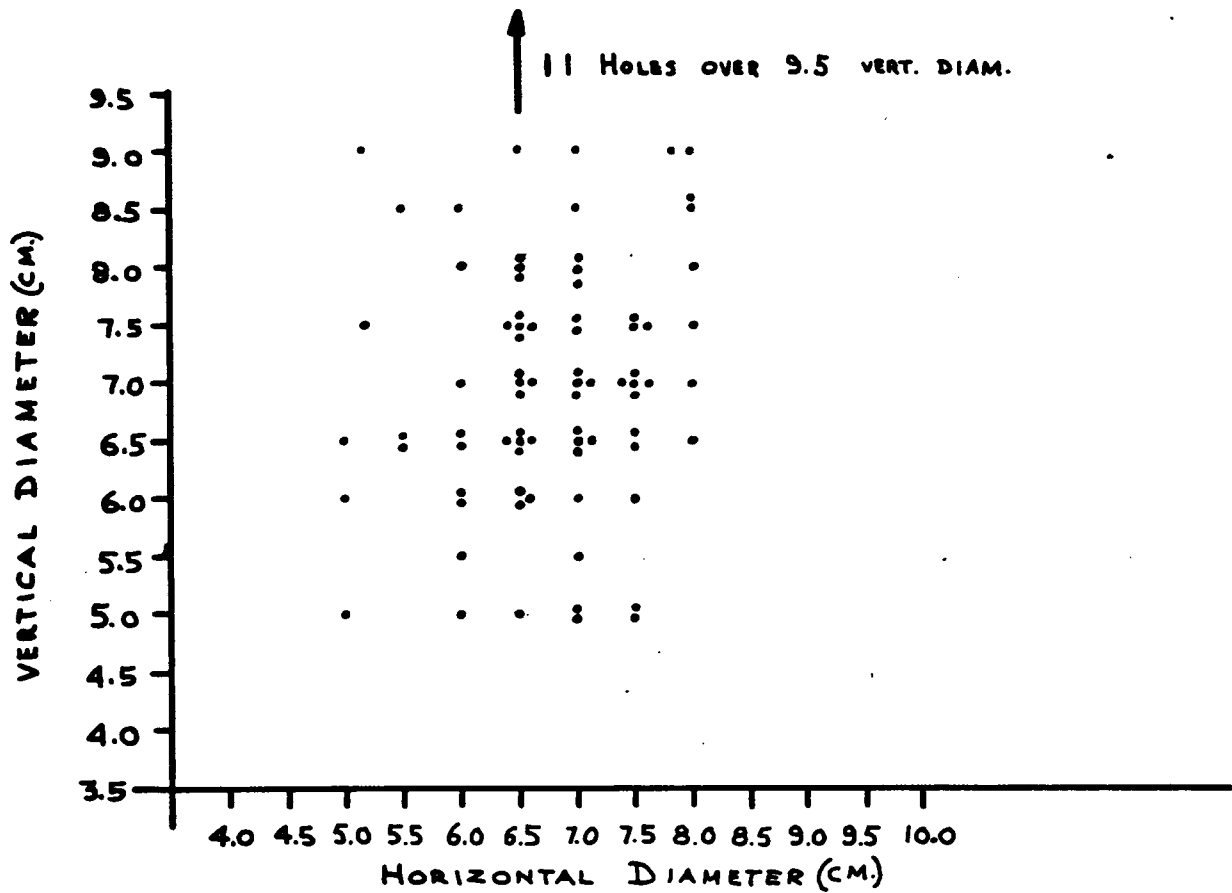


FIG. 10: ENTRANCE SIZES: FLICKER

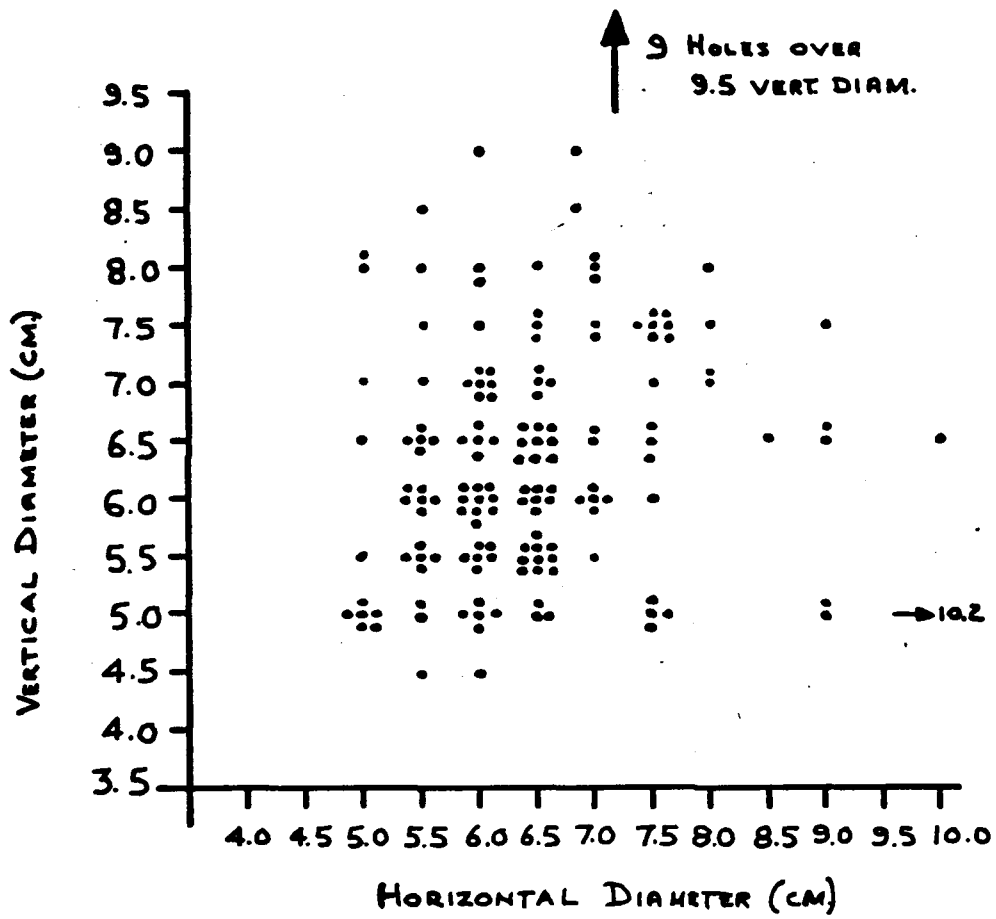


FIG. II: ENTRANCE SIZES: STARLING

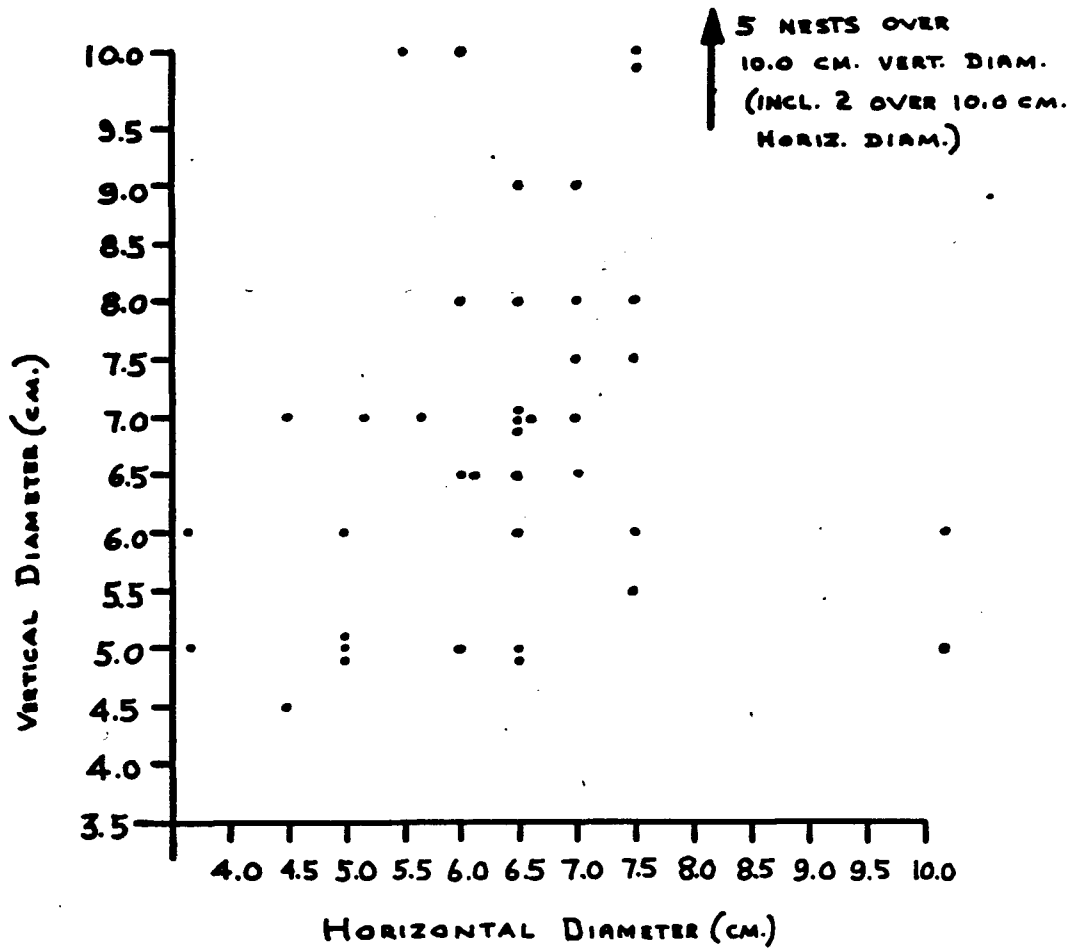


FIG. 12: ENTRANCE SIZES: BLUEBIRD

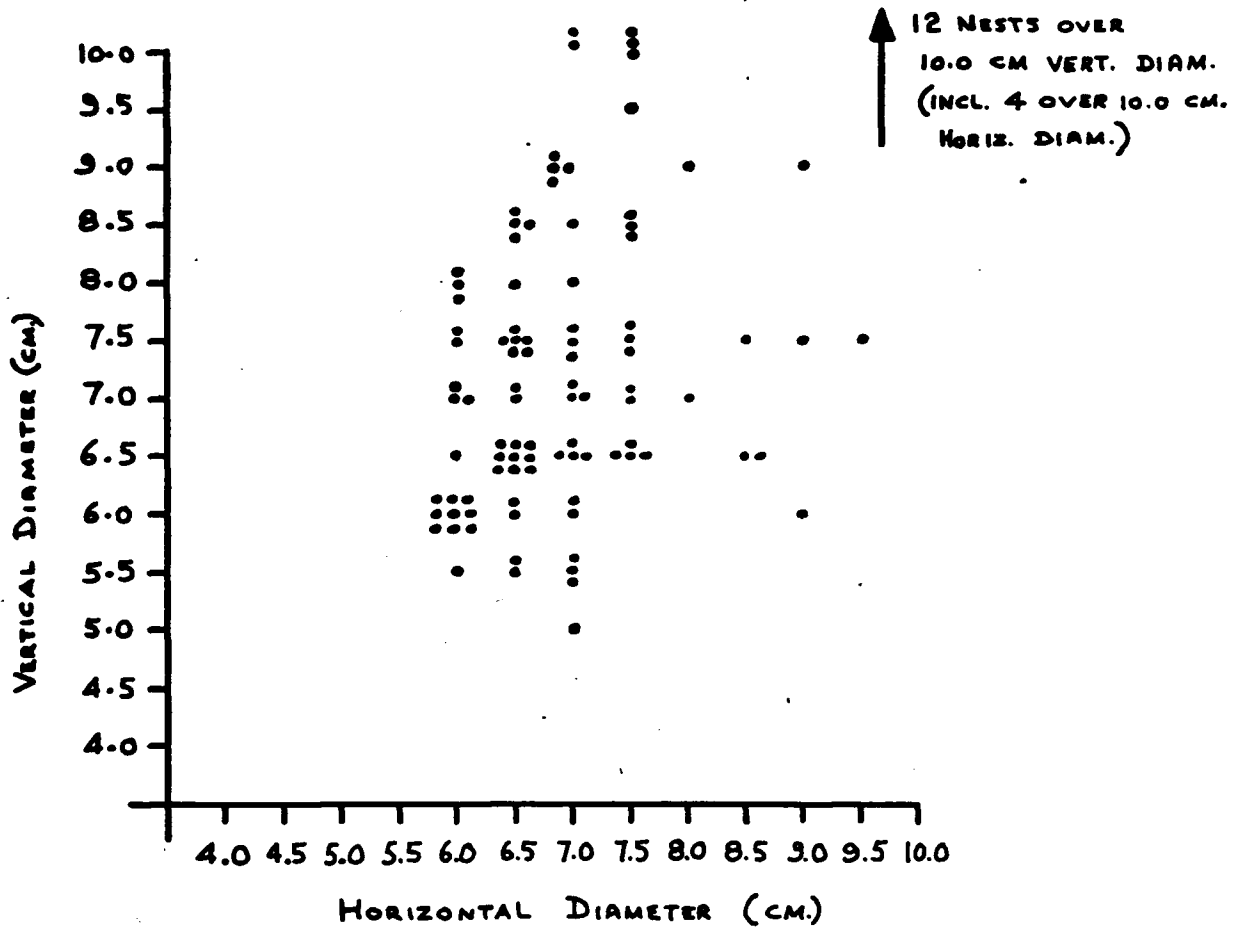


FIG 13: ENTRANCE SIZES: BUFFLEHEAD

Vertical diameter exhibited somewhat greater variability than did horizontal diameter, particularly in terms of the upper limit. This tendency may well be imposed by the nature of the sites selected, as a considerable proportion (approximately 10%) of Flicker holes could still be seen, even when complete, to have been started in a vertical crack.

Sill Size

Data on sill size are summarized in Table V and Figures 14 to 16. This parameter showed one of the most sharply defined ranges in values, with 94% of all measurements in a sample of 436 falling within the range between 1.2 and 7.1 cm. Figure 14 represents per cent frequency distribution of data on occupied Flicker nests, and on all sites established as having been constructed by Flickers. Data for Bufflehead (Bucephala albeola) and Tree Swallow (Iridoprocne bicolor) in Flicker-source sites are shown in Figure 16 and clearly follow the same pattern of sill size distribution. Figure 15, however, is somewhat less clear: the data shown in this figure are from nests occupied by Starling (Sturnus vulgaris) and Mountain Bluebird (Sialia currucoides). The sample for Sturnus, representing 168 nests, should be representative for the species, and seems on first inspection to represent a tendency in Sturnus vulgaris to select somewhat thicker sills, while the Sialia data seem to show a skew toward thinner sills. The size range from 1 to 4 cm. includes 49.1% of all Starling nests, and 81.8% of Bluebird nests. The interval 4 to 6 cm. includes a further 37.6% of Starling and 9.2% of Bluebird nests.

The difference between the sill size-class distributions for Sturnus and Sialia, then, seems striking, but at present it cannot be explained. A possible explanation would be competitive exclusion by Sturnus of Sialia from holes with thicker sills: this is militated against, but not precluded, by the fact that 49.1% of Sturnus nests also occur in the size range occupied by 81.8% of Sialia nests. It would be most instructive to examine data on a series of Sialia nests

