BIOSYSTEMATICS AND ECOLOGY OF PICOIDES VILLOSUS (L.) AND P. PUBESCENS (L.), (AVES: PICIDAE)

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ABSTRACT

A systematic study was undertaken to assess' generic and subspecific limits in taxa previously described as <u>Dendrocopos</u> <u>villosus</u> and <u>pubescens</u>. <u>Dendrocopos</u> is restricted here to Palaearctic taxa. As a result Nearctic and Neotropical species are reclassified in the Holarctic genus Picoides.

A comprehensive analysis of geographical variation in several morphological characters provides the basis for subspecific reevaluation of forms in wide-ranging <u>P</u>. <u>villosus</u> and <u>pubescens</u>. Variation is often clinal and agrees with ecogeographical rules except Allen's Rule. Subspeciation appears to have taken place primarily during the Pleistocene.

These non-migratory woodpeckers have evolved strategies that allow them to coexist sympatrically: tree species selection, foraging stations, foraging techniques, nesting habitats, and insect preys. Allopatric <u>villosus</u> occupies the niche of <u>pubescens</u> on the Bahamas. Morphological sexual dimorphism in body dimensions corresponds with " intersexual ecological differences in <u>villosus</u>. Intersexual ecological differences exist in <u>pubescens</u> but dimorphism in body dimensions is lacking.

RÉSUMÉ

On a entrepris une étude des limites génériques et sousspécifiques des taxa antérieurement désignés comme <u>Dendrocopos</u> <u>villosus et pubescens</u>. On assigne les espèces paléarctiques à <u>Dendrocopos</u>, tandis qu'on réfère les taxa néarctiques et néotropicaux à Picoides.

A partir d'une analyse détaillée de la variation géographique de plúsieurs caractères morphologiques on a réévalué les sous-espèces de <u>P</u>. <u>villosus</u> et <u>pubescens</u>. La variation est souvent clinale et en accord avec les règles écogéographiques sauf celle d'Allen. La formation des[®] sous-espèces semble s'être manifestée surtout au cours du Pléistocène.

Ces deux pics sédentaires ont recours à des stratégies écologiques qui leur permettent de vivre sympatriquement: sélection d'essences forestières, postes et modes de recherche de nourriture, biotopes de nidification et insectes-proies. Aux Bahamas, <u>villosus</u> occupe allopatriquement la niche de <u>pubescens</u>. Chez <u>villosus</u>, le dimorphisme sexuel dans les dimensions corporelles correspond à des différences écologiques intersexuelles, par contre ces différences ne correspondent pas à un dimorphisme sexuel morphologique chez pubescens.

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GENERAL ABSTRACT

A systematic study of woodpeckers was undertaken to assess generic and subspecific limits in taxa previously described as <u>Dendrocopos</u> <u>villosus</u> and <u>D</u>. <u>pubescens</u>. Morphological, ecological, and behavioral information was used. Evidence and arguments are presented for the restriction of the generic name <u>Dendrocopos</u> to Palaearctic taxa. <u>D</u>. <u>obsoletus</u> is referred to the genus <u>Dendropicos</u>. As a result Nearctic and Neotropical species, including <u>villosus</u> and <u>pubescens</u>, are, reclassified in the Holarctic genus Picoides.

A comprehensive analysis of geographical variation in several morphological characters (body weight; wing, tail, culmen, and tarsus length; color; color patterns) provide the basis for the subspecific reevaluation of all the forms in two wide-ranging Nearctic taxa, <u>Picoides</u> <u>villosus</u> and <u>P. pubescens</u>. Tables of measurements are provided. Variation is often clinal and is usually in accordance with ecogeographical rules except Allen's Rule. Subspeciation appears to have taken place primarily during the Pleistocene.

These non-migratory woodpeckers, sympatric over vast areas, have evolved strategies such as tree species selection, foraging stations of specific sizes, peculiar foraging techniques, nesting habitats, and choice of insect preys that allow them to coexist sympatrically. <u>P</u>. <u>villosus</u> is allopatric on the Bahama Islands and occupies there the niche in which <u>P</u>. <u>pubescens</u> is found in the areas of sympatry. Morphological sexual dimorphism in body dimensions corresponds with intersexual ecological differences in <u>P</u>. <u>villosus</u>. In <u>P</u>. <u>pubescens</u> intersexual ecological differences exist, but dimorphism in body dimensions is lacking. It thus appears that in spite of a lack of morphological sexual dimorphism intersexual ecological differences exist in certain avian species.

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RÉSUMÉ GÉNÉRAL

On présente ici les résultats d'une étude systématique dont l'un des buts était de déterminer les limites génériques sous-spécifiques des taxa antérieurement connus comme <u>Dendrocopos villosus</u> et <u>D</u>. <u>pubescens</u>. Cette étude est fondée sur une analyse de données morphologiques, écologiques et éthologiques. On en conclut que le genre <u>Dendrocopos</u> doit être restreint aux taxa de la région Paléarctique et on assigne <u>obsoletus</u> de la région Ethiopienne au genre <u>Dendropicos</u>. Conséquemment, les espèces des régions Néarctique et Néotropicale, y compris <u>villosus</u> et <u>pubescens</u>, sont classifiées dans le genre holarctique <u>Picoides</u>.

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Une analyse poussée de la variation géographique de plusieurs caractères morphologiques (poids corporel; longueur de l'aile, de la queue, du culmen et du tarse; couleur; motifs de coloration) permet la réévaluation de toutes les sous-espèces de deux pics de la région Néarctique à vaste répartition, <u>Picoides villosus et P. pubescens</u>. Les mensurations sont groupées sous forme de tableaux. La variation est souvent clinale et est habituellement en accord avec les règles écogéographiques, sauf celle d'Allen. Le processus de sous-spéciation semble se situer surtout durant le Pléistocène.

Ces pics sédentaires, sympatriques dans de vastes secteurs de leur aire de répartition, ont adopté des stratégies qui leur permettent de coexister sympatriquement comme le choix des essences d'arbre, de postes d'alimentation, de techniques de recherche de la nourriture et d'insectesproies. <u>P. villosus</u>, en l'absence de <u>P. pubescens</u> dans les îles Bahamas, y occupe la niche de ce dernier. Des différences morphologiques sexuelles dans les dimensions corporelles correspondent à des différences écologiques intersexuelles chez <u>P. villosus</u>. Par contre, de telles différences existent chez <u>P. pubescens</u> en l'absence de dimorphisme sexuel morphologique. On conclut donc qu'une absence de dimorphisme sexuel morphologique peut néanmoins correspondre à des différences écologiques intersexuelles chez certains oiseaux.

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PREFACE

This thesis is presented as a series of three inter-connected papers in publication format as permitted under the regulations of the Faculty of Graduate Studies and Research of McGill University. Those regulations require statements as to the elements of the thesis considered to be "contributions to original knowledge". They are as follows:

- A proposal, different from the most recent generic treatment, for a new classification of the species of woodpeckers formerly included in the genera <u>Dendrocopos</u> and <u>Picoides</u> is based on an analysis of morphological, ecological, and ethological characters.
- 2. New data on geographic variation obtained as a result of a comprehensive analysis of various morphological characters provide the basis for a taxonomic revision of all the subspecies of <u>Picoides villosus and P. pubescens</u>. Hypotheses are presented in an attempt to explain the present geographic variation patterns, considered to have occurred mainly as a consequence of the isolation of populations by the glacial retreats and advances during the Pleistocene.
- 3. Bill and tarsus lengths are inversely proportional to the values expected from Allen's Ecogeographic Rule.
- 4. The data available demonstrate, contrary to current assumptions, that <u>Picoides villosus</u> and <u>P. pubescens</u> are not migratory, although some wandering outside the breeding season and nesting

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areas has been recorded particularly in the latter species.

- 5. Niche partioning allows both birds to coexist sympatrically in the same habitat. Marked differences in habitat selection in areas of sympatry, in foraging stations, in foraging and nesting ecology, and insect preys have been recorded and contribute to maintain interspecific competition to low levels at all times of the year.
- 6. Sexual dimorphism varies geographically. It is strong in <u>Picoides Villosus</u> and can be correlated to marked intersexual ecological differences. On the other hand, intersexual ecological differences in <u>P</u>. <u>pubescens</u> do not correspond to intersexual morphological differences. Thus, a lack of sexual dimorphism in morphological characters may correspond to intersexual ecological differences. On the Bahama Islands, in an area of allopatry, in the absence of other congeners, <u>Picoides villosus</u> displays strong sexual dimorphism which corresponds to marked intersexual ecological differences. These may be the result of limited food resources in the insular pine forest, thus producing an additional partioning of the habitat.
- 7. The problem of reversed sexual dimorphism in tail length remains unresolved but the current results indicate that it may be artificial due to an excessive wear of the rectrices. However, true reversed sexual dimorphism in wing length exists in one population of <u>P. pubescens (turati</u>) but the phenomenon

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cannot be correlated with intersexual ecological differences. It is believed that interspecific competition and pressures from other sympatric congeners may have led to such a situation.

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GENERAL INTRODUCTION

Hairy and Downy woodpeckers are widely distributed and easy to observe in suitable habitats of southeastern Canada. Both species of birds are similar in their general coloration and color pattern but the Downy has considerably smaller body dimensions than the Hairy in most of the areas where they occur sympatrically. They are sympatric over large areas but the range of the Downy is much less extensive, thus allowing for sizeable regions of allopatry on the Queen Charlotte Islands (Canada), in Mexico, in Middle America, and in the Bahama Islands (A.O.U. 1957; Dickey and Van Rossem 1938; Godfrey 1966; Land 1970; Miller 1957; Slud 1964; Wetmore 1968).

The problem of generic affinity of the North American species of the genus <u>Dendrocopos</u> to which the Hairy and Downy woodpeckers have traditionally been referred during the last 25 years has been raised as a result of recent studies and diverging taxonomic proposals (Delacour 1951; Goodwin 1968; Mayr and Short 1970; Ruge 1975; Short 1971a, 1974; Voous 1947). Recent classification proposals (Mayr and Short 1970; Short 1971a, 1974; Ruge 1975) are not unanimous. In view of the controversial opinions expressed heretofore (Peters 1948, Voous 1947; Short 1971a) it was felt necessary to investigate in this study the relationship of the species referred to the genera <u>Dendrocopos</u> and <u>Picoides</u> in the light of a thorough analysis of the characters of each genus (Bibliography, Part I).

The extensive geographic variation observed in both species throughout their range has been recognized for a long time and has led taxonomists to describe variation and recognize a number of forms

(A.O.U. 1957; Jenkins 1906; Oberholser 1896, 1911; Peters 1948;
Ridgway 1914). The availability of several thousand museum specimens of the Hairy and Downy woodpecters offered an excellent opportunity to investigate the patterns of geographic variation in size, color, and color pattern and to re-evaluate the numerous subspecies described for those two birds (A.O.U. 1957; Burleigh 1960; Jackson 1970b; Jenkins 1906; Miller 1957; Oberholser 1896, 1911; Ridgway 1914) in the light of extensive series of specimens originating from parts of their range previously unavailable to taxonomists, more adequate methods of analysis of variation, and different evolutionary concepts (Mayr 1969, 1970; Sokal 1965; Sokal and Rohlf 1973)
(Bibliography, Part II).

The study of interspecific competition between two closely related species of similar color and color pattern but of different size continues to be challenging (Lack 1971). Little was known about this problem (Bent 1939) with regard to the Hairy and Downy woodpeckers when I began my field studies in the fall of 1964. Other workers have since provided new information (Conner 1974; Conner <u>et al.</u> 1975; Grubb⁴ 1975; Jackson 1970a, 1971; Kilham 1961, 1962, 1965, 1966a, 1969, 1970, 1973; Kisiel 1972; Lawrence 1967; Selander 1966; Short 1970a, Smith 1973, Williams 1975). In addition to the field data obtained in the areas of sympatry of the two birds, I recorded material on the Bahama Islands where only the Hairy Woodpecker occurs in order to compare my results from a zone of sympatry with those from an area of allopatry, as well as with the information provided by other workers. (Bibliography, Part II).

Sexual differences in foraging behavior are often associated with sexual morphological differences in several species of woodpeckers (Kilham 1965; Ligon 1968b; Selander 1965, 1966; Sélander and Giller 1963; Short 1970) and may contribute in reducing competition for food (Rand 1952) between individuals of a single species or between individuals of two or more species (Lack 1971). Attempts have been made to correlate morphological sexual differences with intersexual differences in foraging behavior and to analyze those results upon comparison of the information obtained in the regions of sympatry against that recorded in the sectors of allopatry with regard to earlier findings (Kilham 1965; Ligon 1968b, 1973; Selander 1966; Short 1970) (Bibliography, Part III).

Thus the present study comprises:

- A generic re-evaluation of the genera <u>Dendrocopos</u> and <u>Picoides</u> on the basis of an analysis of morphological, ecological, and ethological characters (Part I).

- A thorough analysis and description of the morphological variation of <u>Picoides villosus</u> and <u>pubescens</u>. This provides the basis for a revision of the subspecies of each species and sexual dimorphism is investigated for all body characters (Part II).

- A review and comparison of the ecology of the two birds on the basis of new ecological information. Data are provided on the various aspects of the ecological differences between the two species and on the intersexual differences of each bird (Part III).

An historical statement appears in the introduction of each section and provides a topical survey of the literature relevant

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An account of the material and methods used in the study is given following the introduction of each section and an extensive bibliography is provided in each part.

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PART ONE

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Relationships of woodpecker genera Dendrocopos.

Koch and Picoides Lacépède, (Aves: Picidae)

ABSTRACT

On the basis of a comprehensive analysis of morphological, behavioral, and ecological data a new arrangement of the species of woodpeckers heretofore grouped in the genus <u>Dendrocopos</u> is proposed. The genus <u>Picoides</u> comprises all the North and South American species previously referred to the genus <u>Dendrocopos</u> in addition to the two <u>Picoides</u> species. The genus <u>Dendrocopos</u> includes all the Palaearchic taxa currently classified in it except one, <u>Dendrocopos</u> <u>obsoletus</u>, which is best referred to the genus <u>Dendropicos</u>. The Oriental <u>Dendrocopos</u> species are provisionally maintained in that genus.

RESUME

A la lumière de nouvelles données morphologiques, éthologiques et écologiques, on propose une nouvelle classification des Pics du genre <u>Dendrocopos</u>. Le genre <u>Picoides</u>, tel que défini dans cette étude, comprend toutes les espèces des Amériques antérieurement attribuées au genre <u>Dendrocopos</u>, en plus des deux taxa du genre <u>Picoides</u>. Le genre <u>Dendrocopos</u> est maintenant restreint à toutes les espèces Paléarctiques couramment placées dans ce genre sauf une, <u>Dendrocopos obsoletus</u>, qui est reportée au genre <u>Dendropicos</u>. Les <u>Dendrocopos</u> de la région Orientale sont provisoirement retenus dans ce genre.

INTRODUCTION

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Woodpeckers, notably those referred to as the "pied" or "ladder-backed" species of the Old and New worlds, have been the subject of several studies. These have both answered many questions and given rise to much speculation about the history, phylogeny, and evaluation of the group (Goodwin 1968; Blume 1971; Short 1970, 1971a and b, 1973, 1974; Voous 1947; Peters 1948). The purpose of this section is to provide a generic assessment of the group made necessary by the lack of agreement on the recent classification proposals for the genus <u>Dendrocopos</u> Koch (1816).

Peters (1948) listed 33 species in the genus <u>Dendrocopos</u>, representatives of which range in the Holarctic, Oriental, Neotropical, and Ethiopian regions. More recently, Goodwin (1968) has suggested that the only Ethiopian representative of the group, <u>obsoletus</u>, is closer in plumage pattern to the <u>Dendropicos</u> species and he proposed that it be treated as such, contrary to Short (1970) who considers it a <u>Picoides</u> (= <u>Dendrocopos</u>). Goodwin's treatment seems reasonable in view of the color pattern and general color of the bird, in spite of the fact that it may superficially resemble the diminutive dendrocopine species of south Asia (Voous 1947). Notwithstanding Voous's evaluation (1947) and Short's recommendation (1970) I concur with Goodwin's treatment of the species because that bird is morphologically different from those assigned to the other genera.

Delacour (1951) proposed that the Holarctic genus <u>Picoides</u> Lacépède 1799 does not differ significantly from the genus <u>Dendrocopos</u>

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- TABLE 1.
 - w white or whitish
 - bf buffy or brownish
- fl fulvous
- bk black '
- 1. on lower back and rump
- 2. extends on sides of neck
- 3. very faint
- 4. gold and dusky brown, forehead smoky gray
- 5. yellowish green tinge
- 6. dull blond
- 7. not joining the mandible
- 8. small and very restricted
- 9. extends onto posterior part of crown

- MARINA P

10. in certain populations only

	wing markings	dorsal . markings	crown, occipit markings	a 1		facial markings	dorsal coloration	
·· ·	white scapular patches barred wings (or blotches)	barred back white dorsal stripe	red occipital markings red crown markings yellow crown markings	red on underparts	barred external rectrices	black malar stripe black eye marking	black coloration brown coloration underparts coloration	Y Proposed genera
Dendrocopos 1. major 2. leucopterus 3. syriacus 4. assimilia 5. himalayensis 6. darjellensis 7. medius 8. leucotos 9. cathpharius 10. hyperythrus 11. auriceps 12. atratus 13. macei 14. mahrattensis 15. minor 16. canicapillus 17. wattersi 18. kizuki 19. moluccensis 20. maculatus 21. teminckii 22. obsoletus 23. dorae 24. albolarvatus 25. villosus 26. pubescens, 27. borealis 28. nuttallii 29. scalaris 30. arizonae 31. stricklandi 32. mixtus 33. liguarius Picoides tridacty		* * * * * * * * * * * * * * * * * * *	* * * * * * * * * * * * * * * * * * *	***	*****	************	* bf * v * v * v * v * v * fl * fl * fl * fl * fl * bf * v * v * v * v * v * v * v * v	Dendrocopos " " " " " " " " " " " " " " " " " " "
" arcticus	*	1	*		*	* *	*	"

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TABLE 1



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Figure 1.

Selected Palaearctic species of 'pied' woodpeckers showing dorsal,

caudal, and facial patterns:

1	Dendrocopos	major,	male and	d female	(head	only)	, •
2.	······································	syriacus	11	••	11 × ₂ .	11	
3.	11	medius	**	**	**	.")	1
4.	-) H	<u>leucotos</u>	11	**	11	n	
5.	, 11 .	minor ,	tt 2	**	u .	**	
6.	11	auriceps	17	**	11	"	

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Figure 2.

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Selected Nearctic species of 'pied' woodpeckers showing dorsal, caudal, and facial patterns:

1.	<u>Picoides</u>	<u>villosus</u> ,	male and	female	(head	only)	•
2.		pubescens,		Ħ 、	"	11	
ъ 3.	11	<u>albolarvatus</u> ,	17	11 -		"	
4.	**	stricklandi,	11	11	11		`
5.	, . , .	<u>nut/tallii</u> ,	**	11	"	"	
6.		borealis,	17	.,	**	11	
7.	•••••	<u>scalaris</u> ,	18	11	11	11	I
8.	, 11	tridactylus,	17	**	11	17	
9.	ಭಾ 11	arcticus	**	"	**	**	

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and that the latter be merged with <u>Picoides</u> for nomenclatural reasons. Goodwin (1968) suggested a similar treatment which was later adopted by Short (1970, 1971a and b, 1973). I agree partly with these conclusions as to be demonstrated later in this study.

For comparative purposes I have selected a series of characters considered to be of significance for a taxonomic evaluation at the genus level. They appear on Table 1 for the thirty-three dendrocopine and two picoidine species recognized by Peters (1948). The analysis of characters is based on specimen examination for the majority of the species and on a careful study of the published descriptions for those species I could not examine. Numerical taxonomy methods have not been used in this analysis because quantitative data were not available for many species dealt with here. Furthermore most of the characters used in this study cannot be quantified.

RESULTS

Wing markings

Barring is present on the outer primaries in all species with the exception of <u>D</u>. <u>albolarvatus</u> in which it becomes a continuous white streak near the distal end of the outer primaries (Figures 1, 2). In the other species wing barring varies considerably in quantity and form but is always present. This pattern, although not unique to the dendrocopine species (e.g. <u>Sphyrapicus</u> and several other genera), appears to have attained its greatest development in the dendrocopine species. In <u>Picoides arcticus</u> and <u>P</u>. <u>tridactylus</u>, the white markings at the outer edge of the outer primaries are very
similar to those of the dendrocopine-species.

Dorsal markings

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Within the genus Dendrocopos (sensu Peters 1948), the dorsal markings are highly variable. In eight species, which range mainly in the Palaearctic region but which occasionally spill over into the Oriental region, extensive white scapular patches are present (Table 1). This character is unique in the group. In the other species white or whitish dorsal bars, or a continuous white or whitish dorsal stripe are present, except in D. dorae and D. albolarvatus. For D. arizonae and D. stricklandi, I follow Davis (1965) and consider these two taxa to be conspecific, at least for the purposes of this study. D. stricklandi shares this character with its other congeners, although white dorsal markings are absent or very restricted in most of its subspecies notably arizonae. There is a mid-dorsal white stripe in D. leucotos but it is restricted to the rump region and varies geographically in width and length. The mid-dorsal stripe in D. villosus and D. pubescens is also completely white, or any variation from whitish to smoky gray or fumeus brown. This stripe varies geographically in size, pattern, and color as will be shown later in this study. In the other two dendrocopine species, there are no dorsal markings: D. dorse and albolarvatus have a plain back (Table 1).

In the picoidine species this character is conspicuous only in <u>P. tridactylus</u> where dorsal white markings generally form a stripe which can be very faint and/or broken in the North American form.

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In certain Palaearctic subspecies a solid white dorsal stripe has been described and varies geographically (Vaurie 1959). In <u>P</u>. <u>arcticus</u>, although the back is generally uniformly black, traces of white feathers are found in the mid-dorsal region, especially near the rump, but they never form any definite dorsal pattern (Figures 1, 2). These white feathers are probably the manifestation of an ancestral relictual character which can be interpreted as an indication of its close relationship with its congener P. tridactylus.

Coloration of the under parts

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The coloration of the under parts of this assemblage of woodpeckers is predominantly white in 24 of the 33 species listed here (Table 1). This coloration is highly variable geographically and may range from beige and smoky gray to fulvous brown in various populations of the same species such as in <u>D</u>. <u>villosus</u>. In seven of the eight remaining species, most of which occur in the Palaearctic and Oriental regions, fulvous, brownish or buffy coloration is dominant, white being unknown on the under parts of those species. The remaining taxon, <u>D</u>. <u>albolarvatus</u>, is aberrant in having black under parts and under tail coverts.

A varying amount of crimson or reddish coloration occurs in fourteen species (Table 1), all found in the Palaearctic and Oriental regions. This bright coloration is distributed mainly on the under tail coverts but often extends onto the lower abdomen and flanks. In a few species it is found on the lower breast. This peculiarity is unknown in any of the New World species of the taxon. With the exception of <u>D</u>. <u>auriceps</u> which has yellowish under tail coverts, the coloration of this region is similar to that of the lower abdomen in all the other species, although it tends to be more heavily pigmented and often marked with blackish dots, blotches or stripes. The under parts, including the under tail coverts of <u>P</u>. <u>tridactylus</u> and <u>P</u>. <u>arcticus</u>, are white or whitish, without conspicuous markings except in immature individuals.

Coloration of the upper parts

The main color of the upper parts is black in the majority of the species (Table 1). It varies from a dull to a shiny black, which has often a metallic sheen (\underline{D} . <u>major</u>). On the other hand, this general black coloration is replaced by a dark to medium brown color in six species, of which only one occurs in North America (\underline{D} . <u>arizonae</u>, <u>sensu</u> Peters 1948). The dorsal coloration is almost black in \underline{D} . <u>stricklandi</u>, at least in the species that I have examined. The coloration of the upper parts of the two picoidine species is predominantly black. The fresh plumage of \underline{P} . <u>arcticus</u> is very glossy and often has a metallic sheen.

Crown and occipital markings

Age and sexual dimorphism occur to various degrees in all species of the genus, and is particularly strong in the crown region and/or occipital markings (Figures 1, 2). The red, reddish or orange markings of the crown and/or occiput of adult males are not reproduced in adult females of any species of the genus except

D. medius. Goodwin (1968) has summarized the results of his analysis of this character which is found in the juveniles of both sexes. Ι believe that it has more value here as an ontogenic character in determining the ancestry of the group than as a taxonomic criterion on the relationships of its members. Red pigment is found in the head markings of males of all species of the genus and occurs either on the crown or in the occipital region, or both (Table 1) .. This head marking may be exténsive in the males such as in D. medius, D. leucotos, and D. scalaris or much reduced as in D. borealis and D. moluccensis. In the juveniles of both sexes the crown marking often occupies a more extensive area than in the adult males or may show in an area where no such marking is found in the adult male. In those birds, the quality of the pigmentation is very different and it seldom attains as bright a coloration as in the adult. In some juveniles, irrespective of their sex, there is occasionally no trace of red, reddish or orange. However, the general distribution pattern of colors in the crown and occipital regions, whether red is present or not, varies to some extent within the genus (Table 1). In two species, D. auriceps and D. mahrattensis, yellow or yellowish feathers are present in various amounts in the crown region in addition to the red of the occipital and/or crown regions.

The two picoidine species display no red in the head region, but yellow markings are present in certain plumages of both species. In the adult males, a bright yellow patch, more extensive in <u>P</u>. <u>tridactylus</u>, covers the anterior part of the crown. On the other hand, in the females of both species the forehead is occasionally lightly

marked with white speckles. I have recorded several combinations of characters on the crown of immatures, irrespective of their sex: no yellow patch; crown entirely black; medium to small yellow crown patch; faint to bold white crown markings; white and yellow markings, forming a rudimentary crown patch. The texture of the yellow feathers is somewhat different and coarser than that of the red or reddish areas of the dendrocopine species. However, the yellows and reds of the crown markings are carotenoids which belong to a class of closely related lipochromes.

Facial markings

Within the genus all the species with the exception of <u>D</u>. <u>albolarvatus</u> have a malar stripe (Figures 1, 2). It varies much in intensity, shape, color, and prominence. For example, in <u>D</u>. <u>hyperythrus</u> and <u>D</u>. <u>canicapillus</u> it is very faint but stands out well on a much paler background. In <u>D</u>. <u>dorae</u> it is present but barely distinctive because it blends with the surrounding plumage which is almost as dark as the malar stripes themselves. It is only partial and does not reach the base of the mandible in <u>D</u>. <u>mahrattensis</u>. In both <u>Picoides</u> species, the malar stripe is well marked being broad and continuous from the base of the mandible to the upper parts of the neck.

In 18 of the 33 dendrocopine species there is an ocular stripe, generally black or blackish, which confers onto those species a very different facial pattern when compared with the remaining 15 species in which the ocular region is immaculate (Table 1; Figures 1, 2). The species which have an ocular stripe (through the eye) range

primarily in the Nearctic region, except for <u>D</u>. <u>macei</u> and <u>D</u>. <u>mahrattensis</u> which are restricted to the Oriental Region and <u>D</u>. <u>dorae</u> which is confined to Saudi Arabia. In the latter, the ocular marking is difficult to see due to the overall dark coloration of the head with which it blends. This character is well developed even in <u>D</u>. <u>albolarvatus</u> but it is much reduced in <u>D</u>. <u>borealis</u> where it appears as a faint black line. The absence of an ocular stripe gives the sides of the face a much brighter and different appearance. This plain area can be large as in <u>D</u>. <u>syriacus</u>, <u>D</u>. <u>medius</u> or <u>D</u>. major.

In the two picoidine species the ocular stripe has attained a high degree of development. It is very broad and almost joins with the crown from which it is separated by only a thin white line. Below, the white area between it and the malar stripe is much reduced when compared to the other species which possess this character. Their facial pattern is nevertheless very similar to that of the <u>Dendrocopos</u> species of the Nearctic and Neotropical regions, except <u>D. albolarvatus</u>.

Tail markings

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Dark coloration, varying from black or blackish brown to dark dull brown, is dominant on the central rectrices throughout the genus <u>Dendrocopos</u> (Figures 1, 2). These feathers are nearly always uniformly colored. The outermost rectrices of most species often have a varying amount of white or other light coloration on the distal part. These (5th and rudimentary 6th rectrices) are totally

white or have much lighter coloration than the central ones in a few species. Often the lightness of these feathers has a definite pattern that increases from center to edge. Barring of the external. rectrices is found in nearly all the species, except in most populations of <u>D</u>. <u>villosus</u> where they are totally white or whitish and except in <u>D</u>. <u>albolarvatus</u> where they are completely black. This character was not checked in <u>D</u>. <u>wattersi</u> and <u>D</u>. <u>kizuki</u> because I was unable to examine specimens of these species and because the descriptions consulted did not provide this information.

In the two picoidine species, the central rectrices are black and the others have an increasing amount of white near the end from center to edge. The outermost rectrices are almost entirely white except basally, although black bars or dots occur in certain populations of <u>P. tridactylus</u> and exceptionally in certain individuals of P. arcticus.

Flanks and under parts markings

Nearly all the dendrocopine species have some forms of flank markings (spots, bars, and stripes) which often vary geographically to a great extent. Similar markings are not found on the breast or abdominal regions of most species, although it does occur there in a number of species in the Oriental region. However, these markings are not confined to the species of that region and can be found in a few North American taxa such as <u>D. borealis</u>, <u>D. arizonae</u>, <u>D</u>. nuttalii, and <u>D. scalaris</u> as well.

By contrast, the flanks of the two picoidine species are



Table 2.

Measurements of bill length and bill width and ratio of bill length over bill width for a selected number of <u>Picoides</u> (= <u>Dendrocopos</u> + <u>Picoides</u>) species, for both sexes.