SILL SIZES

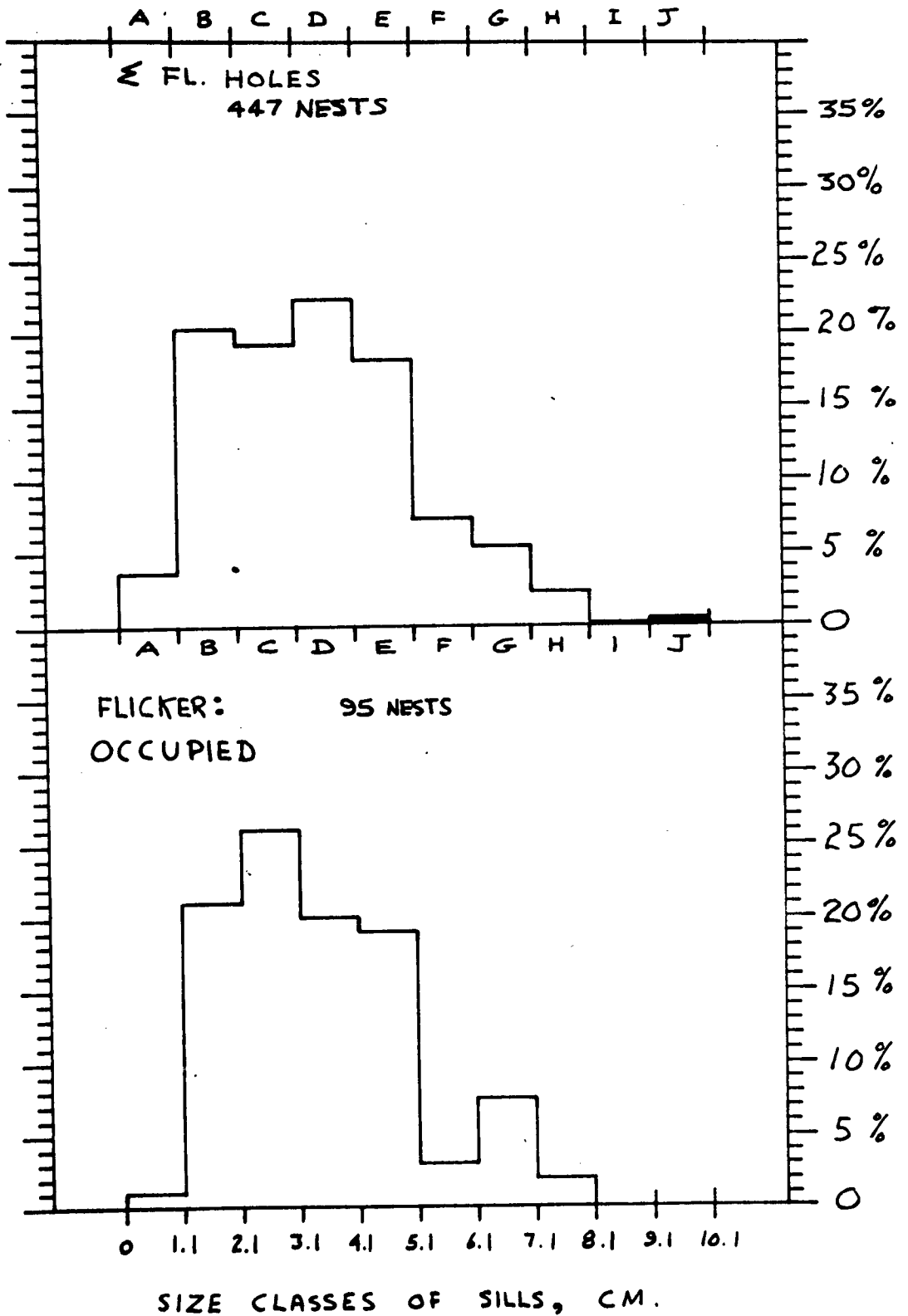


Fig. 14

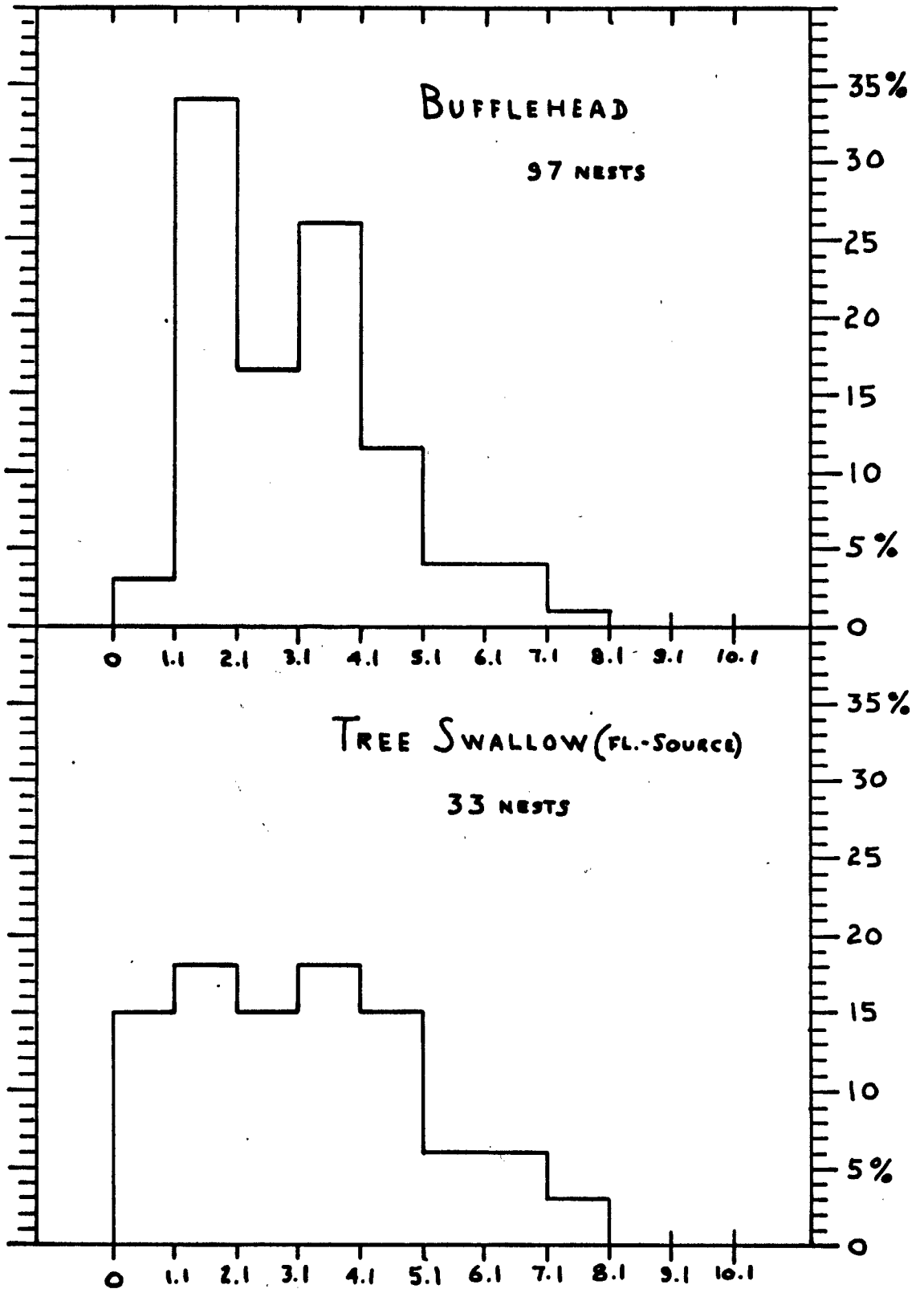
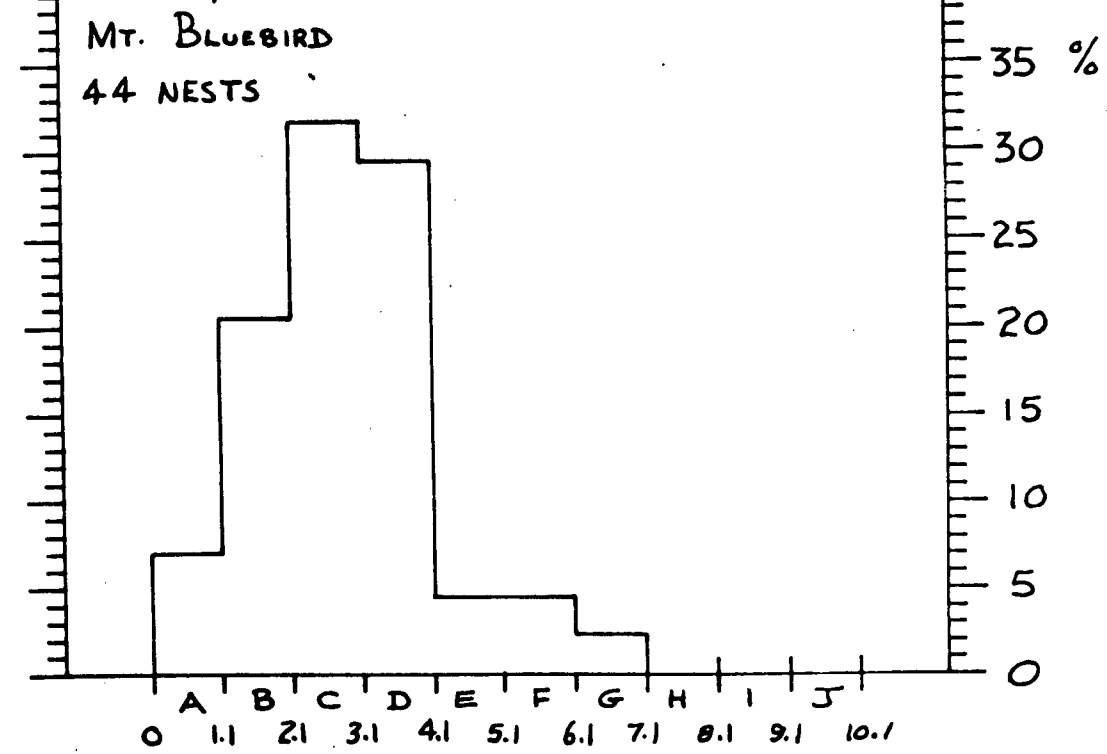
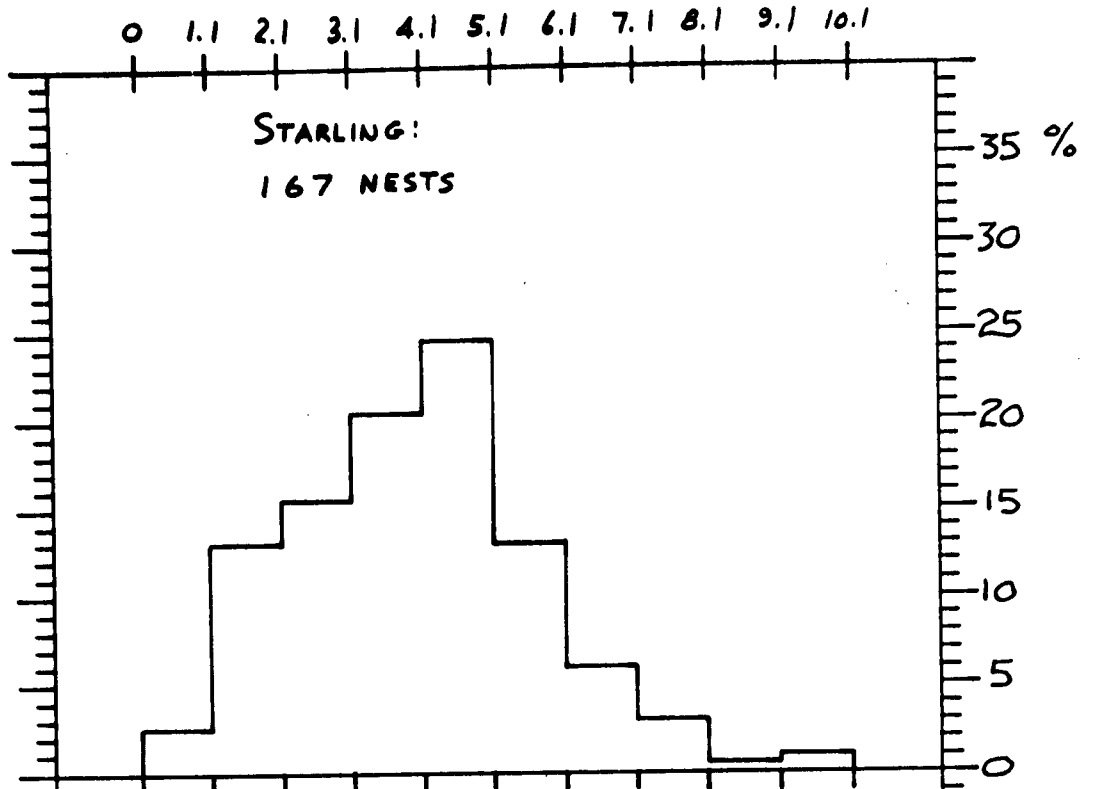


FIG 15: SIZE CLASSES OF SILLS, CM.

SILL SIZES



SIZE CLASSES OF SILLS : CM.

Fig. 16

TABLE V. SILL SIZES: FLICKER CYCLE SUMMARY (BOTH YEARS).