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MALES					FEMALES				-
	Bill Length (a)	Bill Width (b)		Ratio (a/b)	Bill Length (a)	Bill Width (b)		Ratio (a/b)	
Dendrocopos	mean	mean	n	<u> </u>	mean	mean	n		
major	26.95	10.01	11	2.69	25.40	9.40	2	-2.70	
himalayensis	29. 43	10.18	€ 4`∖	2.89	26.80	10.20	1	2.63	,
darjellensis	32.75	9.85	2	3.82					·
medius	24.20	8.60	1	2.81				-	
leucotos	37.55	12.45	2	3.02	33.30	12:40	1	2.69	
cathpharius	18.10	7.70	1	2.35	16.95	6.90	2	2.46	~
hyperythrus	25.60	8.00	2	3.25					
auriceps	· 23.35 ·	8.40	2	2.78					
atratus	~	-		-	25.00	9.60		2.60	
macei	20.88	8.03	4	2.60	21.13	8.75	4	2.41	•
mahrattensis	24.99	8.25	2	3.02	22.08	7.75	-4	2.85	
minor					14.50	6.20	1	2.34	
canicapillus	16.10	6.90	1	2.33	16.48	6.75	4	2.44-	
moluccensis	13.60	5.20	1	2.60	14.13	6.33	3	2.23	
maculatus		· 、			17.85	7.25	2	2.46	
temminckii	15.75	6.90	2	2.28	15.90	6.80	1	2.34	23
obsoletus	17.30	6.80	3	2.54	17.10	6.60	1	2.59	/
albolarvatus	28.55	*9.3 5	4	3.05	25.28	8.70	5	2.91	/
villosus	30.20	10.42	15	2.90	27.72	9.75	13	2.84	
pubescens	16.87	6.73	12	2.51	16.35	6.60	16	2.48	
borealis	20.78	8.77	5	2.37	19.70	7,96	5	2.47	
nuttallii	20.27	7.37	10	2.75	18.18	6.79	10	2.69	
scalaris	22.99	7.94	10	2.90	19.97	7.30	10	2.74	
arizonae	28.05	8.63	4	3.25	23.68	8.45	4	2.80	
mixtus	18.80	6.60	1	2.85	18.80	6.70	1	2,81	
lignarius	19.20	8.65	2	2.22			,	-	
Picoides tridacty	Lus								
bacatus	27.67	10.64	14	2.60	24.83	10.08	9	2.46	. •
tridactylus	28.90	10.50	1	2.75	24.55	9.95	2	2.47	
crissoleucus	· ·		`	_	24.10	9.20	1	2.62	
<u>Picoides</u> arcticus	32.91	12.31	15	2.67	31.15	N 11.82	13	2.63	

TABLE 2

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Figure 3.

Chord of wing, as an indicator of body size, plotted against bill length (exposed culmen) for the North American <u>Dendrocopos</u> species and <u>Picoides</u> populations. Squares indicate males and triangles females. The fact that these fall into three discrete body size groups is purely coincidental.

1.	<u>D. nuttallii</u> M	13.	<u>D. villosus extimus</u> M	
2.	" " F .	14.	" " F /	
3.	" <u>s. scalaris</u> M	15.	" " septentrionalis	М
4.	11 11 F	16.	n n n	F
5.	" <u>stricklandi</u> M	17.	" pubescens medianus M	
6.	" " F	18.	" " F	
7.	" <u>arizonae</u> M	19.	<u>Picoides tridactylus</u> M	
8.	" " F	20.	" F	
9.	" <u>albolarvatus</u> M	21.	" arcticus M	
10.	" F	22.	" " F	
11.	" <u>borealis</u> M			
12.	11 11 F			

Linear regréssion of wing length on bill length is significant as follows:

males: r = 0.834, d.f. = 9, P < 0.01females: r = 0.832, d.f. = 9, P < 0.01both sexes: r = 0.824, d.f. = 20, P < 0.001.

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heavily barred, a character which varies geographically in <u>P</u>. <u>tridactylus</u>. The abdomen and breast of these two birds is usually pure white, although it is not uncommon to find a few black-tipped feathers on the lower abdomen of some of these birds.

Bill

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Bill size is highly variable within the genus. Its length is well correlated with the general size of the birds as indicated by wing length in the North American species of <u>Dendrocopos</u> and <u>Picoides</u> (Figure 3). Bill length (exposed culmen) exhibits also a marked sexual dimorphism in most of the species examined (Figure 3; Table 2) an aspect which will be developed upon more fully with <u>D. villosus</u> and D. pubescens.

Generally speaking, several species appear to have a relatively broad bill. However, upon close scrutiny, this is only a superficial character, due to the shape of the apex of the mandible. The length of the exposed culmen and the width of the bill at the base of the exposed culmen in relation to bill length exhibit little interspecific variation (Table 2). In this context the bill of the <u>Picoides</u> species is not markedly wider than that of several dendrocopine species, as pointed out by Short (1974). Relative bill width reflects a variable sexual dimorphism in bill shape for several species also, notably <u>D</u>. villosus and pubescens.

Tongue

Dissection of the tongue of a number of specimens of Dendrocopos

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Figure 4.

Patterns and gross anatomy of tongue in three species of picoidine woodpeckers:

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A). <u>Picoides villosus</u>

B) <u>Picoides pubescens</u>

C) <u>Picoides arcticus</u>



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<u>villosus</u>, <u>D</u>. <u>pubescens</u>, <u>Picoides tridactylus</u>, and <u>P</u>. <u>arcticus</u> has shown <u>little</u> interspecific differences. Marked sexual dimorphism was observed in those four species, and it was noted (Figure 4) that the tongues of the picoidine species are considerably more brushy at the tip than those of the two dendrocopine species examined. However the general pattern of the picoidine tongue is very similar to those of <u>D</u>. <u>villosus</u> and <u>D</u>. <u>pubescens</u>. I was unable to examine this character in Old World and in other New World dendrocopine species owing to a lack of fresh material.

Feet and toes

All the dendrocopine species have ectropodactyl feet (Bock and Miller 1959), a modified zygodactyl pattern adapted to scansorial habits. The hallux is normally shorter than in other genera. In the two <u>Picoides</u> species the hallux is absent but the feet retain their ectropodactyl condition. Largely on that basis these two species have been placed in a different genus, but such a condition occurs in three other woodpecker genera: <u>Sasia</u>, <u>Dinopium</u>, and <u>Gecinulus</u>. Delacour (1951) considered the genus <u>Picoides</u> congeneric with <u>Dendrocopos</u> claiming that the morphological differences between the two groups are not sufficient to warrant recognition of the two genera.

Within <u>Dendrocopos</u> the size of the hallux is highly variable from species to species, as pointed out earlier by Delacour (1951). However, the absence of the first toe does not necessarily represent an extreme adaptation to arboreal habits (Delacour 1951:50), in spite of the fact that the two <u>Picoides</u> species are probably among the most arboreal species of North American woodpeckers. For instance, it is possible that such an anatomical modification has evolved as an adaptation for the delivery of stronger and more efficient blows (Spring 1965) when the birds are digging in wood in search of food. Spring (1965) has discussed the kinetic aspects of this morphological modification.

Vocalizations and behaviour

According to Short (1974) most vocalizations of the <u>Picoides</u> woodpeckers are similar to those of the <u>Dendrocopos</u> species. On the other hand, Ruge (1975) concluded that the vocalizations of the European <u>Picoides tridactylus</u> differed significantly from those of the European dendrocopine species. I have found some similarity between the calls of <u>Picoides</u> and those of the North American <u>Dendrocopos</u> as judged by ear. The vocalizations of those Palearctic dendrocopine species with which I am familiar sound different from both of the two <u>Picoides</u> species and from the North American <u>Dendrocopos</u> species. Analytical studies on the vocalizations of all these species would probably yield interesting results and demonstrate significant differences between the Nearctic and Palaearctic species.

Short (1974) compared the general behavior patterns in the two groups and found similarities. Ruge (1975) noted that the displays of European populations of <u>Picoides tridactylus</u> are markedly different from those of European dendrocopine species. A number of

specific displays described for the picoidine species in particular situations appear to resemble those of the dendrocopine species in similar situations (Short 1974), but according to my observations the general behavior of the two North American <u>Picoides</u> is to a large extent different from that of the North American <u>Dendrocopos</u> species particularly with regard to their mode of foraging and very different from that of the European dendrocopine species, notably in the feeding, foraging, and social behavior as described by Ruge (1975).

Ecology

Numerous differences have been observed in the ecology of several species of the genus Dendrocopos throughout its range in the Old and New World but the differences are more marked when the Palaearctic species are compared with the Nearctic species (Ali and Ripley 1970; Bent 1939; Blume 1958, 1971; Dement'ev and Gladkov 1966; Géroudet 1961; Hogstad 1971; Jackson 1970; Kilham 1962, 1966a and b, 1969, 1974; Kisiel 1972; Lawrence 1967; Ligon 1968a and b, 1970, 1973; Loehrl 1973; Ruge 1969a; Short 1971a and b, 1973, 1974; Winkler 1972, 1973). The picoidine species have been less studied, particularly in North America (Kilham 1966b; Short 1974), but when the information available is compared with that of the New World dendrocopine species one finds great similarities in their ecology. On the other hand Picoides tridactylus has been well studied in the Palaearctic region notably in Central Europe (Bürkli et al. 1975; Hogstad 1970, 1971; Ruge 1968, 1969b, 1971, 1974, 1975). These ecological studies have revealed numerous differences between it and

the Old World dendrocopine species. Notably, many populations of P. tridactylus have taken the habit of "ringing" the bark trees by their excavating activities (Turcek 1954; Gatter 1972; Ruge 1970). "Ringing" means here making a series of small holes in the bark around a tree, somewhat like <u>Sphyrapicus varius</u>, the exact purpose of which is not clearly known. This is unknown for the dendrocopine and picoidine species of North America, but this has been noted in a number of European <u>Dendrocopos</u> species (Turcek 1954; Gatter 1972).

DISCUSSION

The species currently comprising the genus <u>Dendrocopos</u> occur primarily in the Holarctic and Oriental regions of the world; a few species range in the Neotropical and Ethiopian regions. The history and evolution of the genus have been studied (Voous 1947) and the current classification (Peters 1948) reflects partly these findings. More recently Short (1970, 1971a and b) has proposed that the species of the genus <u>Picoides</u> are so closely related to those of the genus <u>Dendrocopos</u> that only one genus should be recognized: priority dictates that it should be <u>Picoides</u>. I will now consider this proposal in the light of the information presented above.

Comparison of the distribution patterns of the dendrocopine species shows that there are two main groups of species: those of the Nearctic and Neotropical regions, and those of the Palaearctic and Oriental regions.

Examination of the external morphological characters of each species, as summarized on Table 1, has revealed a number of features

that are prevalent in each group. Extensive scapular patches occur in eight Palaearctic species. Crimson or reddish on the lower under parts occurs in fourteen species of the Palaearctic region and is unknown in the New World species. The Nearctic, Neotropical, and the majority of the Palaearctic species, with the exception of <u>D</u>. <u>albolarvatus</u> in the New World, have white (or variants of white) under parts. But this character is not restricted to any one region. For example the species in the Oriental region tend, as a rule, to have buffy or fulvous under parts.

All the <u>Dendrocopos</u> species, <u>albolarvatus</u> excepted, have a conspicuous malar stripe which is particularly well developped in the genus <u>Picoides</u>. The presence of an ocular stripe (stripe through the eye) is restricted to the Nearctic and Neotropical species and gives those birds an entirely different facial pattern when compared with the Palaearctic species. This character is prominent in the picoidine species as well which, on that basis alone, resemble very closely the North American dendrocopine. This character reflects their affinity to this group in spite of the fact that its presence in that genus may be interpreted as a case of convergence because other characters display as well its close affinities with other taxa in the group.

The structure of the bill cannot be used as a criterion to separate the New World species from those of the Old World since it is rather uniform throughout the genus. Short (1974:6) mentions that <u>Picoides arcticus</u> has a relatively "much larger" bill than P. tridactylus. However, my data (Table 2) indicate that it is only

slightly larger in spite of the impression obtained from a visual examination. The impression is caused by the upper surface of the maxilla which is flatter on top in P. arcticus than in P. tridactylus. P. tridactylus has a comparatively longer bill. Since bill length is highly adaptive and often results "from competition or other types of direct interaction between closely related species" (Bock 1964:59) it can hardly be used as a taxonomic criterion at the generic level. When the length of the exposed culmen is plotted against the chord of the wing (indicator of body size) for several dendrocopine and the picoidine species (Figure 3) there is a good correlation and the latter fall well among the North American dendrocopine species on that basis. The differences in tongue structure are well marked between two dendrocopine species, villosus and pubescens, and the two picoidine species. This character is also highly adaptive and . has more value as an indicator of ecological conditions (feeding habits) than as an indicator of relationship (Dorst 1952; Moreau et al. 1969; Rand 1967). No marked differences were recorded in the foot structure of the dendrocopine species except for a slight reduction in relative toe size on the smaller species such as D. pubescens and D. minor. However this reduction, which is inconsistant, does not appear to be correlated with body size as reflected in wing length and affects mainly the hallux. On the other hand, the picoidine foot has undergone important modifications (loss of the hallux) but as pointed out by Delacour (1951:49), "it seems unreasonable to base genera entirely on such an obviously recent and unimportant character as a vanishing organ".

The evidence and arguments presented above show that the genus Picoides is closely related to the North American species of Dendrocopos. The behavior, ecology, and vocalizations of several Dendrocopos and of the Picoides species have been studied by various authors (Bürkli et al. 1975; Hogstad³1971; Kilham 1966a and b, 1969, 1974; Loehr1 1973; Ruge 1968, 1969a and b, 1970, 1971, 1974, 1975; Short 1971a, 1973, 1974). The data provided for the dendrocopine species indicate that the North American taxa are different from those of the Palaearctic and Oriental regions and that they are closely related to the Picoides species. One of the striking ecological differences between the Old World and New World forms is that many of the former have evolved the habit of "ringing" trees which is unknown for the North American dendrocopine and picoidine species, whereas it has been reported in a number of Palaearctic species including P. tridactylus (Gatter 1972; Ruge 1968; Turcek 1954). The tongue of this bird and its congener is particularly suitable for this mode of feeding due to its slightly brushy tip (Figure 4) but such a habit has never been recorded to date for any species of that genus in North America. Hybridization is unknown between the two genera (Gray 1958).

In his review of the historical distribution of the genus <u>Dendrocopos</u> Voous (1947) considered Southeast Asia as the probable center of origin of the group. *This view is quite acceptable and remains valid since no new contradictory facts are available to date. Short (1971a) has recently commented on the history and evolution of the New World species and tentatively considered them

as a monophyletic group (Short 1971a:112) which would include the two three-toed species. This evolutionary hypothesis is generally consistent with my conclusions on the phylogeny of the North American <u>Dendrocopos</u> and <u>Picoides</u> species. However, if Voous's hypothesis (1947) is accepted with reference to southeast Asia as the center of origin of the "pied woodpeckers", the New World species should be considered as having diverged from the ancestral forms after having reached North America during the Tertiary (during the Pliocene or Miocene) or possibly even before, although acceptable species of woodpeckers have not been recorded before the Pliocene (Brodkorb 1970). Similarly the Old World species may have evolved different morphological, ecological, behavioral, and distributional patterns during the same period, when compared to their New World counterparts.

Different hypotheses have been presented to explain the origin of the two species of three-toed woodpeckers (Bock and Bock 1974; Mengel 1970; Short 1971a). It is not unreasonable to speculate that the ancestral picoidine has diverged soon after the mid-asiatic colonizers have invaded North America and that it evolved in the coniferous forests of North America. By the time of the Pleistocene glaciation it had occupied all the northern forest and reached the Palaearctic at the time of the Bering land bridge where it was successful in the coniferous forest. At the height of glaciation, it may have disappeared from the area formerly occupied by the northern coniferous forest except perhaps from Beringia. The population that was displaced south of the ice-cap eventually

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evolved into arcticus. Concurrently, the population occupying Eurasia or Siberia evolved into tridadylus. Following deglaciation tridactylus reinvaded the northern coniferous forest from either Beringia or Siberia and colonized most of the coniferous biome of North America where its modern range is for the most part sympatric with that of arcticus. Recent studies do not suggest a close relationship between the genus Picoides and the Old World dendrocopine species. Ruge (1968, 1969b, 1971, 1974, 1975) has pointed out many divergent aspects of the ecology and behaviour of tridactylus when compared with the European dendrocopine species. Furthermore, it is hard to believe that tridactylus has evolved "where spruce was the only conifer present" (Bock and Bock 1974:402). Certainly, the foraging activities of tridactylus on the breeding grounds are not restricted to spruce trees (Picea sp.). This bird in most of its range in Eastern North America exploits the insect resources of a large number of other trees in the coniferous forest such as fir (Abies sp.), tamarack (Larix sp.), aspen (Populus sp.), and rarely birch (Betula sp.), as I have often observed. Similarly the European data provided by Gatter (1972) and Ruge (1968, 1970, 1971) indicate that tridactylus forages and rings several tree species other than spruce.

To summarize, the <u>Picoides</u> species are more closely related to the North American <u>Dendrocopos</u> than to the Palaearctic and Asiatic Dendrocopos on the basis of their morphology, behavior, and ecology.

PHYLOGENY

Short (1971a) has discussed the phylogeny of the North American species of the genus <u>Dendrocopos</u> in relation to their affinities with the two species of <u>Picoides</u> and in relation to each other. My limited data for the species other than <u>D. villosus</u> and <u>D. pubescens</u> and the two <u>Picoides</u> species are in accordance with his findings and phylogeny (Short 1971a:108-114) to which the reader is referred for more detailed information.

NOMENCLATURAL RECOMMENDATIONS

The data available in the literature and compiled in this study indicate close affinities between the North American Dendrocopos and the two Picoides species, and marked differences between the latter and the Dendrocopos of the Old World. I follow Delacour (1951), Mayr and Short (1970), and Short (1971a), and recommend that the genus Dendrocopos be grouped with Picoides insofar as the American species are concerned. In view of the marked differences recorded between the Old and New World taxa Dendrocopos should be retained for the Palaearctic and Asiatic species (tentatively), whereas the only Ethiopian species, obsoletus, is referred to the genus Dendropicos; and Picoides is restricted to the two picoidine species and to the New World taxa which were formerly contained in the genus Dryobates, prior to Voous's (1947) study and a Peter's (1948) treatment of the group. The Asiatic species with strikingly different under parts coloration from all other species are still poorly known. Additional studies may reveal that they

are in fact different from the <u>Dendrocopos</u> group, but until such studies are undertaken it seems best to treat the Asiatic species as congeneric with other Palaearctic species.

Picoides Lacépède, 1799

all North and South American species of genus <u>Dendrocopos</u> as listed by Peters (1948) and the two species of the genus <u>Picoides</u> (Peters 1948). <u>Dendrocopos</u> Koch, 1816

all the Palaearctic species except <u>Dendrocopos</u> <u>obsoletus</u> as listed by Peters (1948). The Oriental species are provisionally included in this genus pending more detailed studies.

Dendropicos Malherbe, 1849

<u>Dendrocopos</u> <u>obsoletus</u>, after Goodwin's recommendation (1968:19) and contra Short (1970).

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Geographic variation and taxonomy of <u>Picoides</u> <u>villosus</u> (Linnaeus) and <u>P. pubescens</u> (Linnaeus), (Aves:Picidae) ABSTRACT

This study provides a thorough analysis of variation based on several morphological characters in Picoides villosus and P. pubescens across their respective geographical ranges towards a reevaluation of the subspecies previously described and/or recognized in each species. Extensive series of specimens of both species have been examined for geographic and individual variation in color and color patterns (under and upper parts, tail, flanks and sides, and head region) and in size (body weight, wing length, tail length, bill length, and tarsus length). Variation is clinal in several instances and is in general agreement with the well-known ecogeographic rules (Bergmann's, Allen's and Gloger's). Variation follows similar general trends in both species. In spite of the difficulties inherent to the current subspecies concept, the numerous subspecies recognized or described for each bird have been critically examined and new taxonomic proposals have been made in the light of the results obtained in the analysis of variation. Subspeciation probably took place mainly during the glacial cycles of the Pleistocene. Tables of measurements and range maps of the subspecies are provided.

RESUME

Cette étude comporte une analyse de la variation de plusieurs caractères morphologiques chez Picoides villosus et P. pubescens en vue d'une révision taxonomique des sous-espèces décrites et/ou reconnues antérieurement chez ces deux taxa. On a examiné de vastes séries de spécimens en vue d'évaluer l'ampleur et les modes de variation géographique et individuelle aussi bien sur le plan de da couleur et des motifs de coloration (parties supérieures et inférieures, flancs et côtés du corps, et secteur de la tête) que sur le plan des dimensions corporelles (poids du corps, longueur de l'aile, de la queue, du bec et du tarse). La variation est souvent clinale et est généralement conforme aux règles écogéographiques (de Bergmann, Allen et Gloger) et suit des modes similaires chez les deux espèces. On a réexaminé de façon critique les nombreuses · sous-espèces, décrites et/ou reconnues et on a proposé un nouvel arrangement des taxa à la lumière des résultats obtenus à l'analyse des données sur la variation, en dépit des difficultés qui découlent du concept actuel de la sous-espèce. Le processus de formation des sous-espèces s'est probablement manifesté le plus fortement durant cycles climatiques du Pléistocène. Des tableaux de mensurations et des cartes montrant la distribution des sous-espèces complètent cette étude.
INTRODUCTION

Avian taxonomists have long recognized the extensive geographic variation that exists in <u>Picoides villosus</u> and on that basis have described several new forms from various parts of the range such as <u>Picus audubonii</u> Swainson (1831), <u>Picus harrisii</u> Audubon (1838), <u>Picus jardinii</u> Malherbe (1845), and <u>Dryobates picoideus</u> Osgood (1901), to name only a few. Those forms and several others, for a total of at least 24, have been recognized as subspecies at one time or another (A.O.U. 1957; Peters 1948) thus expressing the extent of geographic variation in that species and the application of the subspecies concept at the time.

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Jenkins (1906) has summarized and indicated the main patterns and trends of variation in <u>Picoides villosus</u> in his pioneer study but was hampered seriously by the limited number of specimens available and the intuitive methodology that was prevailing at that time. In spite of the shortcomings he has outlined the major areas of variation in that species and has shown that variation, either in size or coloration, is clinal without having formulated that concept, which is more recent (Huxley 1939).

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A few years later, Oberholser (1911) using over 1,000 specimens from various parts of the range revised the 14 forms recognized then and described 4 new ones in a purely practical taxonomic study. He proposed that a total of 20 subspecies be accepted. Ridgway (1914) followed those proposals very closely. Most of the forms have withstood the test of time but a few have been lumped with other taxa, whereas additional ones have been described later by other authors

(Swarth 1911; Huey 1927; Dickey and van Rossem 1929).

Geographic variation in <u>Picoides villosus</u> has since received little attention except in regional works and in ecological adaptation studies (James 1970). Jackson (1970) has recently studied the problem using numerical taxonomy methods.

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The study of over 2,300 specimens taken across the range confirms that <u>Picoides villosus</u> is a highly variable species. Variability is particularly evident in the coloration of the under parts and in size (general body size, wing length, and bill length) and less perceptible with regard to the coloration pattern of the upper parts, the tarsal length, and the caudal length. Variation in individual characters has been examined for determining trends and their magnitude and for possible general associations with climatic and/or other ecological factors.

The Downy Woodpecker has not previously been examined for variation across its range and only local studies have provided • information on the variation that occurs in the species (Batchelder 1889; Oberholser 1896; Grinnell 1910; Burleigh 1960; Todd 1963; Mengel 1965; James 1970). Ridgway (1914) has however offered the most complete treatment of variation and has been followed for many years except for minor nomenclatural changes. As new specimens became available new subspecies were described and the range of recognized ones was modified accordingly. Concurrently a few forms o were rejected by taxonomists. Ridgway pointed out the difficulty of identifying subspecies in many areas thus indicating, before the concept became widely accepted, that variation is often clinal in this species. Currently, seven subspecies are accepted (A.O.U. 1957).

This widely distributed small woodpecker varies mainly along geographical gradients in size, color, and coloration patterns. It is dimorphic, at least to the extent that females lack the 'red' nuchal band found in adult males.

The study of over 1,200 from all parts of the range confirms in several cases the results obtained by some of the previous writers and provides the basis for new definitions of variation in this bird in a continental perspective.

The following characters were examined: color of under parts, color and coloration pattern of upper parts, general body size, chord of wing, length of tail, length of exposed culmen, tarsus length, and caudal markings. Each characters was examined individually for variation and the results appear in the following sections.

MATERIALS AND METHODS

I collected specimens of both species in various regions of eastern Canada where field studies were undertaken, primarily in Quebec, Ontario, and the Maritime Provinces. Additional specimens from those regions and from other parts of the species ranges were borrowed from or examined at several museums and university collections in Canada and the United States (see acknowledgments). Over 2,500 specimens of <u>Picoides villosus</u> and 2,400 of <u>P</u>. pubescens were thus examined for color and body measurements variation. Worn or soiled specimens, juvenals, and immatures were eliminated from the samples. I tried to avoid samples of less than 5 specimens but it was not possible to do so in a few cases.

Colors were determined visually after Smithe (1974) or after the Munsell System (Anonymous 1929-1960, 1954). Color measurements were taken on a few samples of <u>P</u>. <u>villosus</u> by means of a Spectronic 505 spectrophotometer with reflectance sphere (Bausch and Lomb).

Measurements were taken according to prescribed methods (Baldwin et al. 1931) with dial calipers or dividers, as follows:

- a) <u>Chord of wing</u>: from bend of folded, unflattened, wing to tip of longest primary. Both wings were measured and the longest measurement was recorded.
- b). <u>Tail</u>: from point between central rectrices to tip of longest rectrix.
- c) <u>Exposed culmen</u>: from point where feathers start on ridge of maxilla, between nasal bristles, to tip of maxilla.
- d) <u>Tarsus</u>: from center of middle joint, behind, between tarsometatarsus (tarsus) and tibiotarsus to end of frontal, <u>complete</u>, most distal scute, before joint with central toe.

Standard statistical procedure was followed (Simpson <u>et al.</u> 1960; Mayr 1969; Sokal and Rohlf 1973). <u>P</u> \leq 0.05 was adopted as the level of significance in Student's t-tests used in comparisons of means. For tests of independance, the G-statistic (Sokal and Rohlf 1973) was used and the level of significance set at <u>P</u> \leq 0.01.

The fact that character variation in both Picoides villosus and

P. pubescens is clinal presents difficult problems in specimen and/or population identification. Since it is the role of the practising taxonomist to provide formal names to populations of a given species, I have attempted to provide material on which to base future identifications. Where clines occur it is often near impossible to delimit the range of any subspecies or population unless the analysis of characters provides some indication which may be used to define areas of stability or homogeneity for particular characters. Those cores of homogeneity may be considered as the range of a subspecies and the areas of character overlap can thus be 'treated as areas of intergradation between populations. In such cases, historical antecedents often provide clues for a definition of ranges and, justify them. I have adopted this procedure in my analyses of variation, in determining the range, and in reevaluating the taxonomic status of the various subspecies of Picoides villosus and P. pubescens.

DISTRIBUTION OF <u>PICOIDES</u> <u>VILLOSUS</u> AND <u>P</u>. <u>PUBESCENS</u> Distribution of Hairy Woodpecker

The distribution of the Hairy Woodpecker (<u>Picoides villosus</u>) coincides in the north to a great extent with the range of the central and southern boreal forest region of Canada (Rowe 1972) and Alaska (Aldrich 1963). To the south it reaches the western part of Panama and the northern third of Baja California (Mexico). It has ϕ colonized several offshore islands such as the Alexander Archipelago (Alaska), the Queen Charlotte, Vancouver, Bahama, Cape Breton, Prince

Edward, Newfoundland, St. Pierre and Miquelon, and Anticosti.

Its range is continuous where ecological conditions are suitable. but becomes patchy in several areas. Certain populations appear to be isolated notably in Central America. Its distribution has been compiled from numerous sources (A.O.U. 1957; Bond 1956; Dickey and Van Rossem 1938; Gabrielson and Lincoln 1959; Godfrey 1966; Grinnell and Miller 1944; Land 1970; Miller 1957; Monroe 1968; Oberholser 1974; Phillips <u>et al</u>. 1964; Short and Crossin 1967; Slud 1964; Todd 1963; Wetmore 1968) and is summarized on Figure 1.

Distribution of Downy Woodpecker

To the north the range of the Downy Woodpecker (Picoides pubescens) is similar to that of Picoides villosus for the most part but tends to be somewhat more southerly, especially in Alaska, the Northwest Territories, Ontario, and Quebec. It therefore coincides more closely with the distribution of the central and southern boreal forest region as outlined by Rowe (1972). To date it has not been recorded in Labrador. It fails to reach the U.S.A.-Mexico border to the south and has not been recorded in southeastern California, southern Nevada, western and southern Arizona, southwestern New Mexico, and southwestern and southern Texas. It has colonized a number of offshore islands but is absent from the Bahamas and a few islands of the Alexander Archipelago in Alaska (Gabrielson and Lincoln It has recently been found in the St. Pierre and Miquelon 1959). Archipelago (Tuck and Borotra 1972). Its distribution is patchy in several parts of the range which has been compiled from several





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Figure 1.

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Map showing the known distribution of <u>Picoides villosus</u> (shaded area) based on published and unpublished sources.



sources (A.O.U: 1957; Gabrielson and Lincoln 1959; Godfrey 1966; Grinnell and Miller 1944; Linsdale 1936; Mengel 1965; Miller 1957; Oberholser 1974; Phillips <u>et al</u>. 1964; Todd 1963; personnal records) and plotted on Figure 2.