Code	Size Class Limits	Flicker		Starling		Bufflehead		Bluebird		Tree Swallow		Flicker	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
A	0-1.1 cm.	1	1.1	4	2.4	3	3.1	3	6.8	5	15.2	16	3.7
B	1.2-2.1 cm.	20	22.0	22	13.1	33	34.0	9	20.5	6	18.2	90	20.5
C	2.2-3.1 cm.	25	27.0	26	15.5	16	16.5	14	31.8	5	15.2	86	19.7
D	3.2-4.1 cm.	19	20.0	34	20.5	25	25.8	13	29.5	6	18.2	97	22.2
E	4.2-5.1 cm.	18	19.0	41	24.5	11	11.3	2	4.6	5	15.2	77	17.6
F	5.2-6.1 cm.	3	3.3	22	13.1	4	4.1	2	4.6	2	6.2	33	7.6
G	6.2-7.1 cm.	7	7.4	10	5.9	4	4.1	1	2.3	2	6.2	24	5.5
H	7.2-8.1 cm.	2	2.2	5	2.9	1	1.0	-	-	1	3.1	9	2.1
I	8.2-9.1 cm.	-	-	1	0.6	-	-	-	-	-	-	1	.02
J	9.2-10.1 cm.	-	-	2	1.2	-	-	-	-	-	-	2	.04
K	10.1	-	-	-	-	-	-	-	-	1	3.1	1	.02
TOTALS		95		168		97		44		33		436	
											(Fl. Source Only)		

from an area not occupied by Sturnus. Also, the curve for Sialia might change somewhat with enlargement of the sample: the nature and extent of such a change, if in fact it would occur at all, cannot of course be predicted. In any event, there can hardly be said to be a separation of species in terms of this parameter, although partial competitive exclusion may be hinted at in this one species pair. Finally, it is clear from Table V and Figures 14 to 16 that, in general, there is very little separation of species in terms of sill sizes (except that Starlings (Sturnus vulgaris) seem to show a slight tendency to use wider sills at a rate possibly greater than that at which they are produced).

Hole Depth

Hole depth measurements were made in a total of 446 Flicker-cycle nests occupied by Flicker, Starling, Mountain Bluebird, Bufflehead and Tree Swallow. Depths of 11 Kestrel (Falco sparverius) sites were also measured, but this small sample is not included in the treatment here.

All depth measurements were made without disturbing nests or nest materials, in order to establish the actual space used by the bird.

Data obtained on hole depths are summarized in Table VI, perusal of which quickly reveals several salient factors:

- 1) Holes occupied by Colaptes show that 94.7% of holes were between 20 cm. and 45 cm. in depth, and 83% were between 25 cm. and 40 cm.
- 2) 92.9% of Tree Swallow nests were filled with nest material to the range between 0 and 30 cm.; and 69.4% of the total were between 0 and 20 cm.
- 3) No Starling nests were found to be less than 10 cm. in depth, and only 28 or 17.0% were less than 20 cm. The range 15 to 35 cm. embraced 75.6% of the 165 Starling nests measured.
- 4) No Bufflehead nests were measured with a depth of less than 15 cm., and only 4, or 3.8%, were less than 20 cm. in depth.

84.1 % of Bluebird nests were less than 20 cm.

The placing by secondary hole-nesters of nest material in the cavity is clearly a significant ecological factor in this "competitive" situation. Perusal of Figures 17 and 18, which present the same data as Table VI, shows, as confirmed by direct observation, that the Starling, Sturnus, adds only enough nest material to cover the bottom of the cavity. In most cases, this would not alter a cavity enough to render it unsuitable (in terms of depth) for Bufflehead, or for adoption and further filling by Sialia or Iridoprocne. However, use of a site by Bluebird (Sialia) or Tree Swallow (Iridoprocne) renders a cavity virtually unsuitable for Starling or Bufflehead. 84.1% of Bluebird and 69.4% of Tree Swallow nests were less than 20 cm. in depth, and only 17.0% of Starling and 3.8% of Bufflehead nests were in this range. This definitely constitutes a significant factor in terms of competition, and would tend to reduce competitive pressure on Sialia and Iridoprocne. It could, at the same time, intensify competition between Bucephala and Sturnus; it is important that Bucephala begins laying early in the spring almost before the arrival of Starlings in the area, incubates very closely, and has ceased to use the nest-site before the nesting of Sturnus is completed.

Again, however, it is quite clear that the requirements of all species in the Flicker cycle are very similar. Few cases of actual inter- or intra-specific strife were actually observed during this study, as its mensurational nature required examination of many nests and did not permit detailed observation of single sites. The need for such studies is described below, in suggested further lines of research.

Cavity Sizes

The final parameter related to nest-holes is that defined above as "cavity". It was thought that this could be an important feature, as it is an expression of one aspect of the space within the nest cavity. Measurements were obtained for a total of 446 nests within the Flicker cycle, and these are summarized in Table VII,

TABLE VI. FREQUENCY DISTRIBUTION OF HOLE DEPTHS: FLICKER CYCLE.

SPECIES	DEPTH-CLASSES																			
	0-5		5-10		10-15		15-20		20-25		25-30		30-35		35-40		40-45		45	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Flicker N = 95	-	-	-	-	-	-	-	-	5	5.3	34	35.6	28	29.5	17	17.9	6	6.3	5	5.3
Starling N = 65	-	-	-	-	3	1.8	25	15.2	44	26.8	42	25.4	30	18.2	13	7.9	1	0.6	7	3.3
Bluebird N = 44	10	22.7	11	25.0	7	15.9	9	20.5	3	6.8	1	2.3	1	2.3	1	2.3	0	-	1	2.3
Bufflehead N = 104	-	-	-	-	-	-	4	3.85	9	8.6	22	21.2	33	31.8	17	16.4	6	5.8	13	12.5
Tree Swallow N = 38	5	14.2	8	21.0	7	18.4	6	15.8	4	10.3	5	13.2	2	5.6	0	-	0	-	1	2.6
Flicker Cycle	15	3.4	19	4.5	17	3.8	44	9.6	65	14.6	104	23.4	94	21.0	48	10.8	13	3.0	27	6.0

% values refer to species.

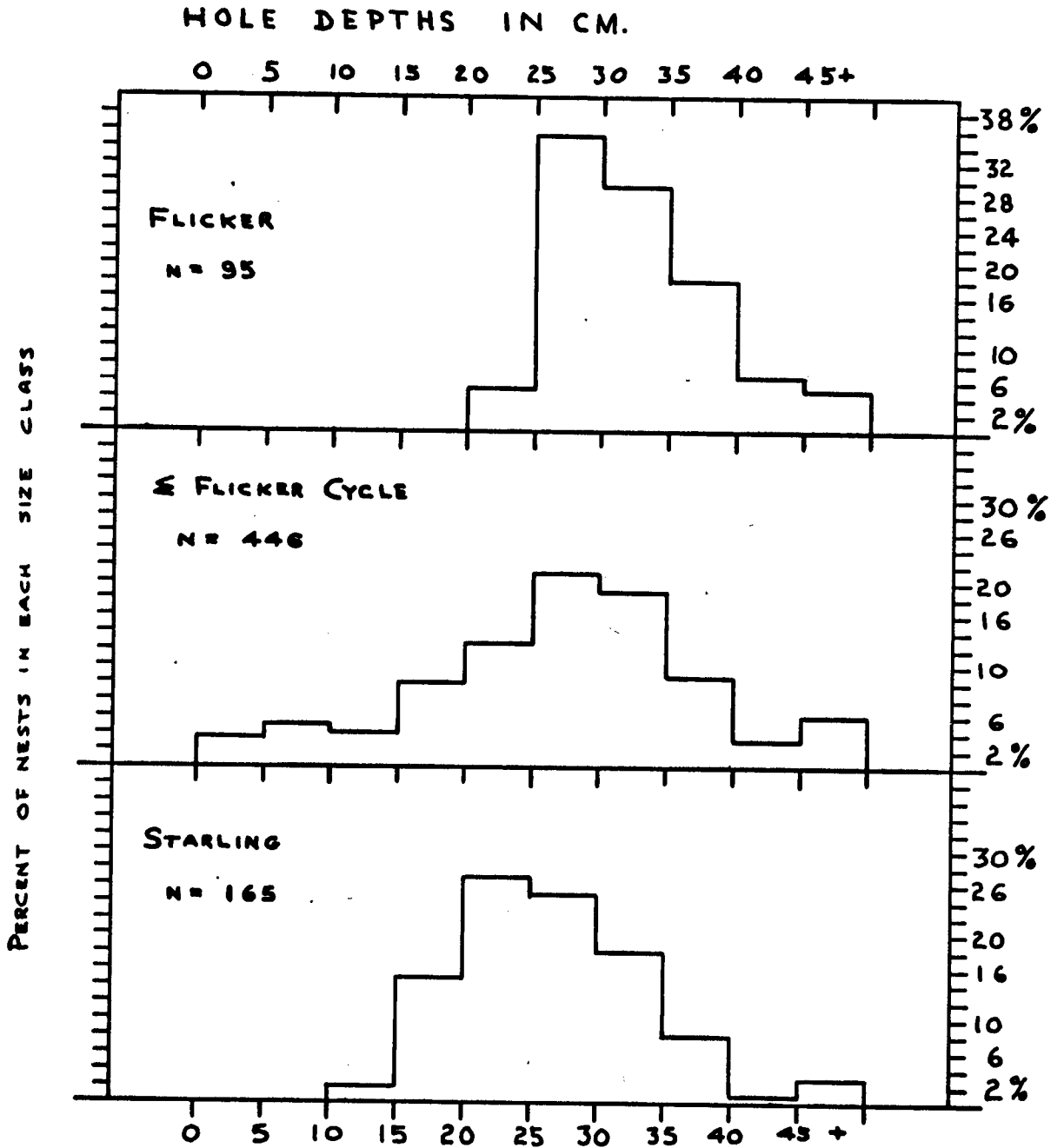


FIG. 17

HOLE DEPTHS FLICKER CYCLE (I)

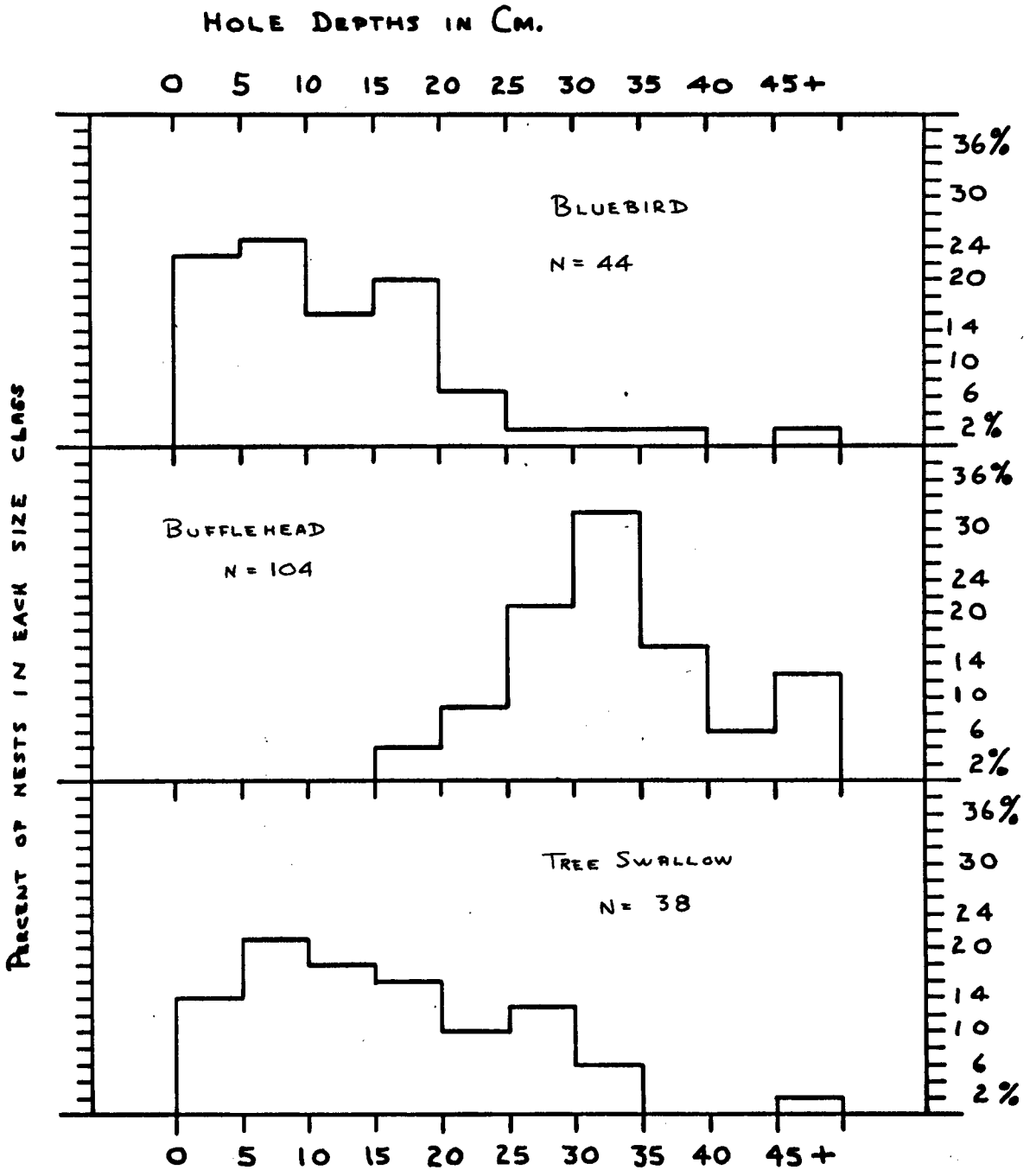


FIG. 18
HOLE DEPTHS FLICKER CYCLE (II)

TABLE VII. SIZE-CLASS DISTRIBUTIONS OF NEST CAVITIES: FLICKER CYCLE.

SPECIES AND SAMPLE SIZE	SIZE CLASSES: CM.																			
	10		10-12		12-14		14-16		16-18		18-20		20-22		22-24		24-26		26	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Flicker Cycle N = 446	27	6.0	83	18.6	96	21.5	68	15.2	56	12.7	36	8.2	42	9.8	15	3.4	14	3.2	9	2.0
Flicker (occ.) N = 95	6	6.3	17	17.9	19	20.0	17	17.9	8	8.4	11	11.6	9	9.5	-	-	5	5.5	3	3.2
Starling N = 166	8	4.8	37	22.4	33	20.0	25	15.1	22	13.3	10	6.0	16	9.9	7	4.2	4	2.4	4	2.4
Bluebird N = 44	4	9.2	13	29.5	9	20.5	7	15.9	3	6.8	4	9.0	2	4.5	-	-	2	4.5	-	-
Bufflehead N = 107	4	3.7	12	11.2	25	23.4	15	14.0	20	18.6	8	7.5	12	11.2	7	6.5	2	1.8	2	1.8
Tree Swallow N = 34	5	14.7	4	11.8	10	29.4	4	11.8	3	8.8	3	8.8	3	8.8	1	2.9	1	2.9	-	-

and shown graphically in Figures 19, 20, and 21. Several points are abundantly clear. Only about 12% of these 446 nests had cavities of less than 10 cm. inside diameter, and only 18, or about 4.5% were over 26 cm. inside diameter. Reference to Figures 19, 20, and 21 shows immediately, as does study of Table VII, that each size class is occupied by roughly the same proportion of the sample for each species. In short, there seems to be no evidence in terms of this parameter to indicate any sort of amelioration of competition.

Another obvious parameter is that of hole volume, which undoubtedly is of importance with relation to body size. However, it can easily be seen that since the cavity diameters selected by the various species are so nearly similar, variations in volume will parallel those in hole depth, and since the latter parameter is analyzed above, a special analysis of hole volumes is redundant.

Recapitulation: Analysis of Competitive Situation

It has now been shown that the 13 common hole-nesting species of the study area are divisible into three natural groups, one of which shows no reason to assume the existence of nest site competition among its component species. Of the remaining two, the large-hole group is too poorly known to permit the forming of definite conclusions, although some qualitative suggestions have been offered.

The final group, that composing of species utilizing nest-holes made by the Flicker (Colaptes), has been examined in considerable detail in terms of some measurable characteristics of nest-sites. It has become clear that, in general, the requirements of the various species, in terms of the parameters considered, show an impressive degree of overlap. A few cases exist in which some evidence is seen for amelioration of competition, but these are minor in comparison with the extent to which broad overlap occurs. Thus it can be presumed on a somewhat more quantitative basis than is usually possible that competition as defined above may be occurring within the medium-hole group of hole-nesting birds in the study area.

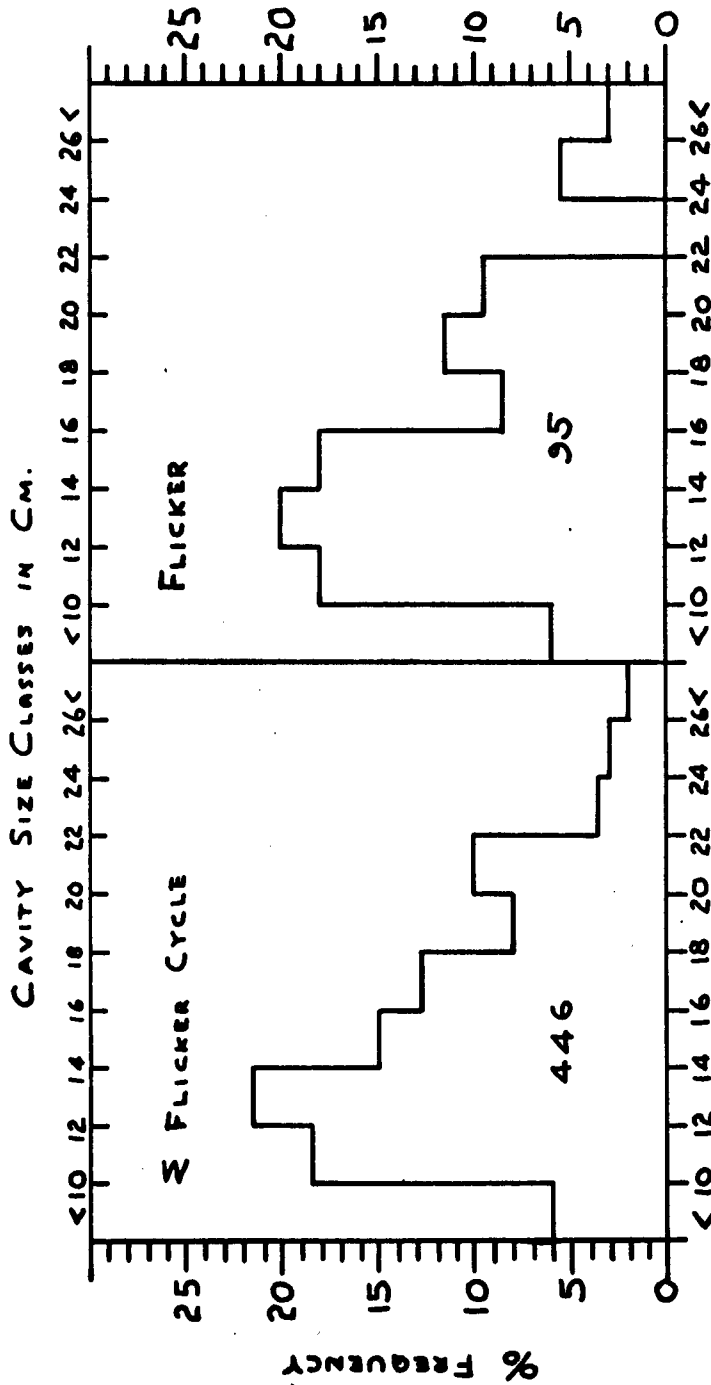


FIG. 19

CAVITY SIZES: FLICKER CYCLE (I)