The geographical ranges of <u>Picoides villosus</u> and <u>P. pubescens</u> are the most extensive of the genus in North and Central America. <u>P. villosus</u> occurs more widely and it is sympatric with <u>P. pubescens</u> over most of its range (Figures i and 2), except south of the U.S.A.-Mexico border, on the Bahama Islands, and on the Queen Charlotte Islands where <u>pubescens</u> is not known to occur. In the vast area of sympatry of <u>P. villosus</u> and <u>P. pubescens</u> other members of the genus occur as well but their geographical ranges are restricted to much smaller areas. Where <u>P. pubescens</u> is not found, <u>P. villosus</u> often ranges sympatrically with other <u>Picoides</u> species. It is however the only representative^Y of the genus on the Queen Charlotte and Bahama islands and in Central America, south of Honduras, where <u>P. scalaris</u> ranges also but in different ecological situations (Monroe 1968). Short (1971) has recently discussed the history and evolution of the two species and I agree for the most part with his conclusions.

A. VARIATION AND TAXONOMY OF PICOIDES VILLOSUS

1. VARIATION IN COLOR AND COLOR PATTERN

1. Variation of under parts

In <u>Ficoides villosus</u> the coloration of the under parts ranges from almost pure white to cinnamon brown. The white may be slightly tinged with yellow or greenish yellow whereas the other colors vary



Figure 2.

Map showing the known distribution of <u>Picoides pubescens</u> (shaded area) based on published and unpublished sources.



extensively in hue, value, and chroma. In spite of the great variability recorded in any given color component on the under parts it is possible to arrange specimens into two different groups which coincide with two well-defined geographical areas, using this single criterion as a basis regardless of any other variable character.

By plotting on a map the distribution of the breeding birds referred to Group I (drab under parts) or to Group II (white under parts), determined by visual methods and color matching, it was possible to outline with a high degree of precision the eastern boundary of Group I and the western limit of Group II. In this manner serious bias was eliminated and subjectivity reduced to that inherent to visual determination of colors.

In the first group, to be referred to as <u>Group I</u>, which occurs from the panhandle of Alaska, along the coast of British Columbia, including the Queen Charlotte Islands, and west of the western foothills of the Rocky Mountains to western Texas, northern Baja California, and western Panama (Figure 3), specimens have drab under parts or any variants of drab from near white to near cinnamon brown. The second group, <u>Group II</u>, comprises all the specimens with white under parts which are often tinged with pale yellow or greenish yellow. These occur from the northernmost parts of the range to southern Florida, including the Bahama Islands, east of the Coast Range (Canada) and of the western foothills of the Rocky Mountains (U.S.A.) as far south as northern New Mexico and western Texas (Figure 3).



Figure 3.

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Range of two main groups of <u>Picoides villosus</u> based on coloration of under parts: Group I (dotted) with "drab" under parts and Group II (stippled) with white under parts.





Figure 4.

Distribution of color sub-groups of <u>Picoides</u> villosus in color Group I:

, A - "grayish drab" Sub-group [A

B - "pale drab" Sub-group IB

C - "brownish drab" Sub-group IC

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1. Colour group I.

Using the terminology provided by Smithe (1975), "drab" is used here to determine a large family of colors which range from "smoke "Drab" has been selected as being near the gray" to "fuscous". mid-point between the lightest and the darkest coloration recorded on the under parts of the birds referred to the current group. Several specimens were examined by means of a spectrophotometer and the values obtained were converted to the Muhsell notation. The following colors (Munsell System) were recorded on specimens from the Queen Charlotte Islands and coastal British Columbia: 10 YR 6.6/2.0; 10 YR 🗉 5.8/2.0; 10 YR 4.5/2.8; 9.YR 5.5/12.5; 7 YR 4.0/4.0; 4.4 YR 7.5/4.0; 4.5 ¥R 5.0/5.0; 2.5 YR 4.2/3.9; 2 YR 3.99/4.8; 7.5 GY 4.16/1.0. It would have been desirable to obtain color values with a spectrophotometer for specimens originating from other regions in Group I but such an instrument was not available when the greater part of the material was studied.

Upon examination of the specimens in Group I, it stands out that those birds from the Queen Charlotte Islands are the darkest ones and are followed closely by those from Vancouver Island and adjacent mainland. There this dark coloration becomes lighter northward and disappears in the Cordova area (Alaska) where individuals classified as belonging to Group II have been recorded. Eastward, Group I ranges as far as the foothills of the Coast Range where Group II replaces it in the mountains and at the head of valleys. To the south the darkest individuals are confined to a narrow coastal belt in the lowlands. They gradually become lighter

southward and are replaced by lighter individuals in Mendocino County, California. All the darker birds can be referred to a well-defined sub-group, Sub-group IA (Figure 4).

A second sub-group Sub-group IB, can be recognized and the specimen's referred to it have lighter under parts but nevertheless belong to the main group, Group I, on the basis of the dominant coloration which is in the "drab" family. Although it was not possible to determine color values on the spectrophotometer for these birds, the following Munsell values have been obtained by visual matching: 2.5 YR 5.0/4.0; 10 YR 5.0/4.0; 10 YR 6.0/5.0. These birds occur east of the Coast Range at the Canada-U.S.A. border, along the Cascades to Mendocino County in California, south to northern Baja California and central Mexico (Mexican Plateau, north of Mexico City) and east along the foothills of the Rocky Mountains to western Oregon, western Nevada, central Utah, southeastern Nevada, southeastern California, central Arizona, southwestern New Mexico, and western Texas (Figure 4).

South of central Mexico, the pigmentation of the under parts becomes darker. The color values were determined visually and converted to the Munsell notation. Although significantly different from the colors of the other two sub-groups, those colors nevertheless belong to the same large family of colors and the following values were obtained 2.5 YR 3.4/2.9; 5.6 YR 3.5/4.7; 7.5 YR 4.2/3.7. Specimens in Sub-group IC occur from central Mexico, to western Panama (Figure 4) and their pigmentation increases in a southeasterly direction from southern Mexico to western Panama

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Region	Pale drab	Grayish drab	Fuscous drab	<u>N</u>
Alaska	91.3 (21)	8.7 (2)	~	23
Queen Charlótte Islands		13.7 (7)	86.3 (44)	51
Vancouver Island and adjacent mainland (a)	3.7 (4)	88.0 (95)	8.3 (9)	108
Coastal Washington (b)	3.9 (1)	92.3 (24)	3.8 (1)	26
Coastal Oregon (c)	6.9 (2)	86.2 (25)	6.9 (2)	29
Coastal -California (d)	18.2 (2)	81.8 (9)		11
Pooled coastal samples (a,b,c,d)	5.2 (9)	87.9 (153)	6.9 (12)	174

Percentage distribution of color classes in Sub-group 1A, in <u>Picoides</u> <u>villosus</u>. Number of specimens of each class appears in parentheses.

Table 1



Figure 5.

Distribution of color classes in <u>Picoides villosus</u> for Sub-group 1A with percentages of each for various samples.

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GRAYISH DRAB FUSCOUS DRAB PALE DRAB Chitina River Glacier ο PCT 100 Cordova Yakutat Juneau 100 100 Calvert Island 100 100 100 Mendocino County

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ALC: NO. OF ALC: NO.

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7 ') 430 a/ Sub-group IA

The distribution of the birds classified in this sub-group appears on Figure 5 and three main colour classes have been identified. Their frequency distribution is shown on Table 1. Darker birds (fuscous drab) are significantly more frequent on the Queen Charlotte Islands (86.3%) where the next lighter class (grayish drab) is uncommon (13.7%). On Vancouver Island and on the adjacent mainland the proportions are reversed (fuscous drab, 8.3%; grayish drab, 88.0%) and a few much paler birds have been recorded (pale drab, 3.7%). Southward, from Oregon to California, the proportions of each color class remain essentially similar (pale drab, 5.2%; grayish drab, 87.9%; fuscous drab, 6.9%). When broken further the proportions of the color classes in this portion of the sample remain similar except in California where an increase in the percentage of the "pale drab" birds is noticeable but this can probably be accounted for by the small size of the sample studied. On the mainland, in coastal Alaska and British Columbia north of Vancouver Island, the proportion of light-colored birds is very high (pale drab, 91.3%) whereas dark birds are rare (grayish drab, 8.7%). Examination of the total sample reveals that lighter individuals occur at the periphery of the range of this sub-group (Figure 5) where it comes in contact in the north and in the east with birds referred to Group II (white under parts), and farther south with birds of Sub-group IC which are characterized by much paler under parts.

In Alaska specimens from Admiralty Island, Juneau, Loring,

Forrester Island, and Stag Bay (Chichagof Island) are among the darkest (grayish drab); those from Sitka, Hoonah Sound, Howkan, Ketchikan are somewhat lighter (medium drab) and those from Yakutat are much lighter (very pale drab). In the Cordova area the under parts are almost pure white. From a series of six specimens taken near Chitina River Glacier, only one (N.M.C. No. 20351) has a faint wash of "drab" on the upper breast. This may be due to an accumulation of dirt on the feathers rather than to pigmentation but I was unable to determine the nature of this coloration. If this "drab" wash is due to natural pigmentation in the feathers, this bird constitutes the morthernmost penetration of Group I into the range of Group II.

The under parts coloration of the Queen Charlotte Islands sample is fairly uniform. Fuscous drab is dominant (86.3%) and grayish drab was recorded only in a small percentage (13.7%). This variation is apparently unrelated to sex, age, time of capture, or origin of the specimens examined. It is unlikely that birds from the mainland, which resemble the lighter insular birds, could fly to the archipelago, at least to the extent that such movements are currently unknown.

In British Columbia, the grayish drab color type is the most frequent (88.0%) on Vancouver Island and its adjacent mainland, whereas fuscous drab is uncommon (8.3%) and pale drab rare (3.7%). The second color type was recorded only on Vancouver Island and at coastal localities in the southernmost part of the province. Lighter birds (pale drab) proved to come mainly from inland

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Region	Range	Mean	SD	SE	<u>N</u>
Queen Charlotte Islands	11.15 - 13.44	12.134	1.615	0.417	15
Vancouver Island and adjacent mainland	9.44 - 16.77	13.598	2.182-	0.546	16
Coastal mainland B.C. and Alaska, north of Rivers Inlet	18.06 - 22.02	19.8 23	1.674	۰ 0.447	14

Percentage brightness of under parts in three samples of <u>Picoides</u> <u>villosus</u> in Sub-group IA.

Table 2

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Figure 6

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Reflectance curves of specimens from three samples of <u>Picoides</u> villosus in Sub-group IA:

triangles: Alaska panhandle

open squares: Vancouver Island and adjacent

Canadian mainland

full squares: Queen Charlotte Islands.

Curves are based on mean values determined in each sample. Sample size appears to the right of each curve.



localities such as Chilliwak and Agassiz. Individuals from Lytton and Lillooet have a light drab wash on the upper breast but the remainder of the under parts is pure white. From Calvert Island and Rivers Inlet northward the under parts are pale drab at localities such as Hagensborg, King Island (Port John), and Kimsquit. On Vancouver Island two pale drab individuals taken during the nesting season were recorded which indicates that this color type can occur also in an insular population which is otherwise highly homogeneous and apparently isolated from the mainland populations. Brightness of the under parts was determined on a spectrophotometer for 3 samples taken in Sub-group I A and the results appear in Table 2 and on Figure 6. Marked differences appear between the sample originating from the mainland north of Rivers Inlet and the other two samples. The difference between the two other samples is more subtle, particularly as shown by the reflectance curves of Figure 10. However the difference in the mean brightness of the two samples is significant ($\underline{t} = 2.10$; df. = 29; $\underline{P} < 0.05$). The color class percentages of the pooled sample from the coastal areas of Washington, Oregon, and California states remain virtually similar and exhibit little difference when compared to the sample of Vancouver Island and adjacent mainland (Table 1). In Washington State, most of the birds from the coastal localities belong to the grayish drab class: Mount Vernon, Rockport, Olympic Mountain, Lake Keechebus, Trout Lake, Neah Bay, Pyallup, Ilwaco, Ocosta, Mount Rainier, Harstine Island, Lake Whatcom, Seattle, Port Angeles, Long Beach, and Suez. One pale drab individual was recorded from Lapush and a fuscous drab bird

from Tenino. It appears therefore, in spite of the relatively small size of the sample (26 specimens) that the geographic distribution of color classes is purely at random in coastal-Washington State.

The sample from Oregon indicates similar trends and the coloration of the under parts is distributed at random (Table 1). Two pale drab specimens were recorded from Reston and Drew, 25 grayish drab individuals from a number of localities (Portland, Tillamook, Summit Prairie, Wedderburn, Mulino, Newport, St. Helen), and two fuscous drab specimens from Salem and Gold Beach. A number of specimens from inland localities display marked affinities with the "pale drab" class of Table 3 but these will be considered under Sub-group IB.

Only 11 specimens "From the northern part of coastal California could be examined for color. Two individuals from Humbolt Bay and Eureka were referred to the pale drab color class. The others from Humbolt Bay, Crescent City, Sherwood, and Eureka belong to the grayish drab class. A bird from Forest Glen, an interior locality, belongs to this color class also. Specimens from localities south of Cape Mendocino are significantly paler than the specimens classified in the pale drab class and will be treated under Sub-group IB, to which they have been assigned with a number of specimens from inland localities which are somewhat darker than the dominant forms in this sub-group.

In summary, the darkest color classes of Sub-group IA (grayish drab and fuscous drab) are predominant in the coastal areas and on the coastal islands but a small proportion of lighter birds (pale

drab) occurs at random within those regions. The "pale drab" color class is more abundant at the periphery of the range of the sub-group and the occurrence of dark individuals beyond the boundaries of Sub-group IA will be treated in the next sub-group.

b/ Sub-group IB

The range has been detailed on Figures 4 and 7 and under the section. "Color group I" where its general color characteristics have been outlined.

Three main color classes have been recognized within this sub-group and the results expressed in percentage values for each color class for representative localities throughout the range including the pooled samples are shown on Table 3. When considering the pooled samples it appears clear that the "whitish drab" color type is dominant whereas the lighter specimens, "creamy white", comprise one third of the total sample. The darker individuals, designated as "pale drab" amount to less than 5 per cent of the pooled samples and have been recorded mainly in areas adjacent to a darker color group.

In Washington State, this color sub-group occupies a narrow area, sandwiched between the dark coastal birds to the west and the white mountain birds to the east. The influence of the two color groups is reflected in the percentage of Table 3, particularly with regard to the light-colored birds, "creamy white", recorded from Entiat, Leavenworth, and Wenachee Lake. A bird, similarly colored, collected at Pyallup in December, but excluded from this analysis, definitely

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Distribution of color classes of <u>Picoidès</u> <u>villosus</u> in Sub-group IB with percentages of each for various samples.

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Region	Creamy White	Whitish drab	Pale drab	N
Washington	12.5 (3)	83.3 (20)	4.2 (1)	24
Oregon	13.9 (5)	86.1 (31)		36
Nevada	25.9 (7)	74.1 (20)		27
California	42.1 (88)	52.2 (109)	5.7 (12)	209
Arizona	36.9 (24)	63.1 (41)		65
Baja California	37.5 (9)	62.5 (15)	` _	24
Northern Mexico	26.6 (25)	61.7 (58)	≥11.7 (11)	94.
Pooled samples	33.6 (161)	61.4 (294)	5.0 (24)	479

Percentage distribution of color classes of <u>Picoides villosus</u> in Sub-group IB. Number of specimens of each color class appears in parentheses.

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belongs to this color class. It may have been an inland bird on a seasonal and irregular movement to the coast. The only dark bird "pale drab" of the sample was collected at Mount Adams, an inland locality, where the next paler color class is dominant. "Whitish drab" individuals which form over 80 per cent of the sample examined were recorded from Yakima, Tampico, Mount Adams, Mount St.Helens, Stehakim, Mabton, Bumping Lake, Wenachee Lake, Leavenworth, and Entiat. Although this sub-group is adjacent to two other sub-groups and occupies a restricted area in Washington State, the variation recorded in the sample analyzed (24 birds) reflects a high homogeneity in the coloration of the under parts.

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The Oregon sample comprises 36 specimens of which 31 were referred to the "whitish drab" color class and the other 5 to the "creamy white class". The former originated from Fort Klamath, Mount Hood, Wiskey Creek, Colestin, Frail, Eagle Point, Prineville, Meacham, and Paulina Lake, whereas the latter where collected at Warmsprings, Lookinglass, and Camp Harney. As expected the lighter individuals were found some distance away from the dark coastal birds of Sub-group IA and closer to the white under parts group. It is unfortunate that specimens from the western and southwestern parts of the State were not available as they probably would be white or at least much 'whiter' than those of the current sample. They could therefore belong to Group II.

The proportion of darker birds in the Nevada sample remains high (74.1%), compared to the "creamy white" individuals. "Whitish drab" specimens were recorded in the lower areas of the western

third of the State: Pine Forest Mountain, Duffer Peak, Schurz, Pyramid, Carson City, Glenn Brook, Sweetwater, and South Twins River. The lighter individuals were identified from Charleston Peak, Mount Callahan, Toquima, Incline, and Las Vegas. Although it was not possible with the material on hand to show any correlation between the lightness of the under parts and the altitude of the collecting stations, I suspect that such a correlation gould be demonstrated if an extensive sample from a larger number of stations were available. All the specimens from the eastern part of the state have white under parts and have been assigned to Group II. The California sample is extensive and comes from various localities east of the range of Sub-group IA (Figure 5) and covers the rest of the state except the southeastern corner (Figure 7). The dark individuals form only a small percentage of this sample (5.7%) and originate from localities adjacent to the range of Sub-group IA (Figure 5), such as Preston, Nicasio, Snow Mountain, Lakeport, and the Siskiyou Mountains. Most of these collecting stations are located at low altitudes but because the representative material from these key areas is not extensive enough, it has not been possible to derive any correlation between the darkness of the under parts and the low altitude. The proportions of the specimens assigned to the other two color classes are not very different (Table 3) and there is an increasing incidence of "creamy white" or paler individuals eastward, towards the Nevada border and the Panamint Range, and southward towards the Mexican border. I was unable, however, to quantify this shift in the proportions of the two color classes.

The Arizona sample is extensive considering the limited range of the birds assigned to the "drab" under parts group. These were recorded in the southeastern corner of the State, mainly from the Tucson area and in the Chiricahua and Huachuca mountains. The "whitish drab" color class is predominant (63.1%) whereas the lighter "creamy white" birds account for the remainder of the specimens examined (Table 3). The latter have been recorded mainly near and north of Tucson, although they appear at random elsewhere in that sector of the State. The high incidence of these lighter birds reflects the influence of the white under parts group which comes into contact with the "drab" group in that area.

The sample from Baja California comprises a high proportion of "whitish drab" birds (62.5%) and the rest of the sample has been referred to the lighter color class (Table 3). Both color classes occur at random in the same localities: La Grulla, Vallecitos, La Ecantada. Pinon, San Diego, and Santa Ulalia. This effect is not due to sexual dimorphism as one color class is as frequent as the other if the specimens are segregated on the basis of their sex.

In northern Mexico, the sample can be divided into the three color classes recognized in this sub-group (Table 3). The paler birds, which comprise over 26 per cent of the individuals examined, originate mainly from northern Sonora, northern and central Chihuahua, and northwestern Coahuila. The "whitish drab" birds form the largest proportion of the sample and range in the southern parts of Sonora and Chihuahua, Durango, central and northern Zacatecas, central and northern San Luis Potosi, Nuevo Leon, and Tamaulipas. The darker

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	Pale		Dark	•	•	
Region	brownish drab	Brownish drab	brownish drab	brown	N	
North central Mexico	32.4 (12)	27.0 (10)	29.7 (11)	., 10.8 (4)	* 37	
Central Mexico		20.8 (20).	29.2 (28)	50.0 (48)	96	
Mexico (Chiapas), Honduras, Nicaragua,	、		•	,		
Guatemala, El Salvador		16.1 (9)	28.6 (16)	55.4 (31)	56	
Costa Rica, Panama			14.8 (12)	85.2 (69)	81	

Percentage distribution of color classes of <u>Picoides villosus</u> in Sub-group IC. Number of individuals in each color class appears in parentheses.

Table 4



Figure 8.

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Distribution of color classes of <u>Picoides</u> villosus in Sub-group IC with percentages of each for various samples.

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individuals, although they have been recorded within the range of "whitish drab" group, occur mainly in central San Luis Potosi, northern Hidalgo, and central Zacatecas. The largest group, "whitish drab", is very homogeneous whereas the other two groups are highly variable which is probably due to their proximity to the paler birds in the north and to the more heavily pigmented birds in the south.

Although the range of Sub-group IB is not continuous (Figure 7) the similarity between the coloration of the under parts of the whole sample is so great that it is preferable not to separate it into two sub-samples. It is not unlikely that these populations may have been continuous in the past and that a hiatus has developed as a result of "recent" ecological changes.

c/ Sub-group IC

The range of this sub-group which comprises birds whose under parts vary from "pale brownish drab" to "cinnamon brown" is shown on Figure 8. The proportions of each of the four color classes in relation to the origin of the sample appears on Table 4.

In the sample from north central Mexico, the four color classes recognized were recorded and their distribution is detailed on Table 6. The paler and the darker individuals together form a high percentage in the sample (43.2%). Although the geographical distribution of the specimens is uniform, the paler individuals come mainly from the northern parts of the sector whereas the darker individuals have been recorded from the southern and western localities. The other two color classes have similar percentage

distributions in the sample and occur randomly throughout the range although they are in concentration in the central district. There is no correlation between sex and any color class. The range of this sample comprises the following regions: southern Hidalgo, Vera Cruz, extreme southern San Luis Potosi, southern Zacatecas, Guanajuato, Queretaro, and northern Jalisco.

In central Mexico the paler birds are absent and the proportion of the darkest individuals jumps up to 50 per cent. The "brownish drab" individuals show a marked decrease whereas the percentage of the "dark brownish drab" remains virtually the same when compared to the first sample. The specimens examined in this sample were collected in southern Jalisco, Colima, Michoacan, Mexico D.F., Morelos, southern Vera Cruz, Guerrero, and Oaxaca. Therefore the lighter individuals do not form an important part of the sample (20.8%) against the darker individuals (79.2%). In the next sample which comprises specimens from Chiapas (Mexico), Honduras, Nicaragua, Guatemala, and El Salvador, the percentage of the darkest color classes increases again, but the shift in proportions is not as marked as in the sample from central Mexico. There is a slight decrease in the lighter birds. The darkest colour class "cinnamon brown" dominates the sample in a very significant manner (Table 4).

The last sample, from Costa Rica and Panama, contains the largest number of dark individuals (85.2%) and only a small number (14.8%) have been referred to the next, and only, paler, color class applicable to it. The other two lighter color classes are totally absent here.

Considering the whole assemblage of specimens referred to Sub-group IC, darkness of the under parts increases from north to south and there is a similar increase in the incidence of specimens referable to the darkest color class. This increase in darkness is so significant that, when comparing the sample from the northernmost part of the range with those of the southernmost part, two color classes have disappeared and the third forms only an insignificant portion of the sample. This shift in color is gradual but less so in the extreme southern part where the percentage of dark individuals increases rapidly and becomes dominant. The results provided by the pooled samples indicate that the darker individuals average more than 80 per cent of the total sample. The remaining part comprises the lighter color classes and originates from the northern part of Subgroup IC. This situation reflects the influence of the paler Subgroup IB which occurs to the north.

Sexual and age dimorphism in color group I

The examination for variation in the under parts coloration of over 1,000 specimens has revealed that sexual dimorphism is unimportant in this large sample. No significant difference in the coloration of the under parts was detected between the sexes in any group of specimens. Some females (less than 1%), however, tend to be slightly darker than the males in certain localities but this tendency is not consistent. This situation occurs mainly in the sample from the Queen Charlotte Islands, from Vancouver Island and its adjacent mainland, and from coastal Washington State. Elsewhere

no difference was recorded.

When immature individuals of both sexes are compared with adults, they tend to be slightly paler but the small number of immature specimens available does not allow me to draw any conclusions, except perhaps that this may be due to a difference in the texture of the under parts feathers. The plumage of the immatures is more fluffy and the tips of the feathers are looser which gives the impression that the under parts have a lighter coloration. This situation was noted primarily in the specimens from coastal British Columbia, Washington, Oregon, and California. A few immatures from Vancouver and the Queen Charlotte Islands appear slightly darker than the adults from these same areas. I believe that this is due to the texture of the under parts feathers also. If a larger sample of immature specimens had been available it would have been possible to evaluate in a better perspective the extent of color variation of the under parts in this age group.

2. Color group II.

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From all the specimens referred to the 'white under parts' group (about 1,700) 1,355 were examined for variation in the whiteness of the under parts. The range of this group is outlined on Figure 3. Although a number of specimens in fresh fall plumage display some pale yellow or greenish yellow in the white of the under parts, this pigmentation fades and these parts become white later in winter. An adult male captured, banded, and color marked at Mont St. Hilaire on 4 November 1964, had a heavy greenish yellow

tinge on the abdomen and lower breast. On 17 December 1964, it was recaptured and the amount of greenish yellow had decreased considerably and showed only as a faint wash. The same bird was captured again on 2 March 1965; its under parts were completely white on that date. I could not verify this observation on any other specimen but expect that this situation would be similar on other individuals as well. The presence of a yellowish wash on the under parts is a current situation in birds with a fresh fall plumage in the northern part of the range (nonnuptial or basic plumage).

• Whiteness of the underparts is variable and four classes have been recognized, based on the purity of the white. All the determinations were made visually by comparison with standard specimens. All the soiled or worn individuals and all those with a yellowish or greenish suffusion in the plumage have been excluded. However, a number of specimens exhibited a "drab" wash in the white of the under parts. These have been referred to Class IV. The other three classes are based on three states of "whiteness" which are visually recognizable: Class I, the whitest; Class II, average white; Class III, dull white.

No sexual dimorphism was recorded in whiteness, birds of both sexes being equally white in given areas. Individuals of both sexes in the first nonnuptial plumage (Basic I) are more frequently tinged with pale yellow or greenish yellow on the under parts than the adults. Specimens, aged as sub-adults, were therefore omitted from this analysis.

a/ Whiteness, Class I.

Although any definition of whiteness by means of visual estimates is highly subjective, the present whiteness class represents an assemblage of birds on which the white of the under parts is pure and intense. It has a brightness found in none of the other three classes recognized in this study and is easily recognizable visually. The samples from which these birds were identified come mainly from the northern and the mountainous western parts of the range (Table In the east, they have been recorded as far south as Maryland 5), and Washington D.C. (2 individuals, 5%). Proceeding northward through the coastal states and provinces this percentage increases regularly though Massachussetts, Rhode Island, New York, Maine, New Brunswick, ħ Nova Scotia, and Prince Edward Island. In Newfoundland it comprises however only 8 per cent of the specimens studied. Farther to the west, the proportion is high in Quebec (16.5%) and rises to over 53 per cent of the individuals examined in Ontario. In the central states and provinces nearly two thirds of the specimens were assigned to this color class (Table 5, kk). It becomes dominant in Alberta, British Columbia, Yukon, the Northwest Territories, Alaska, Montana, Colorado, Wyoming, Idaho, and in the eastern mountainous sectors of Oregon and Washington (Table 5, ss to ww). In the southern part of the western sector, that whiteness class is frequent (43%) in New Mexico, Utah, California, Arizona, and Nevada (Table 5, xx).

In summary, whiteness Class I is dominant in the northern and western sectors of color group II as outlined on Figures 3 and 9.

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Table 5.

Percentage distribution of whiteness classes for selected samples of <u>Picoides</u> villosus: Bahama Islands (Great Abaco and Grand Bahama islands) aa: Bahama Islands (Andros and New Providence) bb: Florida cc: Georgia, Alabama, Mississippi, Louisiana, Arkansas dd: Texas ee: ff: North and South Carolina gg: Tennessee and Kentucky hh: Virginia, West Virginia, Washington D.C., Maryland Missouri, Kansas ii: jj: Pennsylvania, Ohio, Indiana, Illinois kk: Michigan, Wisconsin, Minnesota, Iowa, Nebraska, North and South Dakota 11: Massachussetts, Rhode Island mm: New York and Vermont Maine, New Brunswick, Nova Scotia, Prince Edward Island nn: oo: Newfoundland pp: Quebec qq: Ontario Manitoba, Saskatchewan rr: ss: Alberta British Columbia tt: uu: Yukon, Northwest Territories, and Alaska vv: Montana, Colorado, Wyoming Idaho, Oregon, and Washington ww: New Mexico, Utah, California, Arizona, and Nevada xx:

Class I represents the 'whitest' individuals.

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Sample	Class	I	Class	II	Class	III	Class IV	N
···		1						
aa					05.0	(1)	95.0 (19)	20
bb			17.4	(4)	82.6	(19)		23
cc			27.6	(16)	62.1	(36)	10.3 (6)	58
dd					100.0	(62)		·62
ee					77.8	(7)	22.2 (2)	9
ff					88.4	(38)	11.6 (5)	43
gg			89.7	(26)	10.3	(3)		29
hh`	05.0	(2)	95.0	(38)				40
ii	-		100.0	(20)				20
jj			87.1	(27)	12.9	(4)		31
kk	60.7	(34)	39.3	(22)				56
11	20.0	(8)	80.0	(32)			•	40
mm	19.4	(6)	80.6	(25)				31
nn	10.5	(8)	89.5	(68)				76
00	08.1	(3)	91.9	(34)				37
PP	16.5	(18)	83.5	(91)				109
qq	53.1	(68)	46.9	(60)				128
rr	90. 5	(57)	09.5	(6)				63
88	100.0	(38)						38
tt	91.4	(128)	08.6	(12)				140
uu	96.8	(30)	03.2	(1)				31
vv	94.7	(71)	05.3	(4)				75
ww	91.7	(66)	08.3	(6)				× 72
хх	43.2	(57)	48.5	(64)	08.3	(11)		132

Table 5

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,Figure 9.

Distribution of whiteness classes recognized in white under parts Group II, in <u>Picoides villosus</u>:

- a: pure white ('bright')
- b: average white
- c: dull white ('off white')
- d: 'drab' white
- e: pure white (as in a), but reduced amount of white dorsally.