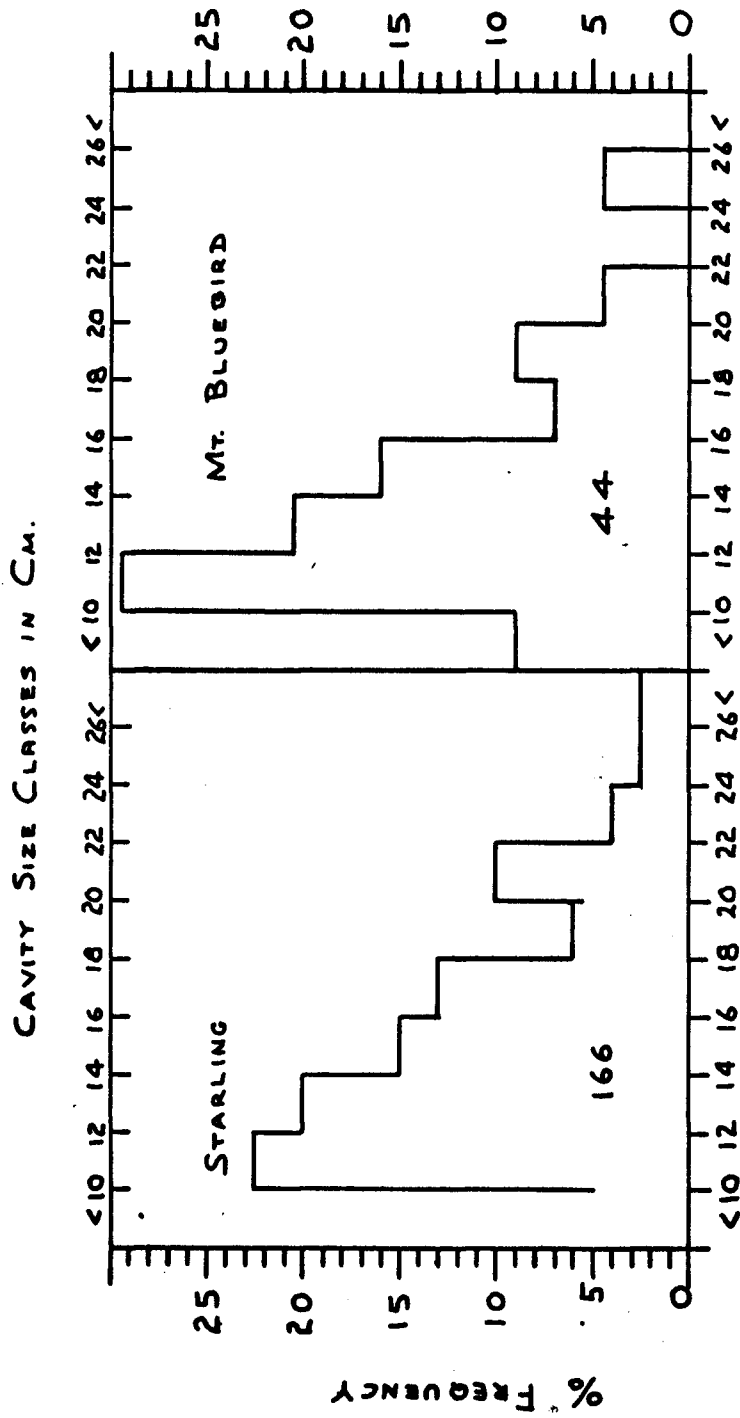


FIG. 20
CAVITY SIZES FLICKER CYCLE (II)

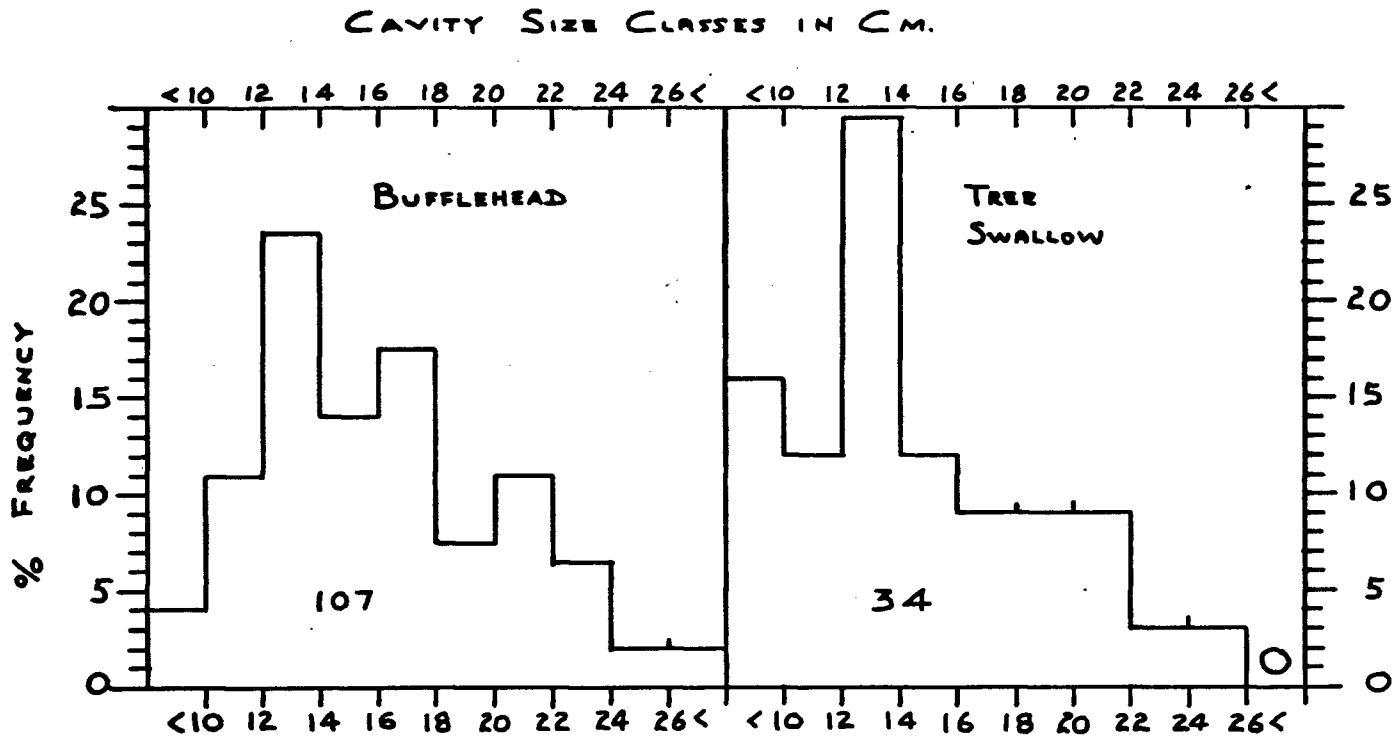


FIG. 21

CAVITY SIZES

FLICKER CYCLE (III)

In the following discussion, the implications and ramifications of this are explored, and a special section has been prepared to suggest future research to examine in greater detail the mechanisms of this competition, as well as its implications in distribution and abundance of the species involved. It should be reiterated at this point that the main role of the work reported here has been to "show the way" in the sense of establishing the extent of occurrence of nest-site competition in the study area.

DISCUSSION

Orientation of This Study and Suggested Future Research

As can be seen in the above presentation, the major role of this study in the overall consideration of nest-site competition among hole-nesting birds in the study area has been to show that the phenomenon may be assumed to occur, and to delimit its extent in terms of the species involved. It is now clear that: (a) not all hole-nesting species may be regarded as being involved in this competition; (b) on the basis of a quantitative study of nest sites, the group designated as the "Flicker cycle" may be accepted as one in which the existence of nest-site competition may reasonably be assumed. Furthermore, since there is broad overlap of all species in the Flicker cycle in terms of nest-site parameters, it is clear that, provided other factors do not limit populations below the level permitted by the supply of holes, the species of this group are likely to remain in competition.

Several avenues of exploration, both experimental and observational, now suggest themselves for further study, particularly of Flicker cycle species. Among those of an observational nature are detailed studies of territoriality and breeding biology and detailed analysis of inter- and intraspecific behaviour. If possible, a general study similar to the present one in an area not yet colonized by the Starling (*Sturnus vulgaris*) would be most instructive, not only in terms of competition per se, but also in terms of the general biology of alien species, and their impact upon the ecosystems which they "invade". Numerous experimental studies are also required: perhaps the most vital and most interesting of these would be to test the hypothesis that the overall population of Flicker cycle species is limited by the number of holes available. This could be accomplished by saturating an area with "standard" nest boxes designed to

approximate the mean measurements of all Flicker-cycle holes, and placed in a randomized arrangement of combinations of height and direction, provided only that each hole have an appropriate flightway before it. Such an experiment should, of course, include an untreated control area of similar ecological characteristics, and would permit the gathering, in addition to population data, of useful information on competitive mechanisms and comparative competitive success. Comparative studies on fecundity and ability to feed young would also be of great value. A further refinement of nest-box studies might involve the providing of boxes of systematically varied geometries, in order to assess the ultimate limits of acceptability of site characteristics for the various species.

Detailed life history studies of individual species are needed to provide data for the fuller description of the ecological niches of the competing species, in order to facilitate better appreciation of the various relationships which may exist.

Many other possible studies could be outlined but it is suggested that those indicated above would be logical steps to follow the present background study.

On the Definition of Competition

The concept of biological competition has been familiar to biologists for many years. This one term has been used in a variety of ways, has been given many different meanings, and in fact has frequently been introduced without definition. This has, of course, given rise to much confusion, and recently, attempts have been made to clarify this situation. Birch (1957) described the broad range of meanings given to the term, ranging from the etymological equivalent of "environment" through a narrow and restricted meaning such as the one used for this study. As is ever the case with terminology, the individual's preference in choice of meaning is largely a matter of taste, but if only for the sake of economy in writing and in the interest of enhanced understanding among ecologists, the plea must be entered for the adoption of the limited and hence clearer

definition. Again, as Birch has also indicated, there exists no need to replace with "competition" the concepts of "environment", "interference phenomena", etc. On the other hand, the perfectly clear reality of the phenomenon described by the restricted definition of competition does require a suitable term.

Milne (1961) reviewed the etymology of the term, as well as the ways in which it has been used, and proposed a definition of his own for use in ecology, genetics and evolution, to cover both inter- and intra-specific relations.

The definition given on Page 1 is essentially similar to those proposed by Birch and Milne, and agrees with them, as well as with Udvardy (1951), in the adoption of a limited meaning. The concept has much potential usefulness, but in order for this to be realized, it must be used consistently. There is, furthermore, as Milne (1961) has pointed out, a need for discerning interpretation.