Ranges are based on the highest incidence of each whiteness class.



b/ Whiteness, Class II

This class comprises all the specimens with 'average white' under parts. Such a 'white' can be defined as pure white without 'brightness', therefore visibly 'duller' than the 'white' of Class I. Its range appears on Figure 9. All the birds referred to it were recorded in a central belt which stretches from eastern California and New Mexico across to Maryland and to the northeast to Newfoundland. It is a highly homogeneous group in most areas, except in a vast area where it has proportions just slightly higher than Class I (Table 5, xx). It attains important proportions in the central states south of the U.S.A.-Canada border (Table 5, kk) where it was primarily recorded in the southern part of the northernmost states. A similar situation prevails in Ontario (46%) where those birds occur mainly in the southern half of the province. The border between it and Class I is not sharply defined as the zone of overlap is broad in Quebec, New Brunswick, Maine, Vermont, and northern New York. The situation is similar in New Mexico, Utah, California, Arizona, and Nevada.

c/ Whiteness, Class III.

Specimens referred to the present whiteness class have white under parts but not as pure or as 'bright' as in the other two preceeding classes. The range of the class is shown on Figure 9 and comprises a large sector in the southern part of the United States from Texas east to North Carolina and Florida, and to the southern Bahama Islands (Andros and New Providence). In that sector the

proportions of specimens referred to Class III are high (Table 5) and the samples are homogeneous except in the northern parts where a number of individuals referred to the next 'brighter' class have been recorded. The Florida specimens assigned to Class II are all concentrated in the northern part of the state while Class. IV specimens originate from the southern part and along the Atlantic coast. Similarly the North and South Carolina specimens assigned to Class IV come from coastal localities. The situation appears to be similar in Georgia. In the Bahama Islands (Andros and New Providence) Class III specimens are the most common but it is surprising to note that more than 17 per cent of the sample is referrable to Class II. Those two whiteness classes are however distributed randomly on both Andros and New Providence islands. Specimens from the lowlands of Tennessee, Kentucky, Illinois, and Indiana referred to Class III delimit the northern range of this class. Whiteness Class III is dominant in Texas (77.8%) but two individuals (22%) were referred to Class IV. This situation reflects the influence of Color Group I which ranges a short distance to the southwest of the localities where those two specimens originated.

To summarize, the plumage of the under parts of the birds referred to this whiteness class is significantly duller than those of the preceding two color classes and occurs at the southern edge of the range of Color group II.

d/ Whiteness, Class IV.

All the specimens referred to this whiteness class display a

faint creamy wash on the under parts. The creamy coloration resembles some pale drabs recorded in Color Group I but it is much paler than any of the drabs and seldom extends beyond a broad central area on the abdomen and lower breast. It is dominant (95%) on Grand Bahama and Great Abaco islands in the Bahama Archipelago. Similarly-colored birds have been recorded in small proportions (10.3%) in eastern Florida and in the eastern parts of North and South Carolina (11.6%). It was found in the sample from Texas but those individuals probably represent the influence of Color Group I, which is dominant in adjacent areas to the west and to the south.

2. Variation of upper parts

In <u>Picoides villosus</u> variation is not as well-marked on the upper parts as on the under parts. Sexual dimorphism, both in color and color pattern, with the exception of the nuchal patch, is slight. On the other hand, geographical variation is well-marked and follows in a general manner the patterns referred to previously in the study of the under parts. A number of dorsal features initially considered and examined for an analysis of variation were found when taken singly to indicate little about the extent or the magnitude of the variation. A combination of these features was therefore used to evaluate each specimen and a 'score' was given to each specimen thus permitting an analysis of variation within given populations and across the range of the species.

a/ Color variation of upper parts

The upper parts are mainly black. The black is shiny after the postnuptial or postjuvenal (Prebasic or subsequent) molts and becomes progressively duller as a result of fading and wear especially toward the end of the plumage cycle. I have recorded 33 cases where the black parts, notably the outer primaries and secondaries and the scapular region, had faded to a dull dark brown. Although I could not determine the age of those specimens with certainty they appear to be in their first year.

The black dorsal color is broken by spots, blotches, bands, and a mid-dorsal stripe the size of which vary geographically. The color of those markings varies geographically also and ranges from pure white to fuscous drab. The markings of the remiges remain white at all times. The markings of the primary and secondary converts, and the mid-dorsal stripe has a coloration that is similar to that of the under parts. The data on the coloration of the under parts assembled on Tables 1, 2, and 4 are applicable to the upper parts as well with the exception that lighter tinges such as 'creamy white', 'pale brownish drab' or 'pale drab' are almost always replaced on the dorsal regions by pure white. A similar situation prevails with regard to the superciliary lines and the malar stripes. The color groups and sub-groups recognized on the basis of the color of the under parts can be maintained in dealing with the upper parts as they appear on Figures 3 to 9.

b/ Dorsal color pattern variation

The mid-dorsal stripe is uniformly white or takes any of the other colors recorded on the under parts in all the populations examined except in specimens from Newfoundland and the Queen Charlotte Islands. In the birds from those two areas, over 4,000 kilometres apart, the uniform dorsal stripe is broken by a series of black bands which gives them a 'ladder-back' effect. It was not possible to quantify this type of variation. Numerous feathers from the dorsal stripe, were measured but no significant variation could be detected. The dorsal stripe may be uniformly white or take any variant of drab in the Queen Charlotte Islands population. Small amounts of black at the tip of the feathers of the mid-dorsal stripe were noted in a number of individuals in fresh plumage. Those black tips appear to wear off by October in any part of the range. Those birds appear to be immature.

The width of the mid-dorsal stripe is highly variable geographically, the broadest being found in the northern parts of the range and the narrowest in the south. It was not possible to measure it effectively with any accuracy due to the mode of preparation of the specimens. It was therefore treated as one of the parameters used in the visual estimation of the dorsal pattern 'score'.

The size and quantity of the markings of the primaries and secondaries are also highly variable but neither could be measured with accuracy or consistency. They were thus treated as an additional parameter in the visual estimation of the dorsal pattern

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Figure 10

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Five types of greater and lesser primary and secondary coverts recorded showing the decreasing amount of white in <u>Picoides villosus</u>.



'score'. These markings tend to be greater and more numerous in the northern parts of the range and more restricted and fewer in the south, and in the Cordillera region.

The white or light-colored markings on the greater and lesser primary and secondary coverts are highly variable also. Five basic types were originally recognized (Figure 10) but it proved impractical to record them accurately for all specimens and to use the data for an analysis since more than one type of markings, sometimes up to three, were noted on the same individual often in various combinations. This character was therefore used in combination with the others to quantify the dorsal pattern. Those markings are more abundant and more extensive in the northern parts of the range and reduced in size and numbers in the Cordillera region and in the southern parts of the species range.

Considering those difficulties it was found to be more practical and less subjective to use a combination of characters and to attribute a score to each specimen. Six dorsal patterns were thus recognized. 'Pattern 1' displays the largest amount of white or any type of other light coloration ('drab') on the dorsal stripe, on the remiges, and on the primary and secondary coverts. At the opposite end 'Pattern 6' has the least amount of white or any other type of light color. A total of 1,687 specimens were examined and 'scored' using those criteria. Approximately 600 additional specimens were omitted from the sample due to their age or plumage condition (immatures, molting, worn, and soiled). The data have been grouped geographically in a north-south direction and the results



Table 6.

Percentage distribution of six dorsal patterns recognized in <u>Picoides villosus</u>. See text for details on dorsal pattern. Number of individuals appears in parentheses.

- aa Interior Alaska, Northwest Territories, Yukon, and northeastern British Columbia
- bb Alberta, Saskatchewan, and Manitoba
- cc Ontario
- dd Quebec
- ee Maritime Provinces and Maine
- ff Newfoundland
- gg New England States and Pennsylvania
- hh Virginia, West Virginia, District of Columbia, Kentucky, Tennessee, and Missouri
- ii North and South Dakota, Iowa, Nebraska, Michigan, Minnesota, and Wisconsin
- jj Ohio, Illinois, and Indiana
- kk Arkansas, North Carolina, Kansas
- 11 South Carolina, Texas, Mississippi, Oklahoma, Alabama, Georgia, and Louisiana
- mm Florida
- nn Bahama Islands
- oo Queen Charlotte Islands
- pp Pacific coast from southwestern Alaska to northern California
- qq Southern California and Baja California
- rr Mexico and Central America
- ss Interior British Columbia, Washington, Oregon, California, Idaho, Colorado, Montana, Wyoming, Utah, New Mexico, Arizona, Nevada, and western Texas.

Sample	Pattern 1	Pattern 2	Pattern 3	Pattern 4	Pattern 5	Pattern 6	N
88	87.9 (29)	12.1 (4)					33
<u>ь</u>	85.3 (64)	12 0 (9)	02.7(2)	2			75
66	51.6 (64)	48.4 (60)	02117 (2)				124
44	16.5(18)	83.5 (91)					109
00	12.2 (9)	87 8 (65)					74
ff	12.2 ())	11 5 (3)	38.5 (10)	50.0 (13)			26
20	20.8 (15)	79.2 (57)	5015 (10)	5010 (15)			72
00 hh	08 5 (6)	88 7 (63)	02 8 (2)				71
44	60.5 (0) 62.6 (16)	57 6 (19)	02.0 (2)				33
44	42.4 (14)	85.0 (17)	15 0 (3)				20
33 kk		83.3 (35)	16.7 (7)				42
11		31 8 (27)	68 2 (58)				85
11 mm		26.5(13)	73 5 (36)				<u>/0</u>
20		19 3 (4)	90 7 (39)				43
00		07.5 (4)	<i>JUT (J)</i>	82 6 (19)	17 4 (4)		23
00		09 5 (7)	25 6 (21)	42 7 (25)	22 2 (10)		20
66		00.5 (7)	23.0 (21)	42.7 (33)	23.2 (17)		138
44			02.2 (3)	16 2 (37)	71 2 (162)	11 3 (26)	220
11	· 05 0 (19)	09 0 (22)	(1.3 (3))	(10.2 (37))	71.2 (103)	11.5 (20)	229
22	0310 (TO)	00.9 (32)	23.4 (04)	JJ.4 (199)	07.2 (20)		229
	<u> </u>		····		· · · · · · · · · · · · · · · · · · ·		<u> </u>

Table⁶

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appear in Table 6.

The examination of single characters has revealed that the 'whitest' individuals occur in the northwestern part of the range. Sample 'aa' (Table 6) comprises the largest number of birds referred to 'Pattern 1.' The small percentage identified as 'Pattern 2' may be explained by the fact that 4 individuals were taken in northeastern British Columbia in an area adjacent to a much darker group of birds (Table 6, aa). In Alberta, Saskatchewan, and Manitoba 'Pattern 1' is frequent and the presence of 'Pattern 3' in central 'Pattern 2' in southeastern Manitoba can be accounted for Alberta. by the presence of darker groups in adjacent areas. The proportions of 'Patterns 1 and 2' are similar in Ontario. The specimens referred to 'Pattern 1' were recorded there mainly north of a line extending from Kenora to Kirkland Lake. In Quebec most of the specimens from the southern part of the province, south of Lake St. John have been referred to 'Pattern 2' whereas those recorded north of it belong to 'Pattern 1'. A number of specimens mainly from the Gaspé Peninsula, although referred to 'Pattern 2' are intermediate between 'Patterns 2 and 1'. The sample from the Maritime Provinces and Maine comprises a very high proportion (87.8%) of individuals referred to 'Pattern 2', whereas only 9 out of 74 individuals have been referred to 'Pattern 1'. Those originate from the northeastern region of New Brunswick and resemble closely the individuals from the eastern Gaspé Peninsula, Quebec. Half of the Newfoundland sample was designated as 'Pattern 4' on the basis of a great reduction in the amount of white and the presence of black markings

on the mid-dorsal stripe. Over 38 per cent of the sample was referred to 'Pattern 3' on the same basis and only 3 birds in the sample (11.5%) were referred to 'Pattern 2'. The New England and Pennsylvania samples contain a high proportion (79.2%) of specimens referred to 'Pattern 2' whereas those assigned to 'Pattern 1' form less than 21 per cent of the specimens examined. The latter were recorded mainly in northern New York and New Hampshire, and in Vermont. The next sample (Table 6, hh) comprises only a small percentage of individuals recorded in 'Pattern 1' (8.5%) from the highlands of Kentucky, Tennessee, and West Virginia. The majority of those birds belong to 'Pattern 2' and two individuals from Virginia are referable to 'Pattern 3'. In the central northern states (Table 6, ii) only two patterns were identified: 'Pattern 2' is slightly more frequent than 'Pattern 1' which comprises specimens originating mainly from the northern parts of Minnesota, Iowa, and Michigan. The birds from Indiana, Ohio, and northern Illinois are all referable to 'Pattern 2' except for three individuals from southern Illinois referred to 'Pattern 3'. In the next sample (Table 6, kk), the percentage of individuals assigned to 'Pattern 3' increases slightly mainly in Arkansas. In the southern states, with the exception of Florida (Table 6, 11) the percentage of individuals scored in 'Pattern 3' increases significantly and the small number of individuals assigned to 'Pattern 2' comes mainly from the highlands of Georgia and South Carolina, and from northern Oklahoma. The Florida sample (Table 6, mm) comprises the highest proportion of 'Pattern 3' individuals, concentrated mainly in the southern third.
of the state whereas 'Pattern 2' (26.5%) is scattered in the northern parts. In the Bahama Islands over 90 per cent of the specimens are referable to 'Pattern 3'. The four individuals scored in 'Pattern 2' come from New Providence and Andros islands but the white is somewhat more reduced than in mainland birds referred to 'Pattern 2'. In the Queen Charlotte Islands 'Pattern 4' is dominant (82.6%) but four individuals were placed in 'Pattern 5'. In the North Pacific Coast sample (Table 6, pp) the individuals scored in 'Patterns 4 and 5' were recorded primarily in the coastal areas of southern British Columbia (including Vancouver Island), Washington, Oregon, and California. 'Pattern 3' occurs mainly in southwestern Alaska and northern California. In southern California and Baja California 'Pattern 4' is dominant and 'Pattern 5' is restricted to Baja California. The large sample from Mexico and Central America indicates a southward increase in darkness (Table 6, rr). The darkest pattern, 'Pattern 6', occurs in Panama and Costa Rica to which it is restricted whereas 'Pattern 5' is the most frequent and ranges from Panama to Central Mexico. It is most frequent in southern Mexico and Central America, except Panama and Costa Rica. 'Pattern 4' replaces 'Pattern 5' in northern Mexico north of Zacatecas. The next sample (Table 6, ss) is characterized by a large number of individuals referred to 'Patterns 3 and 4'. They range in the Cordillera region from central British Columbia to central Arizona and New Mexico. 'Pattern 1' and nearly half of the birds scored as 'Pattern 2' are restricted to northern central British Columbia. 'Pattern 2' was noted also in the sample from



Figure 11.

Diagrams illustrating various rectrix patterns recognized in analysis of data for outer four retrices of <u>Picoides villosus</u> (Number 2, 3, 4, and 5). The types identified for each rectrix are identified in Roman numerals.



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		Rect	rix 2			R	ectrix	3				
		Types				Турев						
Region	I	II	III	N	I	II	III	IV	V	N		
*												
Newfoundland	2	4	6	6	1	0	2	4	0	6		
Maritime Provinces												
and Maine	3	4	13	19	0	11	8	0	0	20		
Quebec	2	10	21	28	0	8	18	2	0	28		
Ontario	6	1	37	49	5	11	29	5	0	50		
Manitoba,												
Saskatchewan,					-							
and Alberta	3	2	29	36	2	11	21	2	0	36		
Dakotas and												
Wisconsin	1	2	7	12	2	4	6	0	0	12		
Illinois	1	1	3	6	1	1	4	0	0	6		
Connecticut	0	3	8	10	0	7	3	0	0	10		
Carolinas and												
Georgia	0	0	13	16	1	5	9	1	0	16		
Florida	0	0	13	13	1	3	9	0	0	13		
Queen Charlotte												
Islands	0	1	17	18	0	0	6	6	6	18		
Coastal British				1								
Columbia	2	5	23	30	1	5	17	7	0	30		
Coastal Oregon												
and Washington	0	0	11	11	0	2	5	4	0	11		
Costa Rica	0	0	3	3	0	0	1	1	1	3		

Distribution of rectrix types for Rectrices 2 and 3 in selected specimens across the range of <u>Picoides</u> villosus.

Table 7

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eastern Montana and northern Wyoming. In southern Arizona and New V Mexico the most numerous birds belong to 'Pattern 5'.

In summary the northern birds display a larger amount of white or light coloration on the upper parts than the individuals from the southern parts of the range. Insular populations have significantly darker dorsal patterns than mainland ones in general but only slightly darker than those adjacent mainland areas.

3. Variation of caudal pattern

Over 300 specimens in fresh plumage from a number of areas across the range were examined for variation in the rectrices. Only a small percentage of the sample on which no wear was evident was used in this survey. The central rectrices (number 1) are always totally black whereas the others are highly variable. Variation is less extensive in Rectrices 2 and 3 and it was found to be independant of sex or age. Five different types of coloration patterns can be recognized in those feathers (Figure 11) and the distribution of the types has been summarized for selected regions on Table 7. As in the dorsal patterns the amount of white or light coloration is reduced in Newfoundland, in the southern states, in ? the Queen Charlotte Islands, in coastal Oregon and Washington, and in Costa Rica (Rectrix 2). The trends are similar as far as Rectrix 3 is concerned and a reduction in the size of the light areas is evident with an extreme reduction in the Queen Charlotte arphi Islands and Costa Rica. In spite of these trends and array of types, Type III is the most frequent in Rectrix 2 irrespective of the

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		R	ectri	<u>x</u> 4					Re	ctrix	5		
			Тур	es	~					Туре	s		
Region	I	<u> </u>	III	IV	<u> </u>	VI	N	I	11	III	1V	<u>v</u>	<u>N</u>
Newfoundland			1	1	3		5		2	2	2		6
Maritime Provinces													
and Maine	13	6					19	11	8	1			20
Quebec	13	10	2`	3			28	21	7				28
Ontario	11	14	13	9			47	52	5				57
Manitoba, Saskatchewan,													
and Alberta	17	7	8	3			35	27	7				34
Wisconsin	6	4	3				13	6	7				13
Illinois	5	1	-		,		6	3		3			6
Connecticut Carolinas	8	2	•		,		10	6	4				10
and Georgia	6	6	3				15	5	11				16
Florida	2	6	3	2			13	3	9	1			13
Queen Charlotte												ì	
Islands Coastal		1			4	13	18	2	1	1		14	18
British Columbia	5	13	5	2	2	2	29	8	10	12		1 -	31
Coastal Oregon and	-		_						1	l			
Washington Costa Rica	2	3	1	2 2		3	10 3	3	4	1	2	3 1	11 3

Distribution of rectrix types for Rectrices 4 and 5 in selected sample's across the range of Picoides villosus.

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Table 8

geographical origin of the specimens. The situation is similar for Rectrix 3.

Six basic types of color patterns were identified for Rectrices 4 and 5 (Figure 11); their distribution has been summarized in Tables 7 and 8. No sexual or age dimorphism has been noted in those feathers. The trends recorded for Rectrices 2 and 3 are applicable here as well with the exception of a significant increase in the amount of white and frequency of lighter feathers in the birds from the northern parts of the range.

4. Variation of flanks and sides

The flanks and sides are usually plain in most populations and have the same general color as that of the under parts although they tend to be slightly duller on the average. In immature birds, prior to the post-juvenal molt, the flanks and sides bear dark markings which are highly variable in quantity, shape, and size, irrespective of their sex or geographical origin except in three populations: Newfoundland, Queen Charlotte Islands, and Bahama Islands. During the first winter (Basic I plumage) faint black markings are sometimes retained for several weeks but wear off later during the plumage cycle until the end of December.

Black markings were recorded however in various amounts and shapes in adults of both sexes in the populations from the Bahama Islands, Newfoundland, and the Queen Charlotte Islands. In the Newfoundland birds, the flanks and sides, from the upper breast region to the lower abdominal area, are lightly marked with poorly

defined black spots, bars or blotches. In immatures those marking's are bolder. In the Bahamas, the populations from Great Abaco and Grand Bahama islands can be separated on the basis of a smaller amount of black markings on the sides of the breast when compared to the birds from New Providence and Andros islands. In the former the adult females and immatures of both sexes have heavier markings than the males. The populations of the latter are more heavily marked on the sides of the breast and the markings extend onto the flanks. They consist mainly of black dots and fine stripes which are more pronounced in adult females and immatures of both sexes.

Birds from the Queen Charlotte Islands have the heaviest markings on the flanks and sides. Black spots, stripes, and bars have been recorded in all the specimens examined. Those markings are bolder on adult females and immatures of both sexes when compared to adult males.

Small black markings at the tip of a few feathers from the flanks were noted on birds from Costa Rica and Panama but those. markings are sparse and irregular.

In summary flanks and sides markings are consistently present only in insular populations and are more prominent in adult females and immatures of both sexes than in adult males.

5. Variation of facial pattern

The facial pattern of <u>Picoides</u> <u>villosus</u> comprises (1) a black crown in the adults, (2) a white supra-orbital stripe which extends from the crown (replaced by red in males in the nuchal region) onto

the lores in certain individuals, (3) a black auricular patch from the lores onto the nuchal region, (4) a white infraorbital or malar stripe from the nasal tufts onto the neck, (5) a black malar stripe from the base of the mandible onto the sides of the upper breast, and (6) nasal tufts.

Much individual variation has been recorded in the width or length of these various stripes or patches but no definite pattern can be correlated to any geographical groups. The lores display individual variation to a great extent but this type of variation is not geographical although Oberholser (1911:596) used that criterion to separate the populations of the Bahama Islands from those of the mainland. The white areas of the facial pattern often have a tinge very reminiscent of the coloration of the under parts but usually much less saturated.

Variation occurs also in the color of the nasal tufts. Birds with colored under parts usually have colored nasal tufts but those are usually significantly paler.

6. Variation of nuchal pattern

The nuchal patch of males extends onto the occiput in a narrow band from the sides of the head, usually interrupted medially. It varies in color from Scarlet to Geranium (Smithe 1974) irrespective of the age or geographical origin of the individuals. Variation in this character appears to be at random throughout the range and can be attributed to individual variation except possibly in Panama and Costa Rica where specimens have a broader nuchal band than those

from adjacent populations as pointed out by Oberholser (1911) but owing to the difficulty of measuring this character I am not at all certain that this possibility holds true in all cases. Ridgway (1914) has indicated that the nuchal band is not interrupted medially in the populations from the Bahama Islands but this applies to less than two thirds of the specimens examined. A continuous nuchal band has been recorded in many individuals across the range in various frequencies and occurs at random. As a result of the examination of a few hundred specimens it appears that this character is inconsistent to the same extent as its coloration and size (width or breadth). It was found also to be extremely variable in individuals from the same geographical area and was consequently not used further in this study.

In females, the red area is replaced by white and the band varies also extensively in width. It is usually continuous but it is sometimes interrupted medially. In populations where the under parts are very heavily pigmented it may, but rarely, have a slight drab wash which is difficult to measure.

7. Variation of crown pattern

The crown of adult males and females is black. In immatures of both sexes the frontal area varies in pattern and coloration. Because this character appears to be independent of sex or geographical origin and because it has been described previously at length by several authors it is not considered here.

2. VARIATION IN SIZE

General size is largest in the northern parts of the range and gradually decreases southward reaching a minimum in the Costa Rica-Panama region. The following characters have been selected and examined for variation on an individual basis for each sex group: body weight, chord of wing, tail length, exposed culmen length, and tarsus length.

A. Variation in body weight

Body weights display a regular and well-marked increase when plotted against latitude from south to north (Figure 12). Correlation between the two parameters is highly significant for both males (r=0.956; P < 0.001) and females (r=0.954; P < 0.001). In spite of the small size of the sample, only 136 weight data being available from a sample of over 2,000 specimens. Those data indicate that variation in this character is gradual. The difference between the largest and the smallest individuals is close to 50 per cent of the weight of the largest individuals. The small sample did not permit a similar analysis along longitude bands particularly in the northern parts of the range where an increase in size from east to west is suspected.

Where the size of the sample permitted, the differences between the weight of males and those of females were compared and tested statistically (Table 9). A larger sample would probably not have yielded different results but the current data indicate at least trends which may hold true in any case. It thus appears that the



Figure 12.

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Linear regression of body weight (in g) against latitude in Picoides villosus. 作品

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Table 9.

This table shows the body weights in <u>Picoides villosus</u> and other statistics calculated for each latitude band where specimens were available. The percentage difference was obtained from the difference between means of males and females expressed as a percentage of the male means.

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Latitude North	N	Sex	Mean	SD	SE	Percentage in sexual dimorphism
48 [°]	9	М	76.59	2.32	0.77	8.34*
	6	F	70.20	2.66	1.09	
45 ⁰	9	М	78.80	4.28	1.43	13.43*
	9	F	68.22	3.26	1.09	
41 ⁰	8	м	73.73	4.05	1.43	12.15*
	6	F	64.77	4.23	1.73	
38 ⁰	7	м	67.61	2.79	1.05	15.99**
	2	F	56.80			
31 [°]	8	м	58.75	2.66	0.94	11.97*
	6	F	51.72	1.51	0,61	
17 ⁰	10	М	47.14	3.26	1.03	6.55
	6	F	44.05	1.99	0.79	
09 ⁰	1	м	40.00			
	2	F	40.00			-رو ^د

BODY WEIGHT IN PICOIDES VILLOSUS

* Indicates significant difference of values obtained from comparison of means using Student's t-test ($\underline{P} < 0.05$).

** Probably significant.

Table 9.

degree of sexual dimorphism in weight is greater in the northern populations and that this difference is less marked and almost nonexistent in the south although the data are incomplete. This aspect will be verified and tested more fully in the analysis of size variation of the other characters for which adequate samples are available.

B. General variation in other body characters

The chord of the wing, the length of tail, exposed culmen, and tarsus all display a gradual and regular increase in size from south to north. All samples were grouped into sections which correspond to bands of 5 degrees of latitude across the range from south to north and the means of the various parameters were calculated and plotted against the mean latitude for each latitude band from 10° to 60° north. A linear regression was obtained for each set of data and plotted (Figures 13 to 16). There is a high correlation (P<0.001 in all cases, except tail lengths of females where P>0.01) between the size of the various body characters selected and their geographical position, the large ones being in the north and the small ones in the south, as demonstrated previously for body weight. Increase in size for these parameters in gradual, continuous, and generally comparable for both sexes.

Those data were tested also for a possible size increase along longitude bands from east to west and no significant changes were found in the southern and central parts of the range. However from latitude 35⁰ north the data show a slight increase from east to west

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Figure 13.

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Linear regression of means of wing length (in mm) against latitude in <u>Picoides villosus</u>.

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---- Figure 14.

Linear regression of means of tail length (in mm) against latitude in <u>Picoides villosus</u>.





Figure 15.

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Linear regression of means of exposed culmen length (in mm) against

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Figure 16.

Linear regression of means of tarsus length (in mm) against latitude in <u>Picoides villosus</u>.



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in a number of populations.

For the following analyses of size variation (chord of wing, tail length, exposed culmen length, and tarsus length) it seemed practical to group the samples according to the divisions recognized in the analysis of the under parts coloration for Group I (Figure 5) and according to the divisions recognized on the basis of both the dorsal and under parts coloration for Group II (Figure 9, Table 6). In Group I, the samples were divided further according to the subgroups recognized as per Figures 4, 7, and 8. For both groups the insular populations were treated separately since they are endemic and non-migratory.

I - VARIATION IN WING LENGTH

1. Wing length: Sub-group 1A

For males, wing length varies in Group I from an average of 102.63 mm in the south to 127.93 mm in the north. Females are significantly ($\underline{P} < 0.05$; t-tests for each sub-samples) smaller (Tables 8, 9, 10, and 11).

The samples assigned to Sub-group IA on the basis of the coloration of the under parts display a slight increase in size from south to north for both sexes (Table 8, Figure 17) and the means of any given sample do not differ significantly from the mean of the pooled samples (P > 0.05). The Queen Charlotte Islands population has means which are slightly smaller than those expected at that latitude and is very homogeneous. The differences between the means of 11 the samples proved to be statistically (P < 0.05)

Latitu'de north	Sex	Range	✓ Mean	SD	SE	cv	N			
$55^{\circ} - 60^{\circ}$	M	123.0-133.0	127.93	2.915	0.752	2,279	10			
	F	124.0-131.0	125.80	1.398	0.442	1.111	8			
Queen	м	~ 122.0-132.0	126.87	2.244	0.410	1.768	30			
Charlotte Islands	F	120.0-129.0	123.93	2.736	0.583	2.208	22			
50 [°] - 55 [°]	М	122.0-132.0	127.00	2.486	0.718	1.957	12			
	F	125.0-131.5	127.00				4			
$45^{\circ} - 50^{\circ}$	м	120.0-131.5	126.27	2.702	0.338	2.140	64-			
	F	119.0-129.0	123.64	2.453	0.317	1.984	60			
$40^{\circ} - 45^{\circ}$	м	121.0-129.0	124.63	2.288	0.660	1.836	12			
	F	118.0-123.0	120.08	1.744	0.712	1.452	- - Ģ			
Pooled	м	120.0-133.0	126.42	2.787	0.277	2.204	98			
<pre>samples *</pre>	F	118.0-131.5	123.87	2.778	0, 310	2.242	78			

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES VILLOSUS

* Excluding the Queen Charlotte Islands sample.