The Detection and Measurement of Competition

Much of the difficulty in the study of any form of biological competition arises from confusion in communication as a result of variations in definition (see pages 1 and 2). However, even when this is overcome, there remain the problems of detecting and measuring competition. These matters are by no means standardized or even well understood, and this study may be regarded as an attempt to facilitate the detection of competition for nest-sites in hole-nesting birds. In this, some success has been achieved, but the measurement or assessment of the competition depends upon the carrying out of a series of experimental studies such as those outlined above. It is suggested that highly interesting and informative data will result from this combination of experimental and observational study.

The method used here to detect nest-site competition is based upon the fact that, although the philosophical concept of "competition" is highly subjective at best, and made more confusing by the variety of uses to which it has been put, there are a number of essentially permanent parameters associated with nest-sites studied,

and the sites chosen by each species could be described in a relatively quantitative fashion.

If the requirements of each species in terms of nest-sites were quite different, then either (a) they were originally quite different or (b) competitive exclusion has occurred in terms of nest-sites. Within the Flicker-based group, as shown by the data presented earlier, this did not prove to be the case. Rather, there appeared to be almost universal overlap in nest-site characteristics within this group, all of which are dependant upon one species for nest-sites. If differences had been detected, there would have remained the problem of whether these differences were due to inherent tendencies of the birds, or whether they were the result of competitive exclusion. In either event, an experimental programme similar to that outlined above would still have been required. In the actual situation, as revealed by the analysis given above, it is clear that in fact nest-site requirements are essentially similar in all species of the Flicker cycle, and there is no reason to assume that competitive exclusion has occurred or is very likely to occur, in terms of nest-sites, or particular parameters of them. There does remain the logical possibility that some species might already have been entirely excluded from the area as a result of nest-site competition. This aspect is discussed separately below.

The actual situation described above is open to another interpretation. The view is widely held by ecologists that if any competition is present between two or more species, one of two outcomes must result: either the species involved will evolve different requirements; or competitive exclusion will occur. As will be shown below, it is virtually impossible to decide whether the range of a species is primarily determined by competitive resistance at its boundary, or by some other limiting factor. In the present study, the European Starling had only recently "invaded" the area, and was probably still increasing its population. There appeared to be few if any surplus holes during the study period but roughly 160 of

450 nests studied (or about 20 to 25%) were of this species. The present study showed nearly all holes examined to be occupied, and the requirements of all species were virtually identical. Thus it is reasonable to assume that competition might now be possible, but what of the situation before the addition of the Starling to the avifauna? The other Flicker cycle species have presumably been in the area since its reforestation after the last glaciation, and have no doubt had time to evolve different nest-site requirements. That this appears not to have occurred suggests that, at least until the advent of the European Starling in the study area, competition for nest-sites in the Flicker cycle may not have occurred, or at least was insignificant as an ecological factor. Thus we find the intriguing possibility that in the avifauna of the Cariboo region we have an opportunity to study the effects upon a group of species, related in only one aspect of their ecological niches, to the relatively abrupt addition to their ecologies of a new and potentially very potent factor. It is unfortunate that data are not available from similar areas not yet supporting Starling populations, in order to better assess the role of the Starling. However, it seems very clear that the impact of any species, which in just over ten years manages to occupy 25% of all holes examined, must be quite considerable. This is particularly so when, as is the case here, its nest site requirements are essentially identical to those of the indigenous species.

Competitive Exclusion

It could be suggested that certain species which are rare or absent from the study area, but present nearby, might have assumed such status as a result of competitive exclusion, and the suggestion should therefore be considered.

Simply stated, the "competitive exclusion principle", or "exclusion principle" states that complete competitors cannot co-exist. Hardin (1960), in a discussion of the nature of this principle, contends that its "truth" rests in theory and

is not subject to proof or disproof by facts, as ordinarily understood. He presents an ingenious argument in defence of this, and points out that isolated laws such as this (and, for example, Newton's first law) are not tested per se, but are tested as parts of a whole conceptual model. From such models, predictions may be made, tested against empirical data, and the model changed if its predictions cannot be verified. He further points out that there is no procedural rule to tell which element of the model should be changed. His final point in this section is that the exclusion principle is one element in a system of ecological thought. Not only are we unable to test the principle itself, but we do not yet know what the whole ecological system is. Cole (1960) offered further remarks on this matter, pointing out that uncritical acceptance of the exclusion principle could lead to neglect of important ecological evidence. Patten (1961) advocated the relegation of this principle from the state of importance given it by some workers to that of a small segment of a broad class of interspecific phenomena.

This, then, is at least a partial delineation of the theoretical context in which to consider the possibility that certain species may be absent from the avifauna of the study area as a result of competitive exclusion.

Several distinct situations which should be reviewed here are presented below. In each such case, it must be borne in mind that no final decision is possible until more information is available on the ecological niches of the species in question. Study of a paper by Bond (1957) has suggested that although two or more species may be in competition for one environmental resource, differences in other aspects of their ecological niches could tend to reduce this competition, and if these differences were great enough, they could even be reflected in different geographical ranges. However, the point can also be made that the presence in a given area of only one of a pair of species which compete elsewhere

could well be a result of competitive exclusion. This question, when it arises, can only be settled with detailed knowledge of the niches of both species.

The Hooded Merganser (Lophodytes cucullatus) is represented in Munro and Cowan (1947) by scattered summer records in the study area. Only two cases of breeding are known to the author at this time: Jackson (pers. comm.) noted a brood in the vicinity of Springhouse, B.C., in 1952, and A.J. Erskine recorded a brood at Phililloo Lake in 1958 (B.C. Nest Records Scheme). Whether this species is excluded from the Cariboo area by nest-site competition is open to dispute. In view of the fact, however, that many more records are available (c.f. B.C. Nest Records Scheme, as well as other sources) from regions to the south of the study area with less severe climates, it appears probable that the study area merely represents marginal habitat. This species is relatively close to the Bufflehead both taxonomically and in terms of size (Johnsgard, 1961), but no conclusions are possible without more data on its ecological niche in B.C.

The Wood Duck (Aix sponsa) represents a case similar to that of the Hooded Merganser, except that no records of nesting are known to me from the study area.

The two species of Chickadee (Parus atricapillus and P. gambeli) are both able to excavate holes, and insofar as is known, seem to exist sympatrically in a stable relationship. No data were obtained on differences in the niches of these two species, but in the light of the exclusion principle, as discussed above, if it is accepted in its usual form, there must be little or no competition in this closely related pair of species.

The possible effects of increasing Starling (Sturnus vulgaris) populations upon those of the Mountain Bluebird (Sialia currucoides) have been of considerable public concern. It now seems clear, in the light of data analyzed in this study, that these two species might be in competition for nest-sites in the study area. The effects upon Bluebird populations, however, cannot be determined without the

aid of census data from times before the appearance of the Starling. These are not available. Some further circumstantial evidence might be forthcoming from a survey of nest-sites in an area occupied by Bluebirds, but not yet reached by Starlings. Some such areas are suggested by Myres (1958).

Competitive exclusion of Woodpeckers via nest-site competition is difficult to envision, nor does it seem possible, at least in summer, that other factors such as food, predation, etc., could virtually exclude the Black-backed Three-toed Woodpecker (Picoides arcticus) and the Hairy and Downy Woodpeckers (Dendrocopos villosus) and D. pubescens). For the former, Jobin (1952) published the first record as a winter visitant, and the only nest record for the study area was made by A.J. Erskine in 1958 (B.C. Nest Records Scheme). The two Dendrocopos species in the study area are very rare, with only occasional nestings reported, and no nests were found in the two years of this study. The two species are, however, present sympatrically in much the same way as the Parus species above. Without further study of the niches of all three woodpecker species, it appears impossible to determine the role of competitive exclusion in determining their abundance in the study area. It is suggested, however, that the reason for their apparent scarcity might more profitably be sought in considerations related to aspects of the niche other than nest-site competition.

Nest-Site Competition as an Ecological Factor in Hole-Nesting Birds

In a situation such as that exemplified by the Flicker cycle, with closely parallel requirements and few primary species, it is easy to envision the supply of nest-sites as a factor controlling the overall population of hole-nesting birds, and to imagine that competition might be occurring among them for these sites. It certainly follows, then, that relative competitive ability may have an important bearing upon the abundance of a given species relative to the number of available holes. Within the study area, few data are yet available on this point, but scattered records are available such as cases of joint clutches of different species

(e.g. Erskine, 1959a) in several combinations, cases of usurpation, etc.

(As mentioned above, the requirements of the present study were such as to preclude the possibility of obtaining many observations of this sort), and there is a clear need for detailed studies on fixed plots to gather more such data.

Competitive success need not be entirely a function of size or aggressiveness. Lohrl (1956) points out that Starlings in northern Europe, although they regularly usurp woodpeckers nests, are less successful in competing with Nuthatches which partially block nest entrances with hard mud. This behaviour is noted also by Seilmann (1958) and has been described to me verbally (von Haartman; Udvardy). This behaviour is represented in the Red-breasted Nuthatch (Sitta canadensis) only by the placing spottily around the hole of "pitch" from coniferous trees.

In the present study, then, it can be seen that at least in the Flicker cycle, nest-site competition appears to limit the overall hole-nester population (except that of the flicker), and it may be speculated that within the group, comparative ability to compete may determine the proportion of the total population taken up by each component species. As noted above, however, it is possible to suggest that this competition may not have been present before the advent of the European Starling in the study area.

The results of the experimental studies suggested above may be expected to reveal many interesting data on this subject. The overall population response to the provision of many new holes should be highly instructive per se, and should also reveal much concerning comparative abilities of the different species to compete one with the other for nest sites.