Table 10

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non-significant for each sex. The percentage difference between the means of males and females is small but nevertheless significant (P < 0.05) and shows little variation except in one case $(55^{\circ}-60^{\circ})$ latitude north) which is probably due to the inadequate size of the sample (females). That percentage is slightly higher on the Queen Charlotte Islands but is nevertheless comparable with that of the other samples. A few larger individuals, intermediate in the under parts and upper parts coloration, taken at a number of inland localities in the coastal beTt from central California to southeastern Alaska were found to have measurements intermediate between those of the main sample and those of the populations that occur in the Cordillera to the east where the under parts are pure white and the body dimensions significantly larger.

2. Sub-group IB: Wing length

The samples of Sub-group IB, although highly homogeneous on the basis of the under parts coloration have been broken into smaller units based on the color pattern of the upper parts. Several such units have been recognized which in turn were split into smaller sub-samples for analysis (Tables 11 and 12).

The coastal California sample, from northern Baja California northward to Mendocino County, when taken as a whole displays a high homogeneity in wing size for both sexes as indicated by the coefficient of variation. When the sample is broken further into bands of two degrees of latitude a size gradient is present (Table 12) and the correlation between wing length increase and latitude

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Region	Sex	Range	Mean	SD	SE	cv	N
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Coastal	M	116.0-131.0	123.01	2.847	0.279	2.315	104
California	F	115.0-125.0	120.76	2.755	0.362	2.281	58
Great	M	123.0-137.0	128.16	3.059	0.293	2.387	109
Basin	F	118.0-129.0	124.74	2.764	0.351	2.215	62
SE Arizona,	М	119.0-131.0	124.33,	2.786	0.581	2.241	23
SW New	F	117.0-128.0	120.69	2.422	0.466	2.007	27
Mexico (a)		Q				,	
Northern '	М	117.0-129.0	123.95	2.878	0.372	2.322	60
Mexico (b)	F	116.0-128.0	120.94	2.566	0.434	2.122	35
Pooled	M	117.0-131.0	124.05	2.837	0.911	2.287	83
samples	F	116.0-128.0	120.83	2.488	0.316	2.059	62
(a and b)		•	t				
Eastern	M	112.0-122.0	118.84	2.588	0.594	2.177	19
Central	F	114.0-119.0	11,6.09	1.514	0.456	1.304	11
Mexico		¢					

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES VILLOSUS

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north is significant ($\underline{P} < 0.05$; r=0.756 for males, and 0.755 for females). Sexual dimorphism is well-marked in the pooled samples for both sexes with a significant ($\underline{P} < 0.05$) difference between means. The pooled samples provide a more accurate estimate of wing length in this population regardless of the smaller mean obtained for the Baja California sample for which the difference proved to be statistically non-significant ($\underline{P} > 0.05$) when compared to the rest of the sample from coastal California. The former population is therefore considered to be at the extreme low of the wing length i and the sample for the sample for the sample for the sample for the former population for the sample for the sample for the former population for the sample for sample for the sample for the sample for the

The Great Basin sample (Figure 4; Table 11) displays a high homogeneity in wing length for both sexes although specimens from the northern parts of the range tend to be slightly larger. Four samples were tested and the difference in means proved to be nonsignificant (P>0.05). A few individuals originating in the extreme eastern part of the range, in areas adjacent to the range of populations with larger body dimensions were included in the present sample in spite of their large wing measurements. Those undoubtedly reflect the influence of the long-winged population immediately to the east. However, those birds are best referred here on the basis of their upper and under parts coloration.

The southeastern Arizona and southwestern Mexico sample, is highly homogeneous for both sexes (Table 11). The larger measurements were recorded on specimens coming from the northeastern sector of this sub-group in an area adjacent to a population of larger individuals. Otherwise, those specimens (6 birds with a wing length
		•				······································		
2 to agree to a state of the st	Region	Sex	Range	Mean	SD	SE	cv	N
	Pooled samples including Baja Calif.	M F	116.0-131,0 115.0-125.0	123.01 120.76	2.847	0.279 0.362	2.315 2.281	104 58
es	Pooled samples excluding Baja California	M F	116.0-131.0 115.0-125.0	123.52 121.32	2.656 2.494	0.283 0.353	2.151 2.056	88 50
	40 [°] -	M F·	122.0-125.0	124.00		* 		3
	38 [°] - 40 [°]	M F	121.0-128.0 118.0-125.0	122.88 121.56	2.603 2.369	0.521 0.749	2.118 1.950	25 10
	36 [°] - 38 [°]	M F	119.0-127.0 115.0-124.0	123.65 120.86	2,036 2.852	0.425 0.762	1.647 2.360	23 [·] 14
	34 [°] - 36 [°]	M F	121.0-131.0 118.0-125.0	123.22 121.25	2.746 2.049	0.573 0.512	2.229 1.690	23 16
್	32 [°] - 34 [°]	M F	122.0-124.0 117.0-123.0	122.60 120.80	1`.949 3.033	0.872	1.590 2.511	5 5
	Baja California	M F	116.0-124.0 115.0-119.0	120.19 117.25	2.167 1.389	0.542 0.491	1.803 1.184	16 8

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES VILLOSUS

Table 12

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ranging from 129.5 to 131.0 mm) display coloration characteristics similar to those of the other specimens in the sample. It is not significantly (P > 0.05) different from the adjacent sample to the south, in northeastern Mexico, for both sexes. Both samples were grouped and the data show that wing length increases slightly along a gradient from south to north. This sample, comprising southeastern Arizona, southwestern New Mexico, and northern Mexico (Table 11), is significantly different (P < 0.05) from that of the Great Basin, north of it, and from that of central Mexico to the south, although its under parts color and dorsal coloration pattern are very similar to that of those two adjacent populations.

The eastern central Mexico sample (Table 11) displays a broad range of measurements particularly in the males. Four small individuals were recorded from the southern part in areas adjacent to populations with small wing length. They were retained in the sample on the basis of the coloration of their under parts. The females are more homogeneous. When compared to the nearest adjacent sample (SE Arizona, SW New Mexico, and northern Mexico) the present sample is significantly different ($\underline{P} < 0.05$).

3. Wing length: Sub-group IC

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The central Mexico sample is more problematic in that it displays a wide range of wing measurements for both males and females (Table 13) but the specimens used here were all referred to the current sub-group on the basis of their under parts color and dorsal color pattern. When the sample, which is inadequate for a more rigorous

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Region	Sex	Range	Mean	SD	SE	CV	N
Central	M	109.0-125.0	116.05	4.212	0.666	4 3.629	40
Mexico	F	106.0-119.0	114.38	3.087	0.545	2 ₇ 699	32
South	м	115.0-121.0	114.14	3.536	0.753	3.098	22
central Mexico	F	110.0-117.0	113.22	2.073	0.488	1.830	18
Southern	М	99.0-112.0	106.62	3.200	0.594	3.001	29
Mexico, Guatemala, Honduras, Nicaragua	F	101.0-108.0	104.33	2.433	0.468	2.331	27
Costa	м	99.0-108.0	103.08	2.374	0.530	2.303	20
Rica (a)	F	96.0-103.0	100.75	2.244	0.501	2.227	20
Panama (b)	м	98.0-107.0	102.18	2.777	0.620	2.717	20
	F	96.0-103.0	99.93	1.886	0.411	_1.887	21
Pooled	м	98.0-108.0.	102.63	2.591	0.409	2.524	40
sample (a and b)	F	96.0-105.0	100.33	2.084	0.325	2. 077	41

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES VILLOSUS

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analysis, is broken into smaller units it nevertheless appears clear that size variation follows a gradient from south to north and from west to east. The chord of the wing is slightly longer in the central highland areas of Mexico. The smaller specimens are concentrated in the southwestern part of the sector occupied by this sample (Mexico, Mexico D.F., Morelos, Puebla, northern Vera Cruz, Hidalgo, and Oaxaca). It is in this area also and just south of it that wing/length decreases abruptly and reaches a size, as indicated by the few specimens examined, similar to that of the populations found much farther south. In spite of the wide range of measurements recorded in wing length, restricted to about 33 per cent of the specimens examined (13 males ranging from 109 to 113 mm and 7 females from 106 to 112 mm), the rest of the sample is fairly homogeneous. The means of this sample are significantly different (P < 0.05) from those of the samples adjacent to it in the northern part of the range.

The western central Mexico sample (Table 13) comprises specimens from southern Jalisco, Colima, Michoacan, and Guerrero states which average slightly smaller wing lengths that those of the populations just to the east. Those differences are however not statistically significant (P > 0.05). Those samples are homogeneous except for a few large males (4) taken in the northeastern sector of the area delimited here and on this basis resemble closely the population to which their range in adjacent.

The small sample from southern Mexico (extreme eastern Oaxaca, and Chiapas), Guatemala, Honduras, El Salvador, and Nicaragua is fairly homogeneous. It was broken into smaller units which indicate

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a slight size gradient from south to north for both sexes and the differences between the various means proved to be statistically nonsignificant ($\underline{P} > 0.05$). The means of the whole sample proved however to be different at a statistically significant level ($\underline{P} < 0.05$) from those of the adjacent sample to the north (Table 13, Southern central Mexico).

The last sample of the sub-group comprises specimens from the central highlands of Costa Rica and western Panama. It is fairly homogeneous with moderate variation between the extremes (less than 10%)

The means, for both males and females, when compared to those of the sample adjacent to it to the north (Table 13, southern Mexico, etc.) proved to be statistically different (P < 0.05). Wing length in the Costa Rica sample is slightly larger than in the Panama specimens but the difference is not statistically significant (P > 0.05). This sample comprises the smallest means Decorded in the specimes and the extreme (smallest)[°] in a size gradient from south to north applicable to all the populations of the species.

4. Wing length: Group II

For the analysis of variation in wing length in this color group (Figure 13) it seemed advisable to divide the large sample into sub-samples as follows: 1) the Cordillera and Colorado Plateau region 2) continental North America east of the Rocky Mountains 3) Newfoundland, and 4) the Bahama Islands, mainly on the basis of natural ecological regions.

The Cordillera and Colorado Plateau sample was separated from

Region	Q	Sex	Range	Mean	SD	SE	CV	° N
								<u> </u>
Mountains		м	124.0-141.0	131.78	2.803	0.206 -	2.127	185
		F	123.0-133.0	128.46	2.315	0.218	1.802	112
Colorado		м	121.0-131.0	126.20	2.406	0.327	1.906	54
Plateau		F	117.0-127.0.	122.89	2.205	0.312	1.795	50

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES VILLOSUS

Table 14

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its adjacent populations on the basis of its dorsal color pattern whereas the large continental sample was kept as one unit in view of the difficulty of separating it into sub-samples using either the color pattern of the dorsal region or the whiteness of the under parts. The insular populations are considered independently because of their isolation from adjacent populations and because of their endemism.

a / The Cordillera and Colorado Plateau sample

This sample comprises specimens from central British Columbia to Arizona, New Mexico, and western California (Figure 9, e). A few individuals from western Texas were assigned to it because they proved to be inseparable from the rest of the sample on the basis of their dorsal color pattern. The sample was split further into two main groups: the mountain population and the Colorado Plateau sample for the purpose of comparison as their wing length appeared to be different. Although wing length proved to vary along a size gradient from south to north (larger individuals) a linear regression against latitude was not revealing, the coefficient of correlation being low (r=0.1264) and statistically non-significant (P>0.05) in spite of a large sample. The difference in the means of each sample, for each sex, proved to be statistically significant (P < 0.05) (Table 14). It is in this sample that the longest wing length was recorded for males (141 mm, one individual) although the mean of the population is not the largest recorded. Sexual dimorphism in wing length is well-marked in both samples. In spite of their similar



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Figure 17.

Linear regression of wing length on latitude for selected samples of <u>Picoides villosus</u> in Group II, in eastern North America. Insular populations are identified.

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dorsal color pattern and under parts those two populations are very distinct on the basis of wing length alone.

b / The continental North America sample

The range of this sample covers continental North America east of the western mountain range from southern Florida and the northern coast of the Gulf of Mexico to southern central Quebec and southern central Alaska (Figure 9) and comprises 947 specimens (Table 15). The sample was split into smaller units which correspond to 5 degrees of latitude across the range from east to west. The wing length mean of all the subsamples was calculated for males and females. A simple linear regression was computed (Figure 17) against latitude and the correlation coefficient obtained is highly significant for both sexes. When each adjacent pair of means was tested for differences, starting in the south $(25^{\circ}-30^{\circ}/30^{\circ}-35^{\circ}; \text{ etc.})$ they all proved to be statistically different ($\underline{P} < 0.05$) from each other for both sexes except for the samples north of 60° latitude north and for the females in samples $55^{\circ}-60^{\circ}/50^{\circ}-55^{\circ}$. When those two sets of samples where pooled (2 for males and 3 for females) the difference between this sample and the next one to the south displays an even greater difference. Considering all the sub-samples it stands out that size increases regularly from south to north (Table 15).

Variation was verified also from east to west along the longitude bands described above. Those were subdivided into smaller units of 5 degrees of longitude and the means were compared. In the bands from 30° to 40° latitude north little variation was

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Latitude north	* Sex	Range	Mean	SD	SE	CV	N
60 [°] - 65 [°]	M	127.0-137.0	132.00	3.082	0.855	2.335	13
o	F	127.0-138.0	129.47	2.855	0./14	2.205	16
550 - 600	M F	127.0-138.0 125.5-132.0	132.61 129.25 _.	2.581 2.478	0.690 0.876	1.946 1.918	14 8
50 [°] - 55 [°]	м	124.0-137.0	130.48	2.841	0.364	2.177	61
	F	122.0-133.0	127.05	2.849	0.456	2.242	39
Newfound- land	M F	^د 120.0–134.0 120.0–132.0	126.11 124.81	3.770 3.763	0.865 0.941	2.989 3.015	19 16
45 ⁰ - 50 ⁰	M F	117.0-135.0 116.0-133.0	125.90	3.687 3.141	0.268	2.928 2.531	188 183
40 [°] - 45 [°]	- M F	116.0-130.0	122.64	2.927	0.343	2.386	73
$35^{\circ} - 40^{\circ}$	м я	112.0-124.0	118.35 115.57	2.942	0.315	2.486	87 43
30 [°] - 35 [°]	M F	110.0-121.0 109.0-118.0	115.27 113.53	2.509	0.316 0.370	2.177 2.187	63 45
25 [°] - 30 [°]	M F	108.0-115.0 109.0-115.0	112.67 111.50	1.819 1.845	0.379 0.393	1.615 1.655	23 22
20 ⁰ - 25 ⁰ (Bahama Is.)	M F	103.0-110.0 101.0-109.0	106.76 103.62	2.328 2.368	0.736 0.655	2.180 2.281	10 13
26 ⁰ (Bahama Is.)	M F	102.0-109.0 100.0-106.0	105.83 103.36	2.345 2.157	0.781 0.650	2.215 2.086	9 11

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES VILLOSUS

Table 15

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recorded from east to west and the difference between means proved to be non-significant (P>0.05) for both sexes. In the $40^{\circ}-45^{\circ}$ latitude north a significant difference (P< 0.05) between the means was recorded in the westernmost blocks $(95^{\circ}-105^{\circ})$ longitude W) for males only and the correlation against longitude from east to west is non-significant (P>0.05). In the next band $(45^{\circ}-50^{\circ}N)$ a similar trend was identified for males west of 95° longitude west and west of 105° longitude west for females. A similar situation prevails in the 50° -55° latitude north band but a significant increase in wing length was detected west of 80° longitude west for males and west of 90° for females. In the latter two sets of samples there is a significant correlation between wing length against longitude (P < 0.05) for both sexes. North of 50[°] latitude north the difference between the means is not significant and no appreciable increase in wing length could be detected along longitude for both sexes (non-significant coefficients of correlation; P > 0.05).

c / The Newfoundland sample

Although displaying a wide spread in wing length (Table 15) for both males and females the samples are acceptably homogeneous. Sexual dimorphism is not as well marked in this sample as in most of the mainland samples. The difference between the means of this insular population and those of the 45° - 50° latitude north is non-significant (P>0.05).

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This sample is separated into two sub-samples on the basis of the under parts color and upper parts and flanks color patterns. The difference between the means of wing length between the two sub-samples is not significant ($\underline{P} > 0.05$) for either males or females (Table 15).

<u> 11 - Variation in tail length</u>

. I have followed here the same procedure used in the analysis of wing length variation in grouping the samples including the insular populations. Tail length is an extremely variable character since the tail is used by those woodpeckers to brace or propel themselves against vertical surfaces. Although the rectrices are stiffer than the other feathers they undergo a rapid wear as a result of constant use. For this reason specimens displaying 'marked wear' were eliminated from the sample and not used in the analysis. 'Marked wear' is applicable here to specimens in any given population where the difference between the shortest and the longest recorded measurements is more than 15 per cent. Although this decision is arbitrary, it helped in eliminating a serious bias due to wear. Wear is more noticeable in late winter, spring, and summer, although some birds in a relatively fresh plumage (November and December) had to be excluded from the sample due to excessive wear. This parameter varies in a similar pattern as that observed for wing length, along a gradient from south to north. It displays a regular increase northward (Figure 14). Sexual dimorphism is well-marked

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Latitude North		Range	Mean	SD	SE	CV	N
55 [°] - 60 [°]	M F	77.0-84.0 77.0-86.0	79.96 81.71	2.434 3.352	0.734 1.267	3.044 4.103	10 7
Queen Charlotte Islands	M F	76.0-85.0 74.0-86.0	79.81 78.48	2.583 3.050	0.527 0.682	3.236 3.886	24 20
50 [°] - 55 [°]	M F	75.0-85.0 77.0-81.0	81.19 79.25	3.927	1.389	4.837	8 4
45 [°] - 50 [°]	M F	74.0-86.0 74.0-87.0	79.86 79.51	3.241 3.313	0.445 0.455	4.058 4.167	53 53
40 [°] - 45 [°]	M F	76.0-82.0 74.0-78.5	77.89 76.63	2.012	0.671	2.583	9 4
Pooled samples *	M F	74.0-86.0 74.0-86.0	79.79 79.40	3.169 3.332	0.354 0.040	3.971 4.196	80 68

TAIL LENGTH (in mm) IN PICOIDES VILLOSUS

* Excluding the Queen Charlotte Islands.

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Table 16

Region	Sex	Range	Mean	SD	ŚE	CV	N
Coastal	м	70.0-82.0	75.76	⊳2.793	0.293	3.687	· 91
California	F	71.0-82.0	76.09	2.925	0.427	3.845	47
Great	м	74.0-88.0	79.65	3.265	0.348	4.100	88
Basin	F	73.0-86.0	79.74	3.212	0.479	4.027	45
SE Arizona,	м	72.0-81.0	77.25	2.712	0.606	3.511	20
SW New	F	75.0-83.0	77.67	2.180	0.445	2.807	24
Mexico (a)			*	•			
Northern	М	73.0-81.0	76.50	2.339	0.401	3.057	34
Mexico (b)	F	72.0-80.0	74.32	2.641	0.528	3.554	25
Pooled	м	72.0-81.0	76.87	2.418	0.322	3.146	54
samples (a and b)	F	72.0-83.0	76.65	2.389	0.364	3.117	49
Eastern	м	70.0-78.0	70.35	5.267	1.277	7.487	17
Central Mexico	F	68.0-74.0	70.50	3.408	1.078	4.833	10

TAIL LENGTH (in mm) IN PICOIDES VILLOSUS

Table 17

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in this character and appears to shift from one sex to the other in some populations (reversed sexual dimorphism).

1. Tail length: Sub-group IA

The geographic range of this sample has been defined previously (Figure 4) and most of the remarks made on wing length (previous section) are applicable here as well. Tail measurements appear in Tables 16, 17, 18, and 19 for this sub-group. The whole sub-group, including the Queen Charlotte Islands specimens, exhibits a high homogeneity and the difference between the means of sample pairs is not significant (P>0.05). Although males have a larger mean than females in most populations, the mean tail length is greater in females in the $55^{\circ}-60^{\circ}$ latitude north sample (Table 16). This situation may be accounted for by the small size of the sample examined and could be considered as a case of reversed sexual dimorphism. Otherwise, sexual dimorphism is present and consistent in this sample, males having regularly longer tails than females.

2. Tail length: Sub-group IB

In this sub-group, the coastal California sample (Table 17) was treated separately (Table 18) as done previously for wing length. Tail length in this sample displays an irregular increase in size from south to north (r=0.4372; $\underline{P} > 0.05$) and the various samples analyzed are not significantly ($\underline{P} > 0.05$) different from each other (Table 18). There is a size gradient from south (smaller) to north (larger) in the other sub-samples of this sub-group (Table 17) and

	TAI	L LENGTH (in m	m) IN <u>PI(</u>	COIDES VI	LLOSUS	. /	
Region .	Sex	Range	Mean	SD °	SE	CV	N
Pooled	M	70.0-82.0	75.76	2.793	0.293	/ 3.687	91
samples	F	71.0-82.0	76.09	2.925	0.427	3.845	47
Pooled	M	72.0-82.0	75.99	2.816	0.315	3.705	80
samples (excluding Baja California)	F	71.0-81.0	76.49	2.856	0.446	3.734	41
40 ⁰	M F	73.0-79.0	75.60		+	میں عور میں کار کی	2
38 [°] - 40 [°]	. M F	73.0-82.0 72.0-80.0	7 <u>6</u> .67 76.86	2.387 2.478	0.689 0.937	3.113 3.225	12 10
36 [°] - 38 [°]	Г	73.0-80.0 74.0-80.0	77.41 76.90	1.698 1.969	0.412 0.623	2.193 2.561	20 10
34 [°] - 36 [°]	M F	73.0-84.0 72.0-82.0	75.97 76.80	1.420 3.709	0.367 1.172	1.869 4.825	18 13
32 [°] - 34 [°]	M F	72.0-77.0 71.0-80.0	73.67 75.75	الله من من بين من م	-		3 4
Baja	м	70.0-77.0	74.09	2.023	0.610	2.730	11
California	F	72.0-76.0	73.33	1.751	0.715	2.388	. 6

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Table 18

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most of the sub-samples are not separable from each other on the basis of tail length, except the coastal California sample from the adjacent sample from the Great Basin (P<0.05) and that from eastern Central Mexico (P<0.05). Sexual dimorphism occurs in all the samples, at least to some extent, and appears to be reversed in certain populations.

3. Tail length: Sub-group IC

In this sub-group tail length varies along a size gradient from south to north although the El Salvador sample averages smaller than " the pooled Costa Rica-Panama sample (Table 19) but the difference between means is not significant (P > 0.05). The difference between means of the Central Mexico and south central Mexico samples is not significant for both sexes (P > 0.05). On the other hand the south central Mexico sample is significantly different from that of southern Mexico and northern Central America (P < 0.05) but the latter is not statistically different (P > 0.05) from the Costa Rica-Panama sample.

Sexual dimorphism is present in all the samples although the difference between each set of means is not statistically significant $(\underline{P} > 0.05)$. Reversed sexual dimorphism was recorded in the Panama sample but this situation may be the result of the small sample examined which has a wide range of measurements but its coefficient of variation is acceptable.

Region	Sex	Range	Mean	SÐ	/ SE	CV	N
Contral	<u>м</u>	68 0-77 0	//	3 026	0 572	. 247	28
Mexico	F	67.0-77.0	71.14	2.601	0.483	3.656	29
South	м	70.0-77.0	, 72.38	2.264	0.800	3.128	8
central Mexico	F	68.0-77.0	70.79	2 .5 47	0.681	3.599	14
Southern	М	60.0-65.0	62,58	1.953	0.448	3.120	19
Mexico, Honduras, Nicaragua, Guatemala	۴	58.0-65.0	61.39	2.291	0.478	3.732	23
Costa	м	58.0-64.0	60.71	1.960	0.475	3.228	17
Rica (a)	F	56.0-62.0	59.33	2.496	0.588	4.206	18
Panama	M	53.0-65.0'	60.2I	3.326	0.7/63	5.523	· 19
(b)	F	57.0-66.0	60.58	2.380	0.532	3.929	20
Pooled	M	55.0-65.0	60.66	2.461	0.416	4.057	35
samples (a and b)	F	5⁄4.Ŏ-66.O	59.93	2 . 495	0.410	4.163	37

TAIL LENGTH (in mm) IN PICOIDES VILLOSUS

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Table 19

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Region	Sex	Range	Mean	SD	∳ SE	CV	N
Mountains	M	75.0-91.0	83.95	3.188	0.248	3.797	164
	F	74.0-89.0	82.50	3.267	0.328	3.960	99
Colorado	M	75.0-88.0	80.33	2.442	0.360	3.040	44
Plateau	F	74.0-85.0	79.02	3.446	0 <u>.</u> 532	4.361	42

TAIL LENGTH (in mm) IN PICOIDES VILLOSUS

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Table 20

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4. Tail length: the Cordillera and Colorado Plateau samples 🐅

The two main samples compared here (Table 20) are acceptably homogeneous. Upon comparison of the means, the differences for each sex proved to be statistically significant (P<0.05). When each of the main samples was broken into smaller units a definite size gradient against longitude north became evident for both sexes (r=0.8143; P < 0.05). Sexual dimorphism is present but not as well-marked as in some of the other samples.

5. Tail length: continental North America sample

The large sample used here was broken into smaller units which comprise all the specimens available from bands of five degrees of latitude running from east to west as in the analysis of wing length variation. It was found also that tail length varies along a gradient from south to north (Table 21). Correlation coefficients (r=0.9132 and 0.9281) were obtained against latitude north for both sexes and indicate a high degree of correlation (P < 0.05). Although this increase in size is regular when the whole sample is considered, it becomes abrupt in certain sectors when the samples are compared among themselves and a number of pairs of means proved to be significantly different (P>0.05) (Table 21). For males all the sub-samples north of 45° latitude north are not significantly (P > 0.05) different from each other.[®] For females a similar situation prevals north of 50° latitude North. The other samples to the south are all separable statistically (P < 0.05) and indicate a progressive "stepped" increase in size, except for females south

Latitude northSexRangeMeanSDSECVN $60^{\circ} - 65^{\circ}$ M $83.0-92.0$ F $79.0-90.0$ 86.000 3.435 1.036 3.994 11 4.579 $50^{\circ} - 60^{\circ}$ M $82.0-95.5$ F 85.14 4.659 1.405 5.472 11 3.601 $50^{\circ} - 55^{\circ}$ M $78.0-92.0$ F 84.16 3.627 0.503 4.309 52 $5.3.424$ $50^{\circ} - 55^{\circ}$ M $78.0-92.0$ F 84.16 3.627 0.503 4.309 52 $5.3.424$ $50^{\circ} - 55^{\circ}$ M $78.0-92.0$ F 84.16 3.627 0.503 4.309 52 $5.3.424$ $100^{\circ} - 55^{\circ}$ M $78.0-92.0$ F 84.16 3.627 0.503 4.309 52 $5.0.990.0$ $80.0-95.0$ B $80.0-95.0$ B 83.29 4.180 1.014 5.018 1.7 1.300 $40^{\circ} - 45^{\circ}$ M $75.0-95.0$ F 80.77 $7.0-90.0$ 80.97 3.231 0.308 0.254 3.990 $40^{\circ} - 45^{\circ}$ M $74.0-85.0$ F 77.21 2.697 0.354 3.139 3.493 58 3.725 $35^{\circ} - 40^{\circ}$ M $62.0-75.0$ F 67.87 2.833 0.368 0.425 4.266 3.725 $30^{\circ} - 35^{\circ}$ M F $62.0-60.0$ 60.96 66.38 2.573 0.407 0.504 3.842 40 $25^{\circ} - 30^{\circ}$ M F $62.0-66.0$ $60.0-71.0$ 66.10 65.09 </th <th></th> <th></th> <th></th> <th></th> <th></th> <th></th> <th></th> <th></th>								
NorthSexRangeMeanSDSECVN $60^{\circ} - 65^{\circ}$ M83.0-92.086.003.4351.0363.99411 $55^{\circ} - 60^{\circ}$ F79.0-90.083.603.8281.2114.57910 $55^{\circ} - 60^{\circ}$ M82.0-95.585.144.6591.4055.47211 $50^{\circ} - 55^{\circ}$ M78.0-92.084.163.6270.5034.30952 F 77.0-90.083.153.4240.5964.11833Newfound-M80.0-95.083.294.1801.0145.01817landF80.0-88.084.072.5560.6833.04014 $45^{\circ} - 50^{\circ}$ M75.0-95.080.773.8010.3084.705152 F 73.0-83.077.212.6970.3543.49358 $40^{\circ} - 45^{\circ}$ M74.0-85.077.212.6970.3543.49358 $50^{\circ} - 30^{\circ}$ M69.0-80.071.653.1390.3754.38070 F 61.0-72.066.962.5730.4073.84240 $25^{\circ} - 30^{\circ}$ M62.0-69.066.381.9360.4222.91621 $20^{\circ} - 25^{\circ}$ M62.0-69.066.381.9360.4222.91621 $20^{\circ} - 25^{\circ}$ M62.0-67.066.104.0231.3416.0869 $80^{\circ} - 25^{\circ}$ M62.0-67.066.10 <td< th=""><th>Latitude</th><th>, 6</th><th>, D====</th><th>Maaa</th><th><u> </u></th><th>CF</th><th><u>O</u>V</th><th>NY</th></td<>	Latitude	, 6	, D====	Maaa	<u> </u>	C F	<u>O</u> V	NY
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	north	Sex	kange	Kean	עפ	· 2E	67	IN
$\begin{array}{cccccccccccccccccccccccccccccccccccc$					· <u>· · · · · · · · · · · · · · · · · · </u>			
F79.0-90.083.603.8281.2114.57910 $55^{\circ} - 60^{\circ}$ M $82.0-95.5$ 85.14 4.659 1.405 5.472 11 $50^{\circ} - 55^{\circ}$ M $78.0-92.0$ 84.16 3.627 0.503 4.309 52 $50^{\circ} - 55^{\circ}$ M $78.0-92.0$ 84.16 3.627 0.503 4.309 52 $80.0 - 55^{\circ}$ M $78.0-92.0$ 83.15 3.424 0.596 4.118 33 Newfound-M $80.0-95.0$ 83.29 4.180° 1.014 5.018 17 $1and$ F $80.0-95.0$ 80.77 3.801 0.308 4.705 152 $45^{\circ} - 50^{\circ}$ M $75.0-95.0$ 80.77 3.801 0.308 4.705 152 $40^{\circ} - 45^{\circ}$ M $74.0-85.0$ 77.21 2.697 0.354 3.493 58 $73.0-83.0$ 77.30 2.880 0.425 3.725 46 $35^{\circ} - 40^{\circ}$ M $69.0-80.0$ 71.65 3.139 0.375 4.380 70 70.90° 2.833 0.526 3.996 29 $30^{\circ} - 35^{\circ}$ M $62.0-75.0$ 67.87 2.896 0.368 4.266 62 $25^{\circ} - 30^{\circ}$ M $62.0-69.0$ 66.38 1.936 0.422 2.916 21 $20^{\circ} - 25^{\circ}$ M $62.0-66.0$ 64.90 1.594 0.504 2.456 10 80.9° M $62.0-72.9$ 6	60° - 65°	М	83.0-92.0	86	3.435	1.036	3.994	11
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		F	79.0-90.0	83.60	3.828	1.211	4.579	10
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$55^{\circ} - 60^{\circ}$	м	82 0-95 5	85 14	4 659	1 405	5 472	11
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		5	82 5-00 5	95 96	2 002	1 140	2 601	7
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	•	r	02.7-90.7	03.00	3.092	1,109	, 2.001	1
F $77.0-90.0$ 83.15 3.424 0.596 4.118 33 Newfound- landM $80.0-95.0$ $80.0-88.0$ 83.29 84.07 4.180 2.556 1.014 0.683 5.018 3.040 17 14 $45^{\circ} - 50^{\circ}$ FM $75.0-95.0$ $75.0-90.0$ 80.77 	$50^{\circ} - 55^{\circ}$	м	78.0-92.0	84.16	3,627	0.503	4,309	52
Newfound- landM F $80.0-95.0$ $80.0-88.0$ 83.29 84.07 4.180 2.556 1.014 0.683 5.018 14 $45^{\circ} - 50^{\circ}$ M F $75.0-95.0$ $75.0-90.0$ 80.77 80.97 3.801 3.231 0.308 0.254 4.705 3.990 $40^{\circ} - 45^{\circ}$ M F $74.0-85.0$ $73.0-83.0$ 77.21 2.697 2.697 0.354 0.308 3.493 58 3.725 46 35^{\circ} - 40^{\circ}M F $69.0-80.0$ $65.0-80.0$ 71.65 70.90 3.139 2.880 0.375 0.375 4.380 1.380 70 3.996 $30^{\circ} - 35^{\circ}$ M F $62.0-75.0$ $61.0-72.0$ 67.87 66.36 2.896 2.573 0.368 0.407 4.266 3.842 $25^{\circ} - 30^{\circ}$ M F $62.0-69.0$ $61.0-70.0$ 66.38 $62.0-67.0$ 1.936 64.90 0.504 2.647 2.456 0.734 10 4.066 26° M $(Bahamas)$ $62.0-72.9$ $62.0-67.0$ 66.10 4.445 2.017 0.608 3.129 11	20	 	77.0-90.0	83.15	3.424	0.596	4.118	33
Newfound- landM F $80.0-95.0$ $80.0-88.0$ 83.29 		-	//.0 /010	03.13	,	0.570	4.110	
landF $80.0-88.0$ 84.07 2.556 0.683 3.040 14 $45^{\circ} - 50^{\circ}$ M $75.0-95.0$ 80.77 3.801 0.308 4.705 152 $40^{\circ} - 45^{\circ}$ F $75.0-90.0$ 80.97 3.231 0.254 3.990 161 $40^{\circ} - 45^{\circ}$ M $74.0-85.0$ 77.21 2.697 0.354 3.493 58 $35^{\circ} - 40^{\circ}$ M $69.0-80.0$ 71.65 3.139 0.375 4.380 70 $55^{\circ} - 40^{\circ}$ M $69.0-80.0$ 71.65 3.139 0.375 4.380 70 $50^{\circ} - 35^{\circ}$ M $62.0-75.0$ 67.87 2.896 0.368 4.266 62 $25^{\circ} - 30^{\circ}$ M $62.0-69.0$ 66.38 1.936 0.422 2.916 21 $20^{\circ} - 25^{\circ}$ M $62.0-66.0$ 64.90 1.594 0.504 2.456 10 $(Bahamas)$ F $62.0-72.9$ 66.10 4.023 1.341 6.086 9 26° M $62.0-67.0$ 64.45 2.017 0.608 3.129 11	Newfound-	М	80.0-95.0	83.29	4.180	1.014	5.018	17
$45^{\circ} - 50^{\circ} \text{ M} = \begin{array}{c} 75.0 - 95.0 \\ F = 75.0 - 90.0 \end{array} \begin{array}{c} 80.77 \\ 80.97 \\ 3.231 \end{array} \begin{array}{c} 0.308 \\ 0.254 \\ 3.990 \end{array} \begin{array}{c} 4.705 \\ 152 \\ 3.990 \end{array} \begin{array}{c} 161 \\ 161$	land	F	80.0-88.0	84.07	2.556	0.683	3.040	14
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	t	-		01101			5.0.0	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$45^{\circ} - 50^{\circ}$	м	75.0-95.0	80.77	3,801	[•] 0.308	4,705	152
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		F	75.0-90.0	80.97	3.231	0.254	3,990	161
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	-			51202		0.,,,,	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$40^{\circ} - 45^{\circ}$	М	74.0-85.0	77.21	2,697	0.354	3,493	58
$35^{\circ} - 40^{\circ} \qquad M \qquad 69.0-80.0 \qquad 71.65 \qquad 3.139 \qquad 0.375 \qquad 4.380 \qquad 70 \\ F \qquad 65.0-80.0 \qquad 70.90 \qquad 2.833 \qquad 0.526 \qquad 3.996 \qquad 29 \\ 30^{\circ} - 35^{\circ} \qquad M \qquad 62.0-75.0 \qquad 67.87 \qquad 2.896 \qquad 0.368 \qquad 4.266 \qquad 62 \\ F \qquad 61.0-72.0 \qquad 66.96 \qquad 2.573 \qquad 0.407 \qquad 3.842 \qquad 40 \\ 25^{\circ} - 30^{\circ} \qquad M \qquad 62.0-69.0 \qquad 66.38 \qquad 1.936 \qquad 0.422 \qquad 2.916 \qquad 21 \\ 61.0-70.9 \qquad 66.36 \qquad 2.151 \qquad 0.469 \qquad 3.242 \qquad 21 \\ 20^{\circ} - 25^{\circ} \qquad M \qquad 62.0-66.0 \qquad 64.90 \qquad 1.594 \qquad 0.504 \qquad 2.456 \qquad 10 \\ (Bahamas) \qquad F \qquad 62.0-66.0 \qquad 64.90 \qquad 1.594 \qquad 0.504 \qquad 2.456 \qquad 10 \\ (Bahamas) \qquad F \qquad 62.0-72.9 \qquad 66.10 \qquad 4.023 \qquad 1.341 \qquad 6.086 \qquad 9 \\ (Bahamas) \qquad F \qquad 62.0-67.0 \qquad 64.45 \qquad 2.017 \qquad 0.608 \qquad 3.129 \qquad 11 \\ \end{cases}$		F	73.0-83.0	77.30	2.880	0.425	3.725	46
$35^{\circ} - 40^{\circ} \qquad M \qquad 69.0-80.0 \qquad 71.65 \qquad 3.139 \qquad 0.375 \qquad 4.380 \qquad 70 \\ F \qquad 65.0-80.0 \qquad 70.90 \qquad 2.833 \qquad 0.526 \qquad 3.996 \qquad 29 \\ 30^{\circ} - 35^{\circ} \qquad M \qquad 62.0-75.0 \qquad 67.87 \qquad 2.896 \qquad 0.368 \qquad 4.266 \qquad 62 \\ 61.0-72.0 \qquad 66.96 \qquad 2.573 \qquad 0.407 \qquad 3.842 \qquad 40 \\ 25^{\circ} - 30^{\circ} \qquad M \qquad 62.0-69.0 \qquad 66.38 \qquad 1.936 \qquad 0.422 \qquad 2.916 \qquad 21 \\ 61.0-70.9 \qquad 66.36 \qquad 2.151 \qquad 0.469 \qquad 3.242 \qquad 21 \\ 20^{\circ} - 25 \qquad M \qquad 62.0-66.0 \qquad 64.90 \qquad 1.594 \qquad 0.504 \qquad 2.456 \qquad 10 \\ (Bahamas) \qquad F \qquad 62.0-66.0 \qquad 66.10 \qquad 4.023 \qquad 1.341 \qquad 6.086 \qquad 9 \\ (Bahamas) \qquad F \qquad 62.0-67.0 \qquad 64.45 \qquad 2.017 \qquad 0.608 \qquad 3.129 \qquad 11 \\ \end{array}$	•	-					••••••	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$35^{\circ} - 40^{\circ}$	м	69.0-80.0	71.65	3,139	0.375	4.380	70
$30^{\circ} - 35^{\circ} \qquad M \qquad 62.0-75.0 \qquad 67.87 \qquad 2.896 \qquad 0.368 \qquad 4.266 \qquad 62 \\ f \qquad 61.0-72.0 \qquad 66.96 \qquad 2.573 \qquad 0.407 \qquad 3.842 \qquad 40 \\ 25^{\circ} - 30^{\circ} \qquad M \qquad 62.0-69.0 \qquad 66.38 \qquad 1.936 \qquad 0.422 \qquad 2.916 \qquad 21 \\ f \qquad 61.0-70.9 \qquad 66.36 \qquad 2.151 \qquad 0.469 \qquad 3.242 \qquad 21 \\ 20^{\circ} - 25 \qquad M \qquad 62.0-66.0 \qquad 64.90 \qquad 1.594 \qquad 0.504 \qquad 2.456 \qquad 10 \\ (Bahamas) \qquad F \qquad 60.0-70.0 \qquad 65.09 \qquad 2.647 \qquad 0.734 \qquad 4.066 \qquad 13 \\ 26^{\circ} \qquad M \qquad 62.0-72.9 \qquad 66.10 \qquad 4.023 \qquad 1.341 \qquad 6.086 \qquad 9 \\ (Bahamas) \qquad F \qquad 62.0-67.0 \qquad 64.45 \qquad 2.017 \qquad 0.608 \qquad 3.129 \qquad 11 \\ \end{array}$		F	65.0-80.0	70.90	2.833	0.526	3,996	29
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		-		,		01010	51770	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$30^{\circ} - 35^{\circ}$	м	62.0-75.0	67.87	2.896	0.368	4,266	62
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		F	61.0-72.0	66.96	2.573	0.407	3.842	40
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		-	0200 / 200		2		5.0.2	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$25^{\circ} - 30^{\circ}$	м	62.0-69.0	66.38	1.936	0.422	2.916	21
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		F	61.0-70.0	66.36	2.151	0.469	3,242	21
$20^{\circ} - 25$ M $62.0-66.0$ 64.90 1.594 0.504 2.456 10 (Bahamas)F $60.0-70.0$ 65.09 2.647 0.734 4.066 13 26° M $62.0-72.9$ 66.10 4.023 1.341 6.086 9 (Bahamas)F $62.0-67.0$ 64.45 2.017 0.608 3.129 11		•	· · · · · · · · · · · · · · · · · · ·				50-12	
(Bahamas)F $60.0-70.0$ 65.09 2.647 0.734 4.066 13 26° M $62.0-72.9$ 66.10 4.023 1.341 6.086 9 (Bahamas)F $62.0-67.0$ 64.45 2.017 0.608 3.129 11	$20^{\circ} - 25^{\circ}$	м	62.0-66.0	64.90	1.594	0.504	2,456	10
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	(Bahamas)	F	60.0-70.0	65.09	2,647	0.734	4.066	13
26°M62.0-72.966.104.0231.3416.0869(Bahamas)F62.0-67.064.452.0170.6083.12911	(2000000)	•		03103				
(Bahamas) F $62.0-67.0$ 64.45 2.017 0.608 3.129 11	26 ⁰	м	62:0-72.9	66.10	4.023	1.341	6.086	9
	(Bahamas)	F	62.0-67.0	64.45	2.017	0.608	3.129	11
	(/	-			2.2.2.		J/	

TAIL LENGTH (in mm) IN PICOIDES VILLOSUS

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of 35° latitude North where the difference between means is not significant (P> 0.05).

Where the number of specimens grouped within the latitude bands was sufficiently large, the samples were split into smaller units representing blocks of 5 degrees of longitude and the means of these sub-samples were compared. A correlation coefficient was obtained also where an increase in size from east to west was recorded. No statistically significant differences were found in most of the samples but a significant increase in size was recorded westward in the following latitude bands $50^{\circ}-55^{\circ}$, $45^{\circ}-50^{\circ}$, and $40^{\circ}-55^{\circ}$. An increase in size appears west of 100° longitude west and is correlated with the longitudinal position of the samples (r=0.8732 for males; r=0.8214 for females) and the correlation coefficient is significant in both cases (P<0.05). In the other samples no significant increase in size westward was recorded.

Sexual dimorphism is present in all the samples and is reduced to a great extent in most populations. Reversed sexual dimorphism occurs in a number of populations. It is not restricted to any given population but was found across the range (Table 21).

6. Tail length: Newfoundland

The Newfoundland sample is somewhat less homogeneous than the other group examined (Table 21). The means of the sample are not significantly different ($\underline{P} > 0.05$) when compared to those of the 50°-55° latitude North band but statistically different ($\underline{P} < 0.05$) from those of the 45°-50° latitude North band. Reversed sexual

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dimorphism was fecorded and appears to be somewhat more important in this sample than in most of the other samples.

7. Tail length: Bahama Islands

The two Bahama Islands samples (Table 21) proved to be inseparable from each other on the basis of their tail measurements $(\underline{P} > 0.05)$. The Bahamas 26[°] longitude north sample is not significantly different ($\underline{P} > 0.05$) from that of the adjacent mainland area at the same latitude ($25^{\circ}-30^{\circ}$), although females of the Bahama sample have on the average a slightly shorter tail.

To summarize, tail length is a highly variable character and variation takes place mainly along a south-north gradient (smaller to larger). East of the Cordillera, variation also takes place in certain areas along an east-west gradient (smaller to larger). Sexual dimorphism is present in all the populations although it appears to be reversed in a few samples. Insular populations display tail length characteristics similar to that of the mainland groups.

III - Variation in bill length

Bill length is based here on the length of the exposed culmen and was measured according to the prescribed methodology. This character varies along a south-north gradient in both sexes (Figure 15). The difference between the mean of the longest bill length for males in the north (35.25 mm) and the smallest in the south (23.7 mm) is 11.46 mm (33%) and 10.55 mm (34%) for females (31.00 mm and 20.45 mm).

Individual measurements were grouped according to the procedure used previously in the analysis of wing and tail measurements. It becomes apparent here that variation in this character exhibits a pattern similar to that of wing and tail lengths. Sexual dimorphism is present and more pronounced here than for the other two mensural characters studied previously.

1. Bill length: Group I

In the coastal samples (Baja California to southwestern Alaska) bill length increases regularly and gradually along a south-north gradient (Tables 22, 23, and 24) and the difference between each pair of samples is not significant (P > 0.05) except for the males of samples 40° -45° and 45°-50°. The Baja California sample is inseparable from the pooled coastal samples of central and southern California (Table 24) and the former, including that of Baja California, is not significantly significant (P > 0.05) from the northern pooled samples (Table 22) for both sexes. The same sample is significantly different however from that of the Great Basin for both sexes (Table 23). Although the southeastern Arizona and southwestern Mexico specimens have bills significantly longer (P 0.05) than those from northern Mexico, a well-marked size gradient (south-north) was recorded in several small samples which had to be pooled due to their inadequate size. The pooled samples are significantly different (P < 0.05) from the Great Basin and the eastern central Mexico samples as well for both sexes (Table 23).

The central Mexico and Middle America samples indicate a

Latitude north	Sex	Range	Mean	SD	SE	CV	N
				<u> </u>			
$55^{\circ} - 60^{\circ}$	М	28.0-33.5	29.10	1.049	0.332	3.604	10
	F	25.5-31.5	26.13	1.642	0.581	6.284	8,
Oueen	М	27.0-32.0	28.71	1.098	0.204	3.825	29
Charlotte Islands	F	24.5-28.5	25.91	1.269	0.271	4.898	22
$50^{\circ} - 55^{\circ}$	м	28.0-34.5	31.71	1,876	0.542	5.917	12
50 55	F	30.0-32.0	31.00				4
$45^{\circ} - 50^{\circ}$	м	28.5-34.5	31.33	1.360	1.170	4.342	64
	F	25.0-31.5	27.71	1.394	0.180	5.031	60
$40^{\circ} - 45^{\circ}$	м	29.0-33.0	30.33	1.854	0.391	4.464	12
	F	26.5-29.0	27.83	1.169	0.477	4.201	6
Yooled '	м	28.0-34.5	31.03	1.571	0.158	5.063	98
samples *	F	25.0-32.0	27.78	1.695	0.190	6.101	78

EXPOSED CULMEN LENGTH (in mm) IN PICOIDES VILLOSUS

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* Excluding the Queen Charlotte Islands

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Table 22

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Sex	Range	Mean	SD	SE	c۷	N
м	27.0-32.0	29.90	1.450	0.156	4.851	87
F	23.0-29.5	26.55	1.379	0.193	5.195	51
м	25.5-34.0	30.82	1.652	0.160	5.358	107
F	25.0-32.0	27.14	1.600	0.203	5.895	62
м	27.0-32.0	28.39	1.446	0.301	5.092	23
F	23.0-27.0	24.96	1.248	0.245	5.001	26
		Ý	•		1	
М	24.0-29.5	26.73	1.281	0.167	4.792	5 9
F	21.0-26.0	23.19	1.249	0.211	5.387	35
М	24.0-32.0	27.20	1.519	0.168	5.586	82 [´]
F	21.0-27.0	23.94	1.522	0.195	6.358	61
М	24.0-28.0	26.42	1.134	0.260	4.291	19
F	20.5-26.0	23.46	1.781	0.537	7.594	11
	Sex M F M F M F M F M F	Sex Range M 27.0-32.0 F 23.0-29.5 M 25.5-34.0 F 25.0-32.0 M 27.0-32.0 F 23.0-27.0 M 27.0-32.0 F 23.0-27.0 M 24.0-29.5 F 21.0-26.0 M 24.0-32.0 F 21.0-27.0 M 24.0-32.0 F 21.0-26.0 M 24.0-32.0 F 21.0-26.0	Sex Range Mean M 27.0-32.0 29.90 F 23.0-29.5 26.55 M 25.5-34.0 30.82 F 25.0-32.0 27.14 M 27.0-32.0 28.39 F 23.0-27.0 24.96 M 24.0-29.5 26.73 F 21.0-26.0 23.19 M 24.0-32.0 27.20 F 21.0-27.0 23.94 M 24.0-28.0 26.42 F 20.5-26.0 23.46	SexRangeMeanSDM $27.0-32.0$ 29.90 1.450 F $23.0-29.5$ 26.55 1.379 M $25.5-34.0$ 30.82 1.652 F $25.0-32.0$ 27.14 1.600 M $27.0-32.0$ 28.39 1.446 F $23.0-27.0$ 24.96 1.248 M $24.0-29.5$ 26.73 1.281 F $21.0-26.0$ 23.19 1.249 M $24.0-32.0$ 27.20 1.519 F $21.0-27.0$ 23.94 1.522 M $24.0-28.0$ 26.42 1.134 F $20.5-26.0$ 23.46 1.781	SexRangeMeanSDSEM $27.0-32.0$ $23.0-29.5$ 29.90 $26.551.4501.3790.1560.193M25.5-34.025.0-32.030.8227.141.6521.6000.203M27.0-32.023.0-27.028.3924.961.4461.2480.3010.245M27.0-32.023.0-27.028.3924.961.4461.2480.3010.245M24.0-29.521.0-26.026.7323.191.2811.2490.1670.211M24.0-32.023.9427.201.5190.1680.195M24.0-28.020.5-26.026.4223.461.1340.537$	SexRangeMeanSDSE CV M $27.0-32.0$ $23.0-29.5$ 29.90 $26.551.4501.3790.1560.1934.8515.195M25.5-34.025.0-32.030.8227.141.6521.6000.1605.358M27.0-32.023.0-27.028.3924.961.4461.2480.3010.2455.0925.001M27.0-32.023.0-27.028.3924.961.2480.2450.2455.001M24.0-29.52.3.1926.731.2490.1670.2114.7925.387M24.0-32.027.2027.201.5190.1680.1685.5866.358M24.0-28.020.5-26.026.4223.461.1340.5370.2607.594$

EXPOSED CULMEN LENGTH (in mm) IN PICOIDES VILLOSUS

Table 23

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Region	Sex	Range	Mean	SD	SE	čv	N
Pooled	м	26.5-33.0	29.87	1.494	0.148	5.002	102
samples	F	23.0-29.5	26.46	1.358	0.178	5.133	58
Pooled	м	26.5-33.0	29.90	1.450	0.156	4.851	87
samples (excluding Baja California)	Fi	23.0-29.5	26.55	1.379	0.193	5.195	51
40 [°] -	м	29.0-32.0	30.17				3
	F						
30 [°] - 40 [°]	м	27.5-31.5	29.32	1.376	0.275	4.693	25
	F	24.5-28.5	26.54	1.405	0.423	5.291	11
36 [°] - 38 [°]	М	28.0-33.0	30.28	1.232	0.257	4.070	23
	F	23.0-28.0	26.89	1.236	0.330	4.702	14
34 [°] - 36 [°]	м	25.0-31.0	30.04	1.356	0.283	4.514	23
	F	24.0-28.5	26.38	1.455	0.364	5.516	16
$32^{\circ} - 34^{\circ}$	м	27.0-32.0	29.38	ينبد خده می جود کم			4
	F	25.5-28.0	26.80	1.037	0.464	3.869	5
Bata	м	[,] 27.0-33.0	29.67	1.769	0.457	5.963	15
California	F	25.0-27.0	25.71	0.906	0.343	3.525	7

EXPOSED CULMEN LENGTH (in mm) IN PICOIDES VILLOSUS

Table 24

Region	Sex	Range	Mean	SD	SE	CV	N.
Central	м	21.0-27.5	25.00	1.260	0.199	5.040	40
Mexico	F	19.0-24.0	21.88	1.256	0.222	5.741	32
South	м	23.0-27.0	24.80	0.983	0.209	3.964	22
central	F	19.0-24.0	21.17	1.434	0.338	6.775	18 -
Mexico						/ i	7
S Mexico,	м	21.0-26.0	23.79	1.039	0.192	4.366	29
Honduras,	F	18.5-23.5	20,94	1.310	0.252	6.254	27
Nicaragua, Guatemala	 ~ _24	4		- ,	₹¥		
Costa	м*́,	21.0-27.0	24.00	1.317	0.294	5.487	20
Rica (a)	F	18.0-22.0	20.45	1.179	0.263	5.765	20
Panama (b)	м	21.5-25.5	23.84	1,167	0.267	4.894	19
, (0)	F	19.5-23.0	21.33	0.963	0.215	4.515	20
Pooled	м	21.0-27.0	23.92	1.232	0.197	5.149	39
a and b	F	18.0-23.0	20.89	1.151	0.182	5.510	40

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Table 25

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south-north size gradient also (r=0.894 for males and 0.921 for females; $\underline{P} < 0.01$). The data appear on Table 25. The El Salvador sample has smaller averages than the other samples. They are considerably smaller than those of the Panama individuals but since only a few individuals could be measured the results are considered as inconclusive, although indicative that a small-billed population may occur in that area. The males of the south central Mexico sample are separable ($\underline{P} < 0.05$) from those of southern Mexico and northern Middle America. The females from Costa Rica are also significantly different ($\underline{P} < 0.05$) from those of Panama. Sexual dimorphism was recorded in all the samples and is better marked than for the wing and tail lengths. Females are considerably smallerbilled than the males.

2. Bill length: Group II

The Cordillera and Colorado samples have means that are significantly ($\underline{P} < 0.05$) different from each other for both sexes (Table 26). Both of these samples are acceptably homogeneous.

For the large sample covering the rest of continental North America, east of the Cordillera, the same procedure was followed as that adopted for the analysis of variation in wing length. Significant differences (P < 0.05) between pairs of means were found in the following samples for males, $55^{\circ}-60^{\circ}/50^{\circ}-55^{\circ}/45^{\circ}-50^{\circ}/40^{\circ}-45^{\circ}/$ $35^{\circ}-40^{\circ}/30^{\circ}-35^{\circ}$, and for females, $55^{\circ}-60^{\circ}/50^{\circ}-53^{\circ}/45^{\circ}-50^{\circ}$, $35^{\circ}-40^{\circ}/$ $30^{\circ}-35^{\circ}$. Although a significant increase in size along a southnorth gradient (r=0.9239 for males and 0.9074 for females: P < 0.01)

Region	Sex	Range	Mean	SD	SE	ĊV	N
Mountains	M	27.0-35.5	31.44	1.724	0.127	5.488	183
1	F	24.5-32.0	27.67	1.503	0.139	5.431	116
Colorado	м	26.0-33.0	29.44	1.447	0.199	4.914	53
Plateau	F	22.5-29.0	25.71	- 1.433	0.205	5.571	49

EXPOSED CULMEN LENGTH (in mm) IN PICOIDES VILLOSUS

Table 26

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is gradual, it is nevertheless "stepped" from one latitude band to the next as indicated by the difference recorded between each consecutive set of means. Those samples (latitude bands) were tested also for an increase in size along a gradient from east to west. Such an increase was detected in several latitude bands as follows:

> $30^{\circ}-35^{\circ}$, west of 95° longitude west $35^{\circ}-40^{\circ}$, " " 95° " " " $40^{\circ}-45^{\circ}$, " " 100° " " " $45^{\circ}-50^{\circ}$, " " 95° " " " $50^{\circ}-55^{\circ}$, from easternmost part of range $55^{\circ}-60^{\circ}$, " " " " " " "

The longest bills, although their means are significantly ($\underline{P} < 0.05$) different occur north of the $45^{\circ}-50^{\circ}$ latitude North band. Those samples display a high homogeneity for both sexes. Sexual dimorphism is well marked and consistent from sample to sample.

The Newfoundland sample exhibits an acceptable homogeneity (Table 27) and its means are significantly different ($\underline{P} < 0.05$) from those of the two nearest mainland samples ($50^{\circ}-55^{\circ}$; $45^{\circ}-50^{\circ}$). Sexual dimorphism is well marked also and consistent with the data recorded in the other samples.

The means of the two Bahama samples are not significantly different ($\underline{P} > 0.05$) from each other and inseparable from those of the adjacent mainland $25^{\circ}-30^{\circ}$ latitude band. Sexual dimorphism is consistent with that of the mainland samples.

In summary bill length increases in size along a south-north gradient in all the samples and along an east-west gradient in several continental samples east of the Cordillera. Sexual dimorphism

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Latitude north	Sex	Range	Mean	SD	SE	CV	N	
$60^{\circ} - 65^{\circ}$	м	32 0-38 5	35.25	1.827	0.488	5,182	14	
	F	28.5-33.0	30.72	1.125	0.281	3.662	16	
$55^{\circ} - 60^{\circ}$	М	32.5-38.0	34.32	1.576	0.421	4.593	14	
<i>.</i> •	F	28.5-34.5	30.88	, 1.996	0.706	6.463	8	
50 [°] - 55 [°]	м	27.0-38.0	33.88	1.892	0.244	5.584	60	
ti M	F	26.0-34.0	29.32	1.421	0.231	4.847	38	
Newfound-	м	24.0-31.5	28.66	.1.724	0.396	6.017	19	
land	F	24.0-27.5	26.23	1.033	0.069	3.937	15	
45 ⁰ - 50 ⁰	- M	24.0-36.0	30.40	1.805	0.132	5.940	188	
	F	23.5-32.5	27.56	1.574	0.118	5.710	177 '	
$40^{\circ} - 45^{\circ}$	м	27.5-32.0	29.67	1.113 -	0.129	3.752	75	
	F	24.5-31.0	26.81	1.325	0,157	4.943	ູ 71	
$35^{\circ} - 40^{\circ}$	M	26.5-32.5	29.22	1.278	0.138	4.373	86	
	F	24.0-28.5	26.35	1.267	0.200	4.808	40	
$30^{\circ} - 35^{\circ}$	м	25.0-32.0	28.12	1.230	0.155	4.376	63	
X	F	23.5-29.0	25.33	1.243	0.192	4.906	42	
$25^{\circ} - 30^{\circ}$	м	26.0-29.0	27.30	1.065	0.227	3.903	22	
	F	23.0-26.5	24.64	1.086	0.237	4.405	21	
$20^{\circ} - 25^{\circ}$	M	25.5-28.5	27.04	0.957	0.302	3.539	10	
(Bahamas)	F	22.5-26.0	23,95	1.104	0.306	4.610	13	
26 ⁰	м	24.0-29.0	27.21	1.529	0.509	5.619	9	
(Bahamas)	F	22.5-25.5	23.68	0.901	0.271	3.804	11	

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EXPOSED CULMEN LENGTH (in mm) IN PICOIDES /VILLOSUS

Table 27

is present in all the populations and is stronger in the eastern populations.

IV - Variation in tarsus length

The procedure adopted for the study of variation of the other mensural characters has been followed here. Tarsus length is the least variable mensural character and increases in length along a south-north gradient (Figure 16). The difference between the largest and smallest means is 4.4 mm (18.5%) for males and 4.2 mm (18.5%) for females. Variation displays here a pattern similar to that of the wing and culmen lengths. Sexual dimorphism occurs and is well marked in all the populations.