Habitat Dispersion as an Ecological Factor

Of the six species of the Flicker cycle, all but the Bufflehead may be described as "edge" species, and even it, as is evident from Erskine (1960), as well as from the fact that it is dependent upon the Flicker for nest-sites, may be so regarded. It is well known that such species are able to achieve much higher

population densities per unit area in a mixed habitat than in a continuous phytocoenosis. Thus, in a very real sense, the population density of any secondary species is dependant not only upon its comparative competitive ability as noted above, but also upon two other sets of factors: (a) those factors satisfying, in terms of the phytocoenosis, various aspects of its own ecological niche; (b) factors permitting the presence and survival of the Flicker (Colaptes).

The latter two groups are, of course, closely related and in most cases there are some aspects in common. Exactly what many of these factors are is not known at present, but in any event, whatever the proximal causation of habitat selection, each species clearly must satisfy a set of habitat requirements, and the amount of "good"-habitat available for each species can be supposed to be related to the interspersion of various phytocoenoses. The final evaluation of the role of habitat dispersion in the ecology of the hole-nesting avifauna of the study area awaits the results of detailed life history studies of each of the component species, to reveal more clearly the details of their ecological niches.

The Tree Swallow (*Iridoprocne bicolor*) as a Competitor

Two points are of importance in the consideration of this species as a nest competitor. Firstly, in terms of the Flicker cycle, is the fact that, so far as is known at present, it is, in a sense, a facultative member of that group. Without more detailed life history data, it must be assumed that individual Tree Swallow pairs choose nest sites at random, and are no more or less likely to use a Flicker hole than one of any other size. This is by no means certain, but it must be accepted as a working hypothesis, although the possibility should be borne in mind that only a proportion of the total population of this species may be potential users of Flicker holes. Secondly, the habit of this species of filling nest holes would be regarded by many workers as an aspect of competition. Whether or not it is accepted as such may be a matter of individual choice, but the ecological effect of rendering the hole unsuitable for certain species is still the same.

Finally, it should be noted that the overall abundance of the Tree Swallow (Iridoprocne) in the study area is definitely not reflected by the sample of nests in the Flicker cycle. These, however, were the only nests of the species which had relevance to the competitive situation. Thus the Tree Swallow is a species which forms part of, but is not confined to, the competing complex.

The European Starling (*Sturnus vulgaris*) as a Competitor

In its original range, this species is well known as a nest-site competitor (c.f. Löhrl, 1956 et al) and might be expected to show similar characteristics here. In the analysis of data above, it is clear that the parameters of the nest site are similar to those of the other species of the Flicker cycle, and since there seemed to be very few unoccupied holes, it is strongly suggested that this species is now a competitor for nest-sites in the study area. Myres (1958) summarized essentially all data on the spread and increase of this species in B.C. from 1947, when it was first noted, to 1957, by which time the population was numbered in tens of thousands. Even if, as suggested above, nest-site competition was absent or negligible before the appearance of this species, the probability that it now exists is greatly enhanced, if only by the sheer numbers of Starlings now present.

The Results of this Study in Relation to General Theory

Much of the previous work on nest-site competition among hole-nesting birds has been done in Europe, with an avifauna considerably richer in hole-nesters of all sizes, and in addition has largely been concerned with nest-box studies.

The present study serves to point out various differences in the extent of competition for nest-holes, which were found in the study area, and was essentially an exploration of a natural situation. On the basis of the finding reported here, it will now be possible to design experiments to study the various mechanisms of this competition, such as aggression, egg-foisting (mixed clutches) (c.f. P. Busse

and J. Gotzman, "Nesting competition and mixed clutches among some birds inhabiting the nest boxes", *Acta Orn.* 7 (1): 1-32, 1962), etc. Various casual observations made during the field work are included above, and these suggest that detailed study will probably show that at least in broad terms, these mechanisms are essentially similar. It has already been pointed out that the data given here may be interpreted to mean that the hole-nesters of the area may not have been in competition before the arrival of the European Starling. This proposal might be further illuminated by study of areas not yet reached by the Starling. If it is correct, we find ourselves in the excellent position of being able to study at first hand the effects of the introduction of biological competition in a situation where it was previously absent. This will, as the quantitative data show essentially no differences in nest requirements, permit the study on a long-term basis of the effects of this newly introduced competition.

In short, then, the present study has revealed the existence of an excellent opportunity to conduct a series of studies, not only on the mechanisms of competition in this case, but, perhaps even more significantly, on the response of populations to this new situation. Apparently no selection of different nest-sites has previously occurred in Flicker cycle species; now, with a new aspect of nest-site competition introduced, an excellent opportunity has arisen to study, from a fairly well-defined time of commencement, a situation in which selection for different nest-sites may well be expected to occur.

SUMMARY AND CONCLUSIONS

1. This work was undertaken as the first of a series of studies designed to explore the extent and nature of nest-site competition among tree-hole-nesting birds in the Cariboo region of British Columbia.
2. The method used was direct measurement of several parameters associated with nest-sites as they were found in nature, and comparison of sites used by each species in terms of overlap in site requirements.
3. The 20 species recorded from the area fell into three distinct natural groups on the basis of hole size, with the exception of one euryoecious species. Of the three groups, one was highly unlikely to show nest-site competition, one is too poorly known to permit generalization, and one clearly shows a likelihood of competition.
4. In the group using medium-sized holes, site characteristics of all 6 species are essentially similar, and only the Flicker (Colaptes cafer) produces holes.
5. Nest-site competition may be deemed to be present among the following species: Flicker (Colaptes cafer), European Starling (Sturnus vulgaris), Mountain Bluebird (Sialia currucoides), Bufflehead (Bucephala albeola), Sparrowhawk (Falco sparverius), and Tree Swallow (Iridoprocne bicolor).
6. Interpretation of quantitative data on nest-sites in the medium-hole group suggests that competition was absent or inconsiderable before the addition of the European Starling (Sturnus) to the avifauna of the area. Data gathered during this study, while populations of this species were still increasing, show that there is good reason to assume that competition is now occurring in that group. It is suggested that if this is the case, one, or a combination of both, of two courses of events may occur: (i) one or more species may be eliminated or reduced in numbers; or (ii) selection for differing nest sites may occur. In either event,

there exists an excellent opportunity to study these events as they occur.

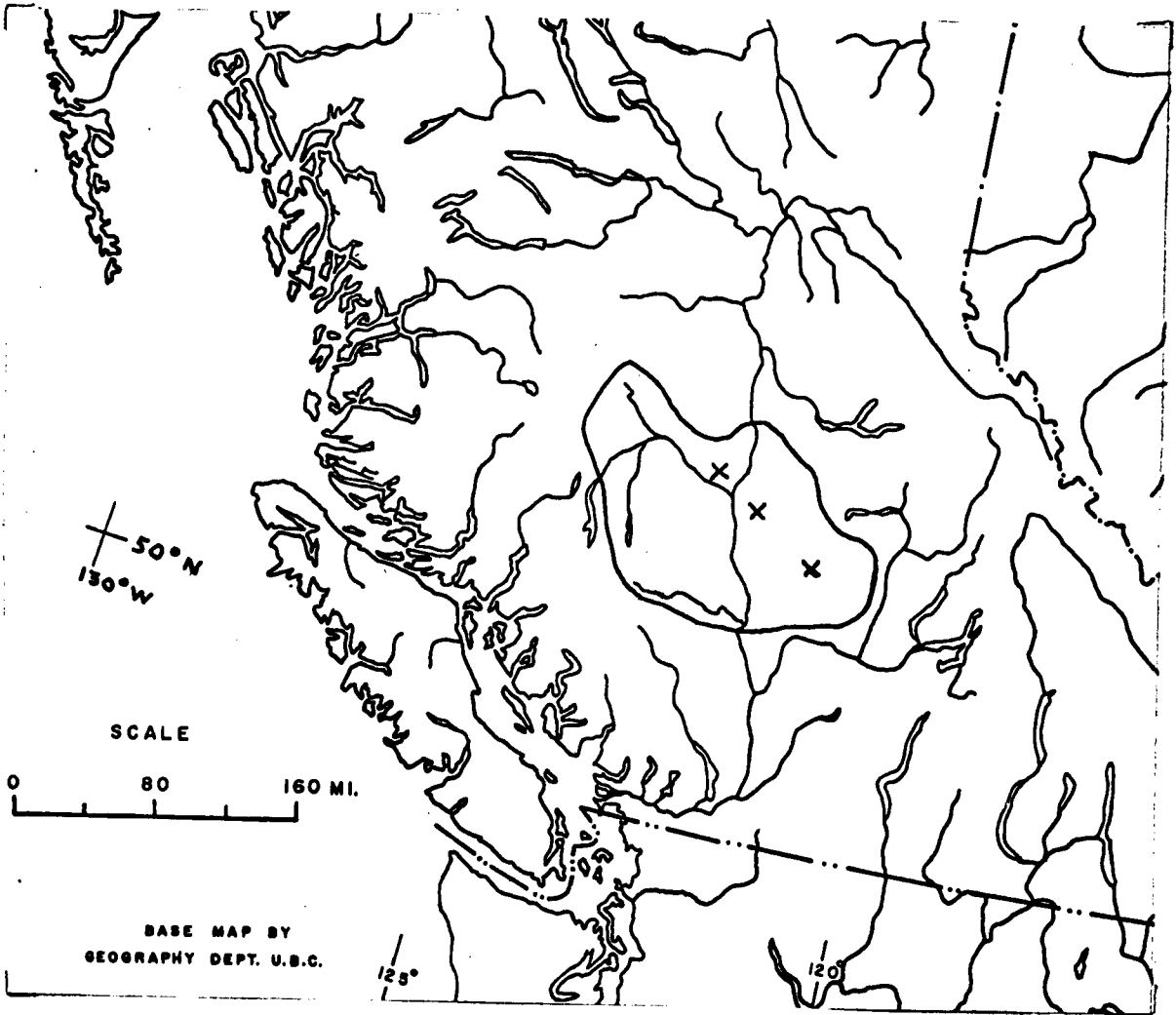
7. The competitive exclusion principle is briefly reviewed, and several possible cases in the study area are considered.

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Appendix I : Map of British Columbia to show Approximate Location of Cariboo Plateau. Major study Locations Indicated by Symbol X .