1. Tarsus length: Group 1

The samples assembled in Sub-group IA vary in size along a south-north gradient (Table 28) but the increase in tarsus length is not very well marked (r=0.591 for males and 0.579 for females; P > 0.05). The sub-samples are highly homogeneous and the difference between each pair of means, from north to south, is not significant (P > 0.05). Sexual dimorphism is present but not particularly strong.

The Queen Charlotte Islands sample has uniform characteristics in tarsus length and its means are statistically different (P < 0.05) from that of the pooled adjacent mainland samples.

The coastal California sample (Table 30) is highly homogeneous and displays strong sexual dimorphism. It presents an increase in

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TARSUS LENGTH (in mm) IN PICOIDES VILLOSUS

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Latitude north	Sex	Range	Mean	SD	SE	CV	N
55 [°] - 60 [°]	· M F	22.5-25.0 20.5-24.5	23.20 22.25	0.978 1.035	0.309 0.366	4.213 4.652	10 8
Queen Charlotte Islands	M F	23.0-24.5 21.5-24.0	23.55 22.73	0.442 0.650	0.081 0.139	1.878 2.859	30 22
50 [°] - 55 [°]	M C · F	22.0-24.5 23.0	23.67 23.00	0.749	0.216	3.163 *	12 4
45 [°] – 50 [°]	M F	22.0-24.5 21.5-23.5	23.21 22.44	, 0.739 0.538	0.092 0.069	3.184 2.395	64 60
40 [°] - 45 [°]	M F	22.0-24.0 21.5-23.5	22.83 22.17	0.615 0.683	0.178 0.279	2.696 3.081	12 6
Pooled samples *	. M F	21.5-25.0 20.5-24.5	23.22 22.43	0.770 0.611	0.077 0.069	3.316 2.724	98 78
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* Excluding the Queen Charlotte Islands



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size along a south-north gradient (r=0.967 for males and 0.979 for females; $\underline{P} < 0.01$). The difference between the means of each pair of samples from south to north (Table 30) is not significant ($\underline{P} > 0.05$) but the difference between the means of the pooled samples and that of Baja California is significant ($\underline{P} < 0.05$). However when the Baja California means were tested against those of the nearest sample to the north no statistically significant ($\underline{P} > 0.05$) difference was recorded.

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The means of the pooled coastal California samples are significantly (P < 0.05) different from those of the Great Basin (Table 29). The means of the Great Basin sample are significantly different (P < 0.05) from those of the pooled southeastern Arizona, southwestern New Mexico, and northern Mexico groups. On the other hand the southeastern Arizona and southwestern New Mexico samples are not significantly different (P > 0.05) from those of northern Mexico and the latter are statistically different (P < 0.05) from those of northern those of the central Mexico sample. Those data indicate well marked sexual dimorphism.

In Sub-group IC (Table 31) 'a south-north size gradient (r= 0.875 for males and 0.914 for females; P < 0.01) was recorded from western Panama to central Mexico and the difference between the largest and smallest means is 1.0 mm (5%) for males and 0.77 mm (4%) for females. The samples are acceptably homogeneous and their extremes fall within a narrow range. The central Mexico sample is significantly different (P < 0.05) from that of south central Mexico for both sexes but all the means of the other samples 172

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TARSUS LENGTH (in mm) IN PICOIDES VILLOSUS

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Region	Sex	Range	Mean	SD	SE	*** GV	• N
Coastal	М	20.0-23.5	22.24	0.747	0.080	3.357	88
California	F	20.0-23.0	21.32	0.733	0.106	3.437	48
Great	м	21.0-24.0	22.70	0.730	0.700	3.216	109
Basin	F	19.5-23.5	21.82	0.850	0.180	3.898	62
SE Arizona,	м	21.5-23.5	2 20	0.494	0.103	2.226	23
SW New Merico (a)	F	20.5-22.0	" 21.17	0.423	0.083	1.997	26
Mexico (a)			r dege j	•			
Northern	М	20.0-23.5	21.23	0.685	0.088	3.229	60
Mexico (bį)	F	19.0-22.5	20.59	0.712	0.120	3.459	35
Pooled	М	20.0-23.5	21.49	0.771	0.085	3.587	83
samples (a and b)	F	19.5-22.5	20.84	0.669	0.086	3.211	61
Eastern	м	19.5-21.5	20.40	0.488	0.112	2.394	19
central	F	19.5-20.5	20.00	0.387	0.117	1.935	11

Table 29

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Region	Sex	Range	Mean	SD	SE	CV	N
Pooled	M	20.5-24.0	22.13	0.763	0.075	3.449	104
samples	F	20.0-23.0	21.24	0.732	0.098	3.448	<u>5</u> 6
Pooled	м	20.5-24.0	22.24	0.742	0.080	3.357	88
samples (excluding	F	20.0-23.0	21.32	0.733	0.106	3.437	48
Baja California)		•	2		\ ,		
40 ⁰ -	M	22.0-24.0	23.00				3
	F		•				
$38^{\circ} - 40^{\circ}$	M	20.0-24.0	22.40	0.777	0,155	3.470	25 11
	r ,	21.0-23.0	21.71	۳ ۰.۵۵	0.1/0	21005	**
36 [°] - 38 [°]	M F	20.5-23.0 20.0-22.0	22.24 21.31	0.655 0.596	0.137 0.165	2.945 2.799	23 13
34 [°] - 36 [°]	М	, 21.5 -23. 0	21.94	0.712	0.148	3.246	23
	F	20.0-21.5	20.82	0.464	0.124	2.230	14
$32^{\circ} - 34^{\circ}$	м	° 21.0-22.5	21.70	0.570	0.255	2.627	5
	F	20.5-21.0	20.63			_~~	4
Baja	м	21.0-22.5	21.50	0.483	0.121	2.247	16
California	F	20.0-21.5	20.75	0.535	0.189	2.576	8

TARSUS LENGTH (in mm) IN PICOIDES VILLOSUS

Table 30

used here (Table 31) are not significantly different $(\underline{P} > 0.05)$. The Costa Rica and Panama samples were pooled but the means of the pooled sample are not statistically $(\underline{P} > 0.05)$ different from those of the pooled, southern Mexico, Honduras, Guatemala, and El Salvador group. The means of the latter sample are nearly as small as those of the Costa Rica and Panama samples which is caused by the presence of small individuals in El Salvador. Since the sample size is inadequate no tests of significance could be performed. However, those specimens have markedly smaller tarsi when compared to adjacent populations and a re-examination of the problem would be warranted should additional material become available. Fourrently it can only be speculated that the El Salvador sample has smaller tail, smaller exposed culmen, and smaller tarsi than those of the populations in adjacent areas.

All the samples used here display sexual dimorphism which varies from sample to sample.

2. Tarsus length: Group II

The means of the Cordillera and Colorado Plateau samples (Table 32) are significantly different ($\underline{P} < 0.05$). The Cordillera sample exhibits an increase in size along a south-north gradient (r=0.874 for males and 0.913 for females; $\underline{P} < 0.05$) and the difference between the means of the sub-samples are not significantly ($\underline{P} > 0.05$) different. Sexual dimorphism is present in both populations but is stronger in the Colorado Plateau individuals.

The large continental sample, east of the Cordillera, was

Region	Sex	Range	- Mean	SD	SE	CV	N
Central	м	19.0-22.0	20.18	0.578	0.092	2.864	39
Mexico	F	18.5-20.5	19.45	0.529	0.093	3.719	32
South	М	19.5-21.0	20.14	0.350	0.074	1.738	22
central	F	18.5-20.5	[.] 19.33	0.542	0.127 🧹	2.803	18
Mexico				c			•
S. Mexico,	м	18.0-20.5	19.23	0.673	0.127	3.499	28
Honduras, Nicaragua, Guatemala	F	18.0-20.0	18.69	0.548	0.107	2.931	26
Costa	м	18.5-19.5	19.25	0.379	0.084	1.968	20
Rica (a)	F	18.0-20.0	18.68	0.465	0.103	2.489	20
Panama (b)	м	17.5-20.5	19.18	0.798	0.178	4.161	20
	F	16.5-20.0	18.69	0.748	0.163	4.002*	21
8 Pooled	м	17.5-20.5	19.21	0.618	0.097	3,216	40
a and b	F	16.5-23.5	18.68	0.619	0.096	3.313	41

TARSUS LENGTH (in mm) IN PICOIDES VILLOSUS

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Table 31

Region	` Sex	Range	Mean	SD	SE	`CV	N
Mountains	M	21.0-25.0	22.92	0.651	0.047	2.839	184
,	F	20.5-23.5	22.14	0.627	0.058	2.831	`113
Colorado	м	20.5-23.0	22.10	0.668	0.092	3.020	53
Plateau	F	20.0-22.5	20.94	0.577 .	0.082	2.756	50

Table 32

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analyzed by comparing the means obtained in grouping specimens along latitude bands of five degrees from south to north, and then in blocks of five degrees of longitude, as described previously for the other parameters analyzed. The difference between the largest and the smallest means is 3.10 mm (13.2%) for males and 2.75 (12.0%) for females (Table 33). Variation takes place regularly along a southnorth gradient (r=0.981 for males and 0.958 for females; P < 0.01) and the difference between pairs of means is not significant (P > 0.05)except in the following bands: $45^{\circ}-50^{\circ}/40^{\circ}-45^{\circ}$, $40^{\circ}-45^{\circ}/35^{\circ}-40^{\circ}$, and $30^{\circ}-35^{\circ}/25^{\circ}-30^{\circ}$ for both sexes, and $60^{\circ}-65^{\circ}/55^{\circ}-60^{\circ}$ for females only. The "stepped" increases were found between the means of latitude bands where an east-west size gradient was recorded as follows: $45^{\circ}-50^{\circ}$ (r=0.718 and 0.834; P<0.05) west of 95° longitude west for both sexes; $40^{\circ}-45^{\circ}$ (r=0.834 and 0.794; P<0.01) west of 100° longitude west; 35°-40° (r=0.6932 and 0.7454; P<0.05) west of 95° longitude west. A slight increase in size from east to west was found also in the sub-samples of latitude bands $50^{\circ}-55^{\circ}$ and $55^{\circ}-60^{\circ}$ but the correlation is not significant (P>0.05). No increase in size westward could be detected in the $30^{\circ}-35^{\circ}$ latitude band.

Sexual dimorphism is well marked and varies from sample to sample and tends to be greater in the northern samples although no significant ($\underline{P} > 0.05$) correlation could be established between its magnitude and the geographical position of the sample.

The Newfoundland sample (Table 33) has significantly different (P < 0.05) means when compared to those of the $50^{\circ}-55^{\circ}$ latitude band sample. Those means are however similar (P > 0.05) to those of the

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TARSUS LENGTH (in mm) IN PICOIDES VILLOSUS

Latitude north	Sex	Range	Mean	SD	SE	CV	N
60 [°] - 65 [°]	м	22.0-25.0	23.54	0.828	Ø.230	3,. 518	13
	F	21.5-24.0	22.91	0.800	0.200	3.494	16
55 ⁰ (0 ⁰	v		22.46	0 720	0 107	2 067	3 4
<u> 55 - 60</u>	M F	22.3-23.0	23.40	0.720	0.132	1 677	14 8
	r	22.0-23.0	22.19	0.572	0.132	T.0//	0
$50^{\circ} - 55^{\circ}$	м	21.5-25.0	23.33	0.662	0.085	2.836	60
	F	21.5-24.0	22.36	0.761	0.124	3.406	38
~	-						
Newfound-	M	21.0-24.0	22.68	0.901	0.207	3.971	19 ·
land	F	21.0-24.0	22.59	0.688	0.172	3.047	16
$45^{\circ} - 50^{\circ}$	M	21.0-24.0	22.52	0.737	0.055	3.278	183
;	F	20.0-24.0	21.89	0.779	0.058	3.560	179
0 0		/		~			
40° - 45°	M	20.5-23.5	22.06	0.616	0.072	2.791	74
-	F	20.5-23.0	21.52	0.642	0.078	2.984	67
							,
35° - 40°	M	20.0-23.0	21.16	0.639	0.069	3.022	87
	F	19.5-22.0	20.64	0.570	0.087	2.763	43
			<u> </u>	0 501		0 771	<i>(</i>)
30° - 35°	M	19.5-22.5	20.97	0.581	0.073	2.//1	63
	F	19.5-21.5	20.42	0.505	0.078	2.4/4	42
250 200	м	10 5 91 F	20 44	0 494	0 101	2 269	22
25 - 30	M	19.5-21.3	20.44	0.404	0.101	1 02/	23 "
	< "	19.5-21.0	20.10	0.390	~ 0.003	1.734	22
200 - 250	м	19.5-20.5	19.83	0.407	0.128	2.052	10
(Rahamac)	ri T	17.5-20.0	18.68	0.700	0.194	3.748	13
(nationas)	r		10.00	51700	J 4 4 / 4	51740	
26 ⁰	M	19.5-21.5	20.42	0.615	0.205	3.011	9
(Bahamas)	F	18.0-20.0	19.05	0.687	0.209	3.607	11
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Table 33

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45⁰-50⁰ latitude band sample. Sexual dimorphism occurs in this sample but is much reduced.

The means of the males in the Bahama Islands samples (Table 33) are significantly different (P < 0.05) whereas those of the females are not separable (P > 0.05). Sexual dimorphism is present and stronger than in the mainland samples referred to Group II.

To summarize, tarsus length displays size variation along a south-north gradient, the longest measurements occuring in the northern parts of the range. A number of populations can be isolated from adjacent populations on the basis of tarsus length alone. The insular populations have tarsal lengths that are different from those of the mainland populations. Sexual dimorphism occurs for this character in all the samples examined and males have consistently longer tarsi than females.

3. Taxonomy

Since Oberholser's (1911) revision of the races of <u>Picoides</u> <u>villosus</u> several new forms have been described and Peters (1948) listed 21 across the range. Such a situation clearly indicates the variation recognized for a long time in this species. The results of this study, as demonstrated previously, emphasize the extent and delimit the range of variation for various characters. It was found, in addition to individual variation, that geographical variation occurs in populations mainly along gradients for color, color patterns, and various body measurements. Variation in body characters along geographical gradients was formally recognized in this species by

Ridgway (1914: 202-203) who pointed out the difficulty of delimiting the range of the various subspecies that he had been studying and expressed "his inability to offer a satisfactory treatment of the subject, which can only be done when the necessary material can be brought together". Some 50 years later, although the material assembled is adequate for most parts in the range the problem indicated by Ridgway still exists, at least for large areas in the species range.

Huxley (1939) used the term 'cline', which was widely accepted thereafter, to describe gradual variation in color, size, and other parameters, along certain gradients. Although the genetics and evolution of this type of variation is better understood now (Mayr 1970; Dobzhansky 1970) only little progress has been made towards a better understanding of this type of variation and its relation to environmental causes. Furthermore, clinal variation has yet to be recognized in many of the more 'plastic' species in which isolated populations have been described and recognized ever since.

Once identified, clines remain a problem for the practicing taxonomist. Hagmeier (1958) and Jolicoeur (1959) have pointed out the difficulty of reconciling this problem to the current subspecies concept. Based on the currently accepted taxonomic definitions and criteria (Mayr 1969) variational overlap in various characters between different populations is acceptable in the contact areas. It is usually possible to determine the presence (or absence) of character overlap (qualitative or quantitative) without too much difficulty with the present geographical isolates. On the other

hand it is often difficult (sometimes impossible) to delimit the present range of former populations when past isolates are considered and the amount of variational overlap that has taken place since these populations have been in contact. In the case of narrow intergradation areas the ranges of individual populations can be plotted but where intergradation takes place over wide areas and becomes clinal many of the characters, if not all, used in analyses may become taxonomically useless and add little to the comprehension of the problem.

The divisions recognized in the preceding parts of this study are based on the color of the under parts (Figures 3, 4, and 9) and correspond closely to several of the subspecific units described by various authors. The use of this important character, in combination with the color and color pattern of the upper parts, the caudal > pattern, the sides and flanks pattern and color, the facial pattern, and various body measurements permit a subspecific reevaluation of the taxa described for that species. Using the data obtained from the various analyses of variation it is now possible to provide a list of the subspecies which are considered to be acceptable in the light of the current taxonomic procedure (Mayr 1969).

The synonymy has been treated thoroughly by Ridgway (1914) and revised by Peters (1948). The latter's sequence is adopted here. Only the forms considered to be invalid and the names previously used in Peters (1948) will be listed here as synonyms. The other older synonyms are available in the works mentioned above, but especially in Ridgway (1914).

The range of the various subspecies and their areas of intergradation have been plotted on Figure 18. The following have been recognized on the basis of the information provided in the previous parts of this study:

Picoides villosus septentrionalis (Nuttall)

Dendrocopos villosus septentrionalis (Nuttall)

The largest and 'whitest' of all the populations examined, it occurs at the northwestern end of a long south-north cline. The reason for recognizing it as a separate taxon stems from the fact that a break in the size gradient appears just south of 50° latitude north and west of 75° longitude west. The purity of the white on various parts of the body and the amounts of white particularly in the dorsal pattern increase significantly in the same area. Even if it intergrades extensively with <u>villosus</u> and <u>monticols</u> over broad areas, it can be separated from those subspecies in the area designated on Figure 18.

Picoides villosus terraenovae (Batchelder)

This insular endemic population can easily be differentiated from any of the adjacent mainland populations on the basis of its dorsal color pattern which displays a greatly reduced amount of white and the presence of black bars on the white mid-dorsal stripe. The outer rectrices often have black markings (spots or bars) on the outer vane. The body measurements are not different from those

Dendrocopos villosus terraenovae (Batchelder)



Figure 18.

Distribution of the subspecies of <u>Picoides</u> <u>villosus</u>. Shaded areas indicate sectors of intergradation.

1. <u>septentrionalis</u>

2. <u>terraenovae</u>'

3. villosus

4. audubonii

5. piger

6. <u>maynardi</u>

7. picoideus

8. <u>harrisi</u>

9. hyloscopus

10. orius

11. monticola

12. leucothorectis

13. icastus

14. intermedius

15. jardinii

16. sanctorum

17. extimus

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of adjacent mainland populations.

Picoides villosus villosus (Linnaeus)

Dendrocopos villosus villosus (Linnaeus)

It occupies a central area east of the Rocky Mountains to the Atlantic coast between the large and 'very' white <u>septentrionalis</u> and the small and 'darker' <u>audubonii</u> with which it intergrades over vast areas. It intergrades also with <u>monticola</u> in the foothills and with <u>leucothorecthis</u> in the southwest. Although its coloration and size are intermediate between those of <u>septentrionalis</u> and <u>audubonii</u> the central core of the population presents homogeneous size and coloration characteristics. To the west the intergradation areas are narrow and present little difficulty. The main difficulty with this group is to define its range due to the broad zones of intergradation but using a combination of characters, it has been possible to define its range (Figure 18) and therefore to treat it as a separate subspecies on the basis of the high homogeneity of the characters found in the core area.

Picoides villosus audubonii (Swainson)

Dendrocopos villosus audubonii (Swainson)-

This subspecies is the smallest at the end of an extensive cline. It cannot be readily separated from <u>villosus</u> but the individuals found south of the area of intergradation (Figure 18) can be identified as <u>audubonii</u> on the basis of the darker color of the under parts and smaller measurements. Because the specimens from that area have highly homogeneous measurements and under parts color, it seems advisable to recognize the current taxon and limit its range to the area shown on-Figure 18.

Picoides villosus piger (G.M. Allen)

Dendrocopos villosus piger (G.M. Allen)

Similar in size to <u>audubonii</u> and <u>maynardi</u> this subspecies is endemic to Abaco and Grand Bahama islands. Its upper parts are on the average darker than those of either subspecies. The white of the under parts is tinged with a faint creamy wash. Black spots are regularly but not always found on the inner vane of the outer rectrices. The black markings of the flanks and sides of breast are heavier than in audubonji and maynardi.

Picoides villosus maynardi (Ridgway)

Dendrocopos villosus maynardi (Ridgway)

Endemic to New Providence and Andros islands it can be distinguished from <u>piger</u> by the pure white under parts and the reduced black markings of the flanks and sides of breast. No significant size difference was found between it and <u>piger</u> or <u>audubonii</u>. It resembles closely the latter.

Picoides villosus picoideus (Osgood)

Dendrocopos villosus picoideus (Osgood)

A well-defined endemic insular population (Queen Charlotte Islands) which is darker on the under parts than the adjacent

mainland populations. It has a barred mid-dorsal stripe and black markings (bars and spots) on the outer rectrices. The flanks and sides of breast are heavily marked with black. The various body measurements are not significantly different from those of the adjacent mainland populations.

Picoides villosus harrisi (Audubon)

Dendrocopos villosus harrisi (Audubon)

Dendrocopos villosus sitkensis (Swarth)

Although the northern segment of this coastal population is significantly paler and has slightly larger body measurements than the central and coastal samples, variation in this group is clinal and the area of intergradation between it, <u>septentrionalis</u> and <u>monticola</u> in the northern sector, takes place over a broad area. At the eastern periphery of its range intergradation with <u>monticola</u> and <u>orius</u> takes place in a narrow belt. The northern segment has been previously described as a different taxon, <u>sitkensis</u>, on the basis of its lighter under parts (Swarth 1911) when compared with specimens from Vancouver Island. In view of the fact that variation in this group is clinal both in mensural and color characters I see no valid reason to retain <u>sitkensis</u>, which is nothing more than an intergrade between <u>septentrionalis</u> and <u>monticola</u> and <u>harrisi</u> in the northern coastal area.

Picoides villosus hyloscopus (Cabanis and Heine)

Dendrocopos villosus hyloscopus (Cabanis and Heine) Dendrocopos villosus scrippsae (Huey)

The intergradation area between <u>harrisi</u> and <u>hyloscopus</u> is narrow and characters such as color of under parts, color pattern of upper parts, and body measurements change abruptly in central California. From Mendocino County southward to Baja California variation in all the characters examined is clinal (Figure 18). The population previously recognized as <u>scrippsae</u> is therefore treated as a synonym of <u>hyloscopus</u> from which it cannot be separated.

Picoides villosus orius (Oberholser)

Dendrocopos villosus orius (Oberholser)

This subspecies has 'whitish drab' or 'creamy white' under parts. The white areas of the dorsal areas are reduced in size and quantity, particularly on the wing coverts which often have more black than <u>monticola</u>. The body measurements are large. The range is confined for the most part to the mountainous regions and highlands of the Great Basin but extends north to southern central British Columbia (Figure 18). It intergrades with adjacent populations but the contact areas are narrow and limited.

Picoides villosus monticola (Anthony)

Dendrocopos villosus monticola (Anthony)

A large bird with pure white under parts and with much reduced white areas on the dorsal regions. It has large body measurements

which are acceptably homogeneous although variation in body size is clinal (Figure 18). It intergrades with <u>harrisi</u> over a broad area in the northwestern part of its range and with <u>septentrionalis</u> in the interior of the same area. To the south some intergradation takes place with <u>leucothorectis</u> but on a limited basis.

Picoides villosus leucothorectis (Oberholser)

Dendrocopos villosus leucothorectis (Oberholser)

This subspecies is very similar to monticola but has appreciably less white on the dorsal regions and significantly smaller body measurements. It intergrades with monticola in a restricted area. Intergradation with orius at the northwestern periphery of its range is somewhat more extensive and a few individuals have a light buffy suffusion on the under parts, otherwise they are typical (Figure 18).

Picoides villosus icastus (Oberholser)

Dendrocopos villosus icastus (Oberholser)

The coloration of the under parts and color pattern of the upper parts are very similar to those of <u>leucothorectis</u> but the body measurements are considerably smaller. On that basis it is different from the adjacent populations. The sample has homogeneous body measurements although these display a slight clinal variation from south to north, the smallest individuals being recorded in Coahuila (Mexico) (Figure 18).

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Picoides villosus intermedius (Nelson)

Dendrocopos villosus intermedius (Nelson)

The body measurements of this subspecies are significantly smaller than those of <u>icastus</u>. The under parts color is appreciably darker and the amount of white of the dorsal region is much reduced. It does not intergrade with any of the adjacent populations as far as I could determine it and seems to be restricted to the states of Tamaulipas, San Luis Potosi, Hidalgo, Nuevo Leon, eastern Guanajuato and Queretaro, extreme eastern Jalisco, and northern Vera Cruz (Figure 18).

Picoides villosus jardinii (Malherbe)

Dendrocopos villosus jardinii (Malherbe)

This subspecies has under parts that on the average are appreciably darker than those of <u>intermedius</u>. Its body measurements are slightly smaller than those of <u>icastus</u> and <u>intermedius</u> and much smaller than those of <u>sanctorum</u>. It intergrades slightly with <u>icastus</u> in the northwestern part of its range and with <u>intermedius</u> in Vera Cruz (Figure 18). The subspecies recognized here comprises the two forms described by Oberholser (1911): <u>Dryobates villosus</u> <u>enissomenus</u> and <u>hylobatus</u> which cannot be recognized as a result of the study of the current material. It displays a high degree of variation in the color of the under parts and the problem should be reexamined when additional material becomes available. Variation in body measurements appears to be clinal (east to west) and the specimens from Guerrero and Michoacan average slightly larger than

those from western Vera Cruz and northern Oaxaca. The specimens from the states of Mexico and Morelos (Huitzilac) are intermediate between the other two populations both in color of the under parts and in body size. It seems best to regroup these various populations under one subspecies, at least until additional material can be examined.

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Picoides villosus sanctorum (Nelson)

Dendrocopos villosus sanctorum (Nelson)

<u>Dendrocopos villosus parvulus</u> (Dickey and Van Rossem) <u>Dendrocopos villosus fumeus</u> (Oberholser)

From southeastern Mexico (Chiapas) to central Nicaragua, a slight cline was recorded but the various samples examined are however very homogeneous and statistically inseparable; from each other on the basis of their body measurements. The El Salvador specimens have considerably smaller tails, exposed culmens, and tarsi as pointed out by Dickey and Van Rossem (1929) who described the population as <u>parvulus</u>. Since the sample from El Salvador is too small, it seems preferable not to recognize the taxon at least until more material can be studied to determine the true affinity of that population (Figure 18). The coloration of this group is much darker than that of the population which occur north of it although a number of individuals have rather light under parts. This subspecies does not intergrade with adjacent populations since it is apparently ' completely isolated from jardinii in the area of the isthmus of Tehuantepec and from extimus from which it is separated by an important hlatus. The El Salvador specimens, along with those from the coastal Sierra Madre of Guatemala and southern Mexico (Chiapas) when available, should be examined as they may represent an isolated population with small body measurements and possibly darker under parts than <u>sanctorum</u>. Then the form <u>parvulus</u> may be reinstated if warranted.

Picoides villosus extimus (Bangs)

Dendrocopos villosus extimus (Bangs)

This subspecies is the smallest in general body size, except perhaps the El Salvador birds, and the darkest of the Middle American populations. Although some variation occurs in the color of the under parts and although the lighter individuals resemble <u>sanctorum</u>, this population is isolated (Figure 18) and does not intergrade with any other. No significant difference between the individuals from Costa Rica and those of Panama were recorded in either measurements, color of under parts, or dorsal color pattern. For these reasons those samples are treated as belonging to the same population.

B. VARIATION AND TAXONOMY OF <u>PICOIDES</u> <u>PUBESCENS</u> I. VARIATION IN COLOR AND COLOR PATTERN

1. Variation of under parts

In <u>Picoides pubescens</u> the color of the under parts varies from nearly pure white to sooty drab. Two main color divisions can be recognized on that basis: a) drab under parts (Division I) and b) white under parts (Division II). 'Drab' as defined here is similar

to the color referred to as "drab" by Smithe (1975). The geographic distribution of these color groups is shown on Figure 19.

A. Division I

This division comprises all the populations where 'drab' appears in any amount on the under parts. In those groups, 'drab' is dominant, but 'white' individuals may occasionally be present in those populations as well but are in minority.

'Drab' varies however in its components (from nearly white to snooty drab) and the following values have been obtained on specimens by visual matching, using the Munsell notation: 2.5 Y 3/2; 10 YR 4/2; 2.5 Y 5/2; 10 YR 7/2; 7.5 GY 5/2; 7.5 YR 4/3; 5.6 YR 4/5.

It proved to be practical to divide the large sample into smaller natural geographical units for analysis where a break was found in their distribution. These are shown on Figure 20. Because no sexual dimorphism in the color of the under parts could be detected all the specimens were examined in the same manner irrespective of their sex. Immature, badly worn, and soiled individuals were removed from the samples. In this large sample three distinct groups were recognized (Figure 19) as each one was found to occupy a distinct area based on the geographic distribution of the specimens examined. I have identified four color classes and their quantitative distribution is shown in Table 34 for each of the three main sub-divisions.

a) Sub-division I

Only 23 specimens were available and referred to this sub-division



Figure 19.

Distribution of four main groups of specimens of <u>Picoides pubescens</u> based on color of under parts: A) intermediate 'drab' to whitish; B) 'drab' to 'sooty drab' group; C) 'light drab' group. The dotted lines represent the limit of the range occupied by the groups with the highest frequencies of dark individuals, from south to north; and white group (light shading). The dotted line displays the approximate extent of penetration of 'drab' under parts individuals.





Figure 20.

Distribution of specimens of <u>Picoides pubescens</u> based on dorsal color pattern. Areas of intermediate conditions are darkened. The stippled area represents the darkest dorsal color classes and the dotted line, the region where the darkest color class is replaced in the central region by the next lighter class.

1



(Table 34). 'Pale drab' is dominant in this sample, whereas only two paler birds, 'whitish drab', were recorded from the Kenai Peninsula, Alaska. The specimens from Homer and Seward (Alaska) are among the darkest in the sample ('grayish drab') and the 'pale drab' individuals originate from Kodiak Island and adjacent coastal localities, and from Graham Island (Queen Charlotte Islands) where the species is not known to occur regularly. On the coastal mainland, the species has not been recorded opposite the Queen Charlotte Islands (Figure 19) and north of Kingcome Inlet (British Columbia). The under parts of the specimens from this area are intermediate in color between that of the current sample and those of Sub-division II. Additional collecting is therefore necessary to establish the relationships in this area. General variation in the under parts color on the coastal belt, from northern British Columbia to the western Alaska (Figure 19, a) thus takes place along a gradient from south to northwest (dark to pale).

b) Sub-division II

The range of the individuals referred to this sub-division is shown on Figure 19 (b). The darkest individuals ('sooty drab') come from Vancouver Island and adjacent coastal areas in Canada and the United States (Table 34). Paleness increases inland where the present population comes into contact with the adjacent populations with white under parts. The under parts become progressively paler to the north and to the south but 'sooty drab' individuals have been recorded in Mashington, Oregon, and northern California. On

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	'Whitish drab'	'Pale drab'	'Grayish drab'	'Sooty drab'	N
Sub-division I	8.7 (2)	69.6 (16)	21.7 (5)	0	23
Sub-division II	7.2 (12)	42.2 (70)	37.9 (63)	12.6 (21)	166
Sub-division III	45.7 (107)	31.9 (74)	22.4 (52)	0	232

Percentage distribution of color classes in Division I in <u>Picoides</u> <u>pubescens</u>. The number of specimens appears in parentheses.

Table 34

the other hand 'grayish drab' birds have been found from Vancouver Island and adjacent areas south to Marin County (California). The 'pale drab' individuals occur mainly on the mainland north of 🕔 Vancouver Island and inland. They are dominant in California south of San Francisco where they form a highly homogeneous population. In spite of the fact that 4 color classes have been recognized in this sample, it is characterized by a high degree of homogeneity when it is broken into smaller units, the darker individuals occuring mainly in a core on Vancouver Island and around the adjacent mainland. 'Pale drab' individuals become dominant near Nicasio and San Geronimo in Marin County, California. In Mendocino County (Sherwood) most of the individuals have 'grayish drab' under parts. The 'whitish drab' or palest individuals of the sample were recorded at inland stations such as Okanagan (B.C.) and localities to the south like Haywards, Boulder Creek, Crafton, Bray, and Alameda (California). Although it cannot be demonstrated very clearly 'lightness' in the under parts coloration increases mainly in two directions, the Vancouver Island region being in the core of darkest under parts: a) to the north, along the coast where it reaches the level of Sub-division I; b) to the south along the coast to central California. It is more difficult to define the area where the paler ('pale drab') individuals become dominant in this sample. This apparently takes place south of San Francisco and the specimens examined from the southern part of coastal California are readily separable from the rest of theindividuals from northern coastal California on the basis of their light under parts. Those birds display little individual variation and the sample is remarkably homogeneous.

c) Sub-division III

This sub-division occupies a broad geographical range (Figure 19) and three color classes have been recognized for the under parts (Table 34). The darkest color class is absent from this sample. It is restricted mainly to the southern area whereas the 'pale drab' group is intermediate in its coloration and geographical position between the other two groups recorded to the north and to the south (Figure 20).

The specimens from coastal North and South Carolina, Georgia, Alabama, southern Mississippi and Louisiana, southeastern Texas, and Florida, were referred for the most part to the 'grayish drab' color class (98%). Two specimens only, one from the southern coast of Georgia and the other from coastal Texas, were referred to the 'pale drab' group. The sample displays a high degree of homogeneity and occurs within boundaries which are sharply defined.

The sample from northern North Carolina, the southern half of Virginia, Tennessee (eastern and western), Kentucky, most of Arkansas, and central Texas can be described as 'pale drab'. It is homogeneous but to a lesser degree and lighter birds, 'whitish drab', were recorded in northern Texas, Kentucky, and northern Arkansas. It is difficult to delimit with accuracy the boundaries of this group ' in view of the small number of specimens available in comparison with the vastness of the area where this color class is dominant.

'Whitish drab' individuals occur in the northern part of the area of Division I (Figure 19, c) but the sample does not display the homogeneity observed in the other two groups and the presence of pure

white individuals is quite evident along the boundary between Division I and Division II. The Anticosti saland and Newfoundland samples have a high homogeneity in this character (whitish drab). Elsewhere the ratio of 'whitish drab' to white individuals is almost 3 to 1. Because of the dominance of this color class, the boundary line was drawn approximately where this proportion is maintained. North of it, in the sector where the proportion shifts in favor of white individuals, 'drab' birds are nevertheless recorded at considerable distance into the area defined as Division II (Figure 19, white, area below dotted line).

In summary, variation in this sub-division takes place from south (dark) to north (light) along a geographical gradient. Homogeneous coloration on the under parts can be defined in two sectors and the rest of the area occupied by this sub-division is intermediate between 'white' and 'drab' birds.

B. Division II

This division occupies a vast area in central North America (Figure 19) and comprises specimens with white under parts. White is generally 'pure white' north of the dotted line (Figure 19) and is 'less pure' south of it where the under parts are often washed medially with a faint grayish or buffy suffusion. Along the southern edge of the area occupied by this group a number of individuals with 'buff' on the under parts have been recorded but their percentage appears to decrease sharply northward. The 'whitest' individuals (quality and amount of white) have been found

in the northwestern sector (interior Alaska, northeastern British Columbia, Northwest Territories, and Yukon).

In summary, the specimens examined originating north of the dotted line of Figure 19 have 'purer' white under parts when compared to those from areas southwof that line. The change in the quality of the white appears to be gradual with a maximum in quality and quantity in the northwestern part of the range although it takes place in a relatively narrow band along that line. This situation therefore implies that variation in this character takes places along a geographical gradient, from east to northwest.

2. Variation of upper parts

The upper parts of <u>Picoides pubescens</u> vary both in color and color pattern. The color of the light areas of the dorsal regions is in general white, except in the coastal region of the West Coast where it often takes a color resembling that of the under parts but which is somewhat paler. In British Columbia (Figure 19, b) 67 per cent of the individuals with 'drab' under parts have 'drab' in various amounts and intensity in the light areas of the dorsal region. All the northern coastal British Columbia and coastal Alaska specimens have white in the light areas of the upper parts. Elsewhere across the range, the light areas of the dorsal regions, including those of the upper surface of the wings, are white.

The extent of the light areas, whether they are 'drab' or 'white', is highly variable across the range, particularly with regards to the rows of white dots of the upper wing coverts. This
character cannot be quantified singly. It was therefore found more practical to evaluate the amount of white in the dorsal regions by using five different classes as a reference, based on the amount of white on the upper wing coverts, on the primaries, and of the middorsal stripe and by 'scoring' in this manner each specimen. Thus the white areas of the wings (coverts and primaries) vary much in pattern but the variation is not related to the sex or geographical origin of the birds. In immature birds in the first plumage cycle (after postjuvenal molt) the white tends to be less pure and variously marked with blotches, vermiculations, and fuzziness at the edges.

Individual variation occurs in this character also, primarily in the shape of the light areas of the wing but no consistent pattern was observed.

The data obtained by assigning nearly 1,000 birds to the five coloration pattern classes recognized appear in Table 35. Class 1 represents the specimens with the largest amount of white whereas Class 5 has the least. Classes 1 and 2 are dominant in most of the samples but the former is absent from the Washington and Oregon, and California samples. Classes 3, 4, and 5 occur only in British Columbia, Alberta, Washington, Oregon, California, Nevada, Utah, Arizona, Idaho, Wyoming, Colorado, Montana, and New Mexico. A single individual from northwestern Texas was referred to Class 5. The range of Classes 4 and 5 is detailed on Figure 21, as well as that of Class 3 which was recognized mainly in areas where Classes 4 and 5 come in contact with Classes 1 or 2. The occurence of Class 1 is



Table 35.

Percentage distribution of dorsal pattern classes for various geographical areas in the range of <u>Picoides pubescens</u>. The number of individuals assigned to each class appears in brackets.

Region	Class 1	Class 2	Class 3	Class 4	Class 5	N
Coastal Alaska	82.6 (19)	17.4 (4)	e		-	23
Interior Alaska 🧠	80.8 (8)-	20.0 (2)				10
Northwest Territories	72.7 (8)	27.3 (3)				11
British Columbia	3.4 (3)	13.5 (12)	° 38.2 (34)	34.8 (31)	10.1 (9)	89
Washington, Oregon		7.6 (6)	24.1 (19)	46.8 (37)	21.5 (17)	79
California	1- 4	21.1 (28)	42.9 (57)	21.8 (29)	14.3 (19)	133
Alberta, Saskatchewan, Manitoba	36.8 (7) 🄽	10 . •5≪(2)		21.7 (4)	31.5 (6)	19
Nevada, Utah, Arizona, Idaho	3.6 (1)	21.4 (6)	3.6 (1)	57.1 (16)	14.3 (4)	28
Wyoming, Colorado, Montana,						
New Merico	20.8 (11)	28.3 (15)	18.9 (10)	18.9 (10)	13.2 (7)	53
N Dekote S. Dakota.						
Nebrecke Kengeg	87.5 (42)	12.5 (6)				48
Alabama Tayas	64.7(11)	29.4 (5)			5.9 (1)	17
Minnogota Wigcongin Towa	0,00 (==)	-				
Tilinoia	88 0 (22)	12.0 (3)		•		25
	71.7 (43)	28.3 (17)	_			60
Michigan Indiana, Ohio	68.8 (11)	31.2 (5)				16
Kontucky Arkangag Miggourt		• •	`			
Relicucky, Alkalisas, Missouri,	82 1 (32)	17.9 (7)			. '	39
Tennessee	02.1 (32)	10.0(2)		-		20
Louisiana, Mississippi, Alabama	88.9 (24)	11.1(3)				27
Vuebec	05.7(44)	4 3 (2)				46
Newroundland	JJ.7 (44)	413 (4)				
New Brunswick, Nova Scotia,	01 7 (00)	0 2 (2)			•	~ 24
Prince-Edward Island	91.7 - (42)	0.3(2)	r		₽	12
Maine, Vermont, New Hampshire	91.7 (11)	0.3 (1)				*-
Pennsylvania, Massachussetts,		٩				
Connecticut, New York, New	((-)	/->	~	×	•	. 67
Jersey, Rhode Island	92.5 (62)	7.5 (5)				07
W. Virginia, Virginia,						55
Maryland, D.C.	92.7 (51)	7.3 (4)				
S. Carolina, N. Carolina,						55
Georgia	96.4 (53)	3.6 (2)				20
Florida	97.4 (38)	2.6 (1)				27

DORSAL COLOR PATTERN IN PICOIDES PUBESCENS

Table 35

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highly consistent across the range, whereas Class 2 is less frequent in the southern part.

To summarize, birds with reduced light markings and areas on the dorsal regions occur in a well-defined sector in the species range. An intermediate group has been recorded between it and the area occupied by the birds with the greatest amount of white on the dorsum.

3. Variation of caudal pattern

A.

The central rectrices (No. 1) are normally totally black whereas the next pair (No. 2) has a varying amount of white at the tip of the outer vane which often extends onto the inner vane. The white portion is similarly located on the third rectrix but occupies a much greater area at the basal third of the feather. The amount of white (or 'buff') in these feathers does not vary geographically as far as I could determine it. Rectrices 4 and 5 are seldom completely white, this situation having been recorded only 6 times upon the examination of 1,233 specimens. These feathers are normally marked with dots,' spots, or bars, which are black and highly variable with regard to their size and quantity. It is possible to recognize three basic patterns based on the amount of black and the shape of the markings present on the outer two pairs of rectrices (Nos. 4 and 5). They are depicted on Figure 21 and each represent an average for the pattern class it illustrates.

Badly worn specimens, those missing the outer pair of rectrices, and immatures were eliminated from the compilation. Upon visual



Figure 21.

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Three rectrix patterns identified in analysis of variation of caudal pattern in <u>Picoides</u> <u>pubescens</u>. Each represent an average amount of black in each class.

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Table 36.

Percentage distribution of rectrix patterns in various regions in the range of <u>Picoides pubescens</u>. Number of individuals appears in brackets.

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RECTRIX PATTERNS IN PICOIDES PUBESCENS

Region	1		2	*	3) N •
Coastal Alaska	69.6	(16)	17.4	(4)	13.0	(3)	23
Interior Alaska	9.1	(1)	9.1	(1)	81.8	(9)	11
Northwest Territories			27.3	(3)	72.7	(8)	11
British Columbia	60.8	(59)	15.5	(15)	23.7	(23)	97
Washington, Oregon	53.4	·(31)	37.9	(22)	8.6	(5)	58
California	66.0	(68)	31.1	(32)	2.9	(3)	103
Alberta, Saskatchewan,							
Manitoba	17.4	(4)	17.4	(4)	65.2	(15)	23
Wyoming, Colorado,		• •				,	
Montana, New Mexico	3.8	(2)	9.6	(5)	86.5	(45)	52
Nevada, Utah, Arizona,							
Idaho	25.0	(4)	62.5	(10)	12.5	(2)	16
N. Dakota, S. Dakota,		• •					
Nebraska, Kansas	25.6	(11)	58.1	(25)	16.3	(7)	43
Oklahoma, Texas	5.9	(1)	88.2	(15)	5.9	(1)	17
Minnesota, Wisconsin,				ı			
Iowa, Illinois			96.0	(24)	4.0	(1)	25
Ontario	35.2	(19)	59.3	(32)	5.6	(3)	54
Michigan, Indiana, Ohio 👘	46.2	(6)	53.8	(7)			13
Kentucky, Arkansas,							
Missouri, Tennessee	10.3	(4)	84.6	(33)	5.1	(2)	39
Louisiana, Mississippi,		I	,	J			
Alabama	66.7	(6)	11.1	(1)	22.2	(2)	9
Quebec	14.3	(5)	85.7	(30)			35
Newfoundland	19.6	(9)	80.4	(37)			. 46
New Brunswick, Nova Scotia,							- Ala
Prince-Edward Island	13.6	(3)	86.4	(19)		*1	22
Maine, Vermont, New					,		
Hampshire, Pennsylvania,					e e		
Massachussetts,							
Connecticut, New York,							
New Jersey, Rhode Island	11.1	(8)	86.1	(62)	2.8	(2)	72
W. Virginia, Virginia,							r
Maryland, D.C.	12.7	(7)	83.6	(46)	3.6	(2)	55
S. Carolina, N. Carolina.						-	
Georgia	30.8	(12)	56.4	(22)	12.8	(5)	39
Florida	7.7	(3)	89.7	(35)	2.6	(1)	39
9							

Table 36

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examination, each specimen was referred to a pattern class. The data thus obtained appear on Table 36 and represent a total of 902 specimens.

Pattern 1 with the largest quantity of black accounts for 30.9 per cent of the sample, compared to Pattern 2 which comprises 53.7 per cent and Pattern 3 with 15.4 per cent of the specimens.

How variation in this character takes place is not very clear due to the overlap of the pattern classes recorded in the majority of the samples. The highest proportion of Pattern 1 occurs in the coastal samples of the western sector of the range. Small samples, such as that from Alabama, must be disregarded. Pattern 3 is dominant in the samples from Interior Alaska, the Northwest Territories, the northern half of the Prairie Provinces, and the Cordillera region. Although not dominant in the British Columbia sample (23.7%), taken as a whole, it reaches a higher percentage in the interior of the Province. Elsewhere, it has been recorded in small proportions in most of the samples. Pattern 2, intermediate between the other rectrix types, was found in all the samples and is dominant over a wide area of the range, primarily east of the Rocky Mountains and south of 55° latitude north. By plotting the distribution of specimens assigned to the various patterns, it was possible to outline three major areas where each type is dominant. These areas are detailed on Figure 22 and represent only an approximation of the range of these rectrix patterns.



Figure 22.

Grouped specimens of <u>Picoides pubescens</u> for analysis of mensural characters based on a combination of color characters and color patterns discussed in previous parts.



4. Variation of under tail coverts

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The under tail converts are usually marked with black blotches, spots, dots or stripes. These markings are usually located near the end of the feathers, nearly as often on or near the rachis as on the vanes. They are bolder in immature birds but not usually more numerous than in the adults. Birds with plain under tail coverts are rare, at least in the fresh plumage but the proportion increases somewhat in birds taken at a later time in the plumage cycle as the dark terminal markings tend to wear off, particularly prior to the following molt, which gives the impression that these feathers are plain. No sexual dimorphism could be recorded for this character and geographic variation was not identified. It appears that the presence or absence of these markings is purely a matter of individual variation as it occurs at random in all the populations examined.

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5. Variation of sides and flanks

The sides and flanks are usually plain in adult birds but in fresh plumage, just after a molt, the tips of many feathers in these regions often bears small terminal black marks. These markings which wear off later in the plumage cycle are usually heavier in the juvenal plumage and often extend medially. They disappear by abrasion and are replaced during the post-juvenal molt by plain feathers. No sexual dimorphism or geographic variation were noted in this character. 6. Variation of facial pattern

Variation in this character is limited to the white malar area which sometimes becomes 'buffy' particularly in those individuals of the West Coast with heavily saturated under parts. 'Buffy' coloration in the white malar area was recorded in less than 15 per cent of the 'buffy' individuals examined. Otherwise the malar area is pure white.

The nasal tufts are highly variable in color but are basically white across the range. However, they are often colored (yellow to deep reddish). This coloration is due to stains acquired in the process of digging into the substrate for food. Otherwise the only variation observed in the nasal bristles is in their length. After a molt they are long but abrasion considerably reduces their size until the next molt. No geographic variation was recorded in size or color of this character.

The width of the black facial markings is variable but this insignificant effect is due to individual, variation and is unrelated to geographic variation.

7. Variation of nuchal crest and crown

[°] Adult males have a bright red nuchal band which is always continuous. It varies from Geranium to Scarlet (Smithe 1975), and less often to Flame Scarlet. ['] The width and length of this band are variable also but I could not establish that it varies geographically. I therefore consider this the result of individual variation.

In adult females the red nuchal band is absent and sometimes replaced by white which varies from a touch to a well-defined band,

usually divided medially by a black area but no variation pattern other than individual variation could be established here either.

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Immature males do not have a red nuchal band but the feathers of the crown and forehead are tipped with red which varies much in hue and chroma. A number of feathers in this area are tipped with white. All those feathers are replaced during the post-juvenal molt by completely black feathers. This character does not vary geographically, at least in the material that I have examined. Immature females resemble juvenal males but lack the red which is replaced in the crown and forehead regions by white at the tip of feathers. The size of the white tips is highly variable individually. Those feathers are replaced also during the post-juvenal molt by typical adult black feathers.' This type of variation is not geographic.

II. VARIATION IN SIZE

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The specimens were examined for size variation in the following characters: body weight, chord of wing, length of tail, exposed culmen length, and tarsus length. The smallest body measurements were recorded in the southeast whereas the largest occur in the northwestern sector of the range and in the Cordillera region. Each character has been treated separately and the results appear in the following sections.

A. Variation in body weight

Only 38 body weight data were available to me from the sample examined. The majority come from the northeastern part of the

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species range (Quebec and Ontario). Each sex was treated separately and the following data were recorded:

	Range	Mean	SE ,	N
Males	24.2-31.2 g	28.11	0.403	20
Females	24.6-30.0 g	27.64	0.399	18

The means were compared (Student <u>t</u>-test) and did not prove to be significantly different (<u>t</u>=0.813; <u>P</u>>0.05). It appears therefore that sexual dimorphism does not occur in this character. It would have been very desirable to have weight data in sufficient number from all parts of the range in order to see if this character varies geographically to the same extent as the other body measurements, and to ascertain that the lack of sexual dimorphism in body weight is general across the range and not restricted to the sample examined here.

B. General variation in other body characters

The other body characters (chord of wing, length of tail, length of exposed culmen, and tarsus length) all display geographic variation. Those characters vary mainly along geographic gradients from south to north.

The samples were first grouped on the basis of their under parts color and the following main groups have been recognized (see section on under parts variation): a) the Pacific Coast group with dark 'buffy' under parts and b) the light 'buffy' or white under parts in the pemaining part of the range. The second group was further divided into two sub-samples on the basis of the dorsal color pattern of the

specimens, as pointed out earlier. The Cordillera sub-sample can in this manner be segrated from the rest of the large sample (Figures 20 and 22). The mensural characters selected were then examined for size variation on the basis of those groupings.

I. Variation in wing length

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The data on wing length measurements are presented in Tables 37, 38, and 39 and comprise a sample of 1,059 specimens from all parts of the range.

The sample from western coastal North America (from southern Alaska to southern California) can be separated into two sub-samples on the basis of the darkness of the under parts: a) darker under parts: from British Columbia and southern coastal Alaska to central California; b) lighter under parts: from interior Washington and Oregon, interior California, and southern California (Table 37). The Marin County (California) specimens have under parts intermediate in coloration between those of these two groups, and for that reason were separated into a different sub-sample. Wing length increases slightly from south to north in the Pacific Coast sample (Table 37) in both sexes (males: r=0.699, df.=5, P>0.05; females; r=0.657, df.=5, P>0.05) and the correlation between latitude and wing length increase is not significant.

The means of all the sub-samples, including those of coastal Alaska, were compared for each sex, from north to south, and the difference between each pair of means did not prove to be statistically different (P < 0.05) except for the females of coastal

Region	Sex	Range	Mean	`SD-ø	SĔ	cv	N
Coastal	м	91.0- 99.0	95.62	2.844	0.789	2.975	13
Alaska	F	89.0-100.0	96.10	3.178	1.005	3.307	10 _
British	м	92.0-100.0	96. 38 ⁷	2.214	0.418	2.297	28
Columbia	F i	93.0- 98.0	96.00	1.651	0.477	1.720	12
Coastal	м	92.0-101.0	96.31	·2.810	0.779	2.918	`14
Washington	F ,	93.0-101.0	96.64	2.274	0.608	2.353	14
Coastal	м	94.0-102,0	95.76	1.437	0.349	1.501	17
Oregon	F	93.0-100.0	97.78	2.489	0.830	2.545	9
Coastal	M	90.0-100.0	94.09	3.448	1.040	3.665	11
northern California	F	91.0-100.0	95.27	2.915	0.753	3.059	14
Pooled	м	90.0-102.0	95.38	4,345	0.476	。 4.555	83 -
northern samples	F	91.0-101.0	96.20	2.584	0.336	2.685	59
Marin	М	90.0- 95.0	92.85	1.631	0.365	1.757	20
County (California)	F	93.0- 97.0	94.07	1.385	0.370	1.472	14
Tratantan	v	»	07 60	2 2 701	0 675	2 765	16
Washington and Oregon	F	96.0-101.0	97.09 98.00	2.449	0.775	2.499	10
P	•		•				
Interior	м	89.0-100.0	92.80	3.167	0.818	3.412	15
California	F	89.0- 99.0	94.40	3.291	0.850	3.486	15
Southern	М	· 88.0- 95.0	91.14	1.922	0.357	2.109	29
California	F	` 90.0- 96.0	93.17	2.125	0.613	2.281	12
Pooled	M	88.0-102.0	93.07	3.615	0.487	3.884	60
southern	F.	89.0-101.0	94.8 5	3.403	0.584 、	3.588	37

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES PUBESCENS

Table 37

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and interior samples 220

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northern California dompared to those of coastal Oregon. The difference between the means of the interior Washington and Oregon is highly significant for both series when compared to those of interior and southern California. The means of the latter sample are comparable to those of coastal Oregon ($\underline{P} > 0.05$). The Marin County (California) samples are not significantly different ($\underline{P} > 0.05$) from those of interior or southern California but are significantly different ($\underline{P} < 0.05$) from the pooled northern samples. All those samples display an acceptable degree of homogeneity as indicated by their low coefficient of variation. The northern samples (pooled) have means that are statistically different (\underline{t} =3.41 for males; \underline{t} =2.23 for females; $\underline{P} < 0.05$) from the southern and interior (pooled) samples (Table 37).

Co

^o Sexual dimorphism occurs in the two pooled samples and is reversed, the females having a longer wing than the males but the difference is significant (P < 0.05); t=2.31) in the southern sample only.

The sample from the Cordillera region and southwest interior displays a reduction in the amount of white in the dorsal region. It has been broken into 4 smaller sub-samples. (Table 38) which are all acceptably homogeneous. The individual sub-samples exhibit an increase in size from north to south, contrary to what has been observed in the other samples, but the correlation between wing length and latitude is not statistically significant (P > 0.05). The difference between the means is statistically significant (P < 0.05) for males in the Washington, Oregon, etc., and the Nevada, Utah, and Colorado samples (Table 38). In females, the British Columbia and

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES PUBESCENS

Region	Sex	Range	Mean	SD	SE	CV	N
British	м ,	95.0-103.0	97.93	2.400	0.641	2.450	14
Columbia, Alberta	F	95.0-101.0	97.60	1.796 °	0.401	1.840	'20
Е.	м	94.0-103.0	98.83	2,205	0.348	2.231	40
Washington, E. Oregon, Idaho, Montana, W. Wyoming	F	93.0-104.0 `	99.29	2.180	0.419	2.195	27
E. Nevada.	м	98.0-103.0	** 100.88	1.884	0.666	1.867	8
Utah, W. Colorado	F	101.0-103.0	101.75				49
Arizona.	м	98.0-105.0	100.25	2.050	0.591	2.044	12
New Mexico,	F	93.0-100.0	97.40				5
and NW Texas		·	, ⁹	e e	·	I	
Pooled '	м	94.0-105.0	99.11	2.338	0.271	2.359	74
samples	F	93.0-104.0	98. 70	/ ^{2.367} .	0.316	2.398	56
1	,	•			•		Ψ.

Table 38

Alberta sample has a statistically different mean (P < 0.05) when compared to that of Washington, Idaho, etc. no significant difference between means was observed in the other cases. Sexual dimorphism was recorded in all the samples but could not be tested statistically in all of them due to inadequate sample size. Females display a longer wing in two of the sub-samples but the difference between the two means are not significant (P > 0.05). In the other cases males have similar wing lengths. A similar situation occurs in the pooled sub-samples (Table 38) where the males have longer wings, but the difference is statistically non-significant (P > 0.05). The means of the Cordillera and southwest interior sample, when compared to those of the Pacific Coast samples (Table 37) is significantly different for both sexes (P<0.05). Furthermore, (Table 38) significant différences (P < 0.05) were found also between the means of males and females and those of all the samples with which its range is adjacent.

In the last large sample, detailed in Table 39, wing length increases markedly for both sexes from south to north and the correlation with latitude is highly significant ($\underline{P} < 0.001$; df.=12; $\underline{r}=0.930$ for males and 0.931 for females; df.=12; $\underline{P} < 0.001$), using the mean of each sub-sample against its average latitude. On the other hand, sub-samples tests were too small to detect increases in size from east to west. A slight size increase was however recorded along longitude in three sub-saples (1, j, and k) but the difference between the means for each 5 degree block is not significant nor is the correlation ($\underline{P} > 0.05$) obtained from east to



Table 39.

a Alaska and Yukon

b 'Northwest Territories

- c Alberta, Saskatchewan, and Manitoba
- d Ontario
- e Quebec
- f Newfoundland
- g Maritime Provinces and Maine 🧹
- h New Hampshire, New York, Rhode Island, Massachussets, and Vermont

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i New Jersey, Connecticut, Pennsylvania, Illinois, Ohio, Indiana, Iowa, and Nebraska

j Michigan, Wisconsin, North and South Dakota, and Minnesota

k Maryland, West Virginia, Virginia, D.C., Kentucky, Missouri, and Kansas

1 North Carolina, Tennessee, Arkansas, and Oklahoma

- m South Carolina, Georgia, Alabama, Louisiana, Mississippi, and Texas
- n Florida

Sample	Sex	Range	Mean	SD	SE	CV	N
a	М	96.0-101.0	98.71	1.603	0.606	1.623	7
I.	Ę	97.0-102.0	99.00			1945 - 1945 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 - 1946 -	3
Ъ,	М	96.0-101.0	98.14	1.670	0.633	1.707	• 7
	F	97.0-100.0	<u>)</u> 99 . 00				4
с	М	92.0-102.0	· 96.03	2.499	0.464	2.602	29
	F	91.0-100.0	96.65	2.047	0.373	2.117	30
đ	м	92.0-100.0	95.51	1.965	0.310	2.057	40
,	F	91.0-100.0	95.73	2.307	0.452	2.409	26
e	۳ M	. 92.0-99.0	94.81	1.691	0.369	1.783	21
*	F	91.0-99.0	94.91	2.256	0.680	2.377)_ 11
f	м	90.0-99.0	94.15	1.804	0.353	1.916	26
	F	93.0-99.0	95.29	1.553	0.338	1.629	21
\$ g	M	93.0-98.0	95 . 42	1.729	0.499	1.812	12
,	F	93.0-98.0	95.83	1.531	0.395	1.597	1.15
h	м	90.0-98.0	93.96	2,084	0.401	2.217	27
	F	90.0-98.0	94,43	1.832	0.399	1.940	21
1	M	90.0-97.0	93.67	1.806	0.329	1.928	30
κ.	F	91.0-100.0	94.33	1.961	0.377	2.078	- 27
j	м	92.0-102.0	96.73	2.897	0.617	2.995	22
· · · ·	F	91.0-101.0	97.33	2.894	0.747	2.973	15
k	M ·	87.0-97.0	91 .9 5	2.172	0.292	2.362	55
、"	F	88.0-99.0	93.80	2.137~	0.302	2.278	50 *
1	M	88.0-96.0	91.41	2.061	0.396	2.254	27
	F	87.0-97.0	92.20	2.966	0.663	3.216	20
m	·M	84.0-96.0	89.77	2.311	0.348	2.574	44
_	F	87.0-95.0	90.19	2.320	0.446 /	2.572 [.]	27
n	, W	, 84.0-93.0	88.18	2.789	0.676	3.162	17.
• ,•	F	86.0-93.0	89.18	1.991	0.424	2.232	22

CHORD OF WING MEASUREMENTS (in mm) IN PICOIDES PUBESCENS

Table 39

west along longitude. The difference between the means of the following pairs proved to be significantly (P<0.05) different: b-c, f-g, 1-m, and m-n, for males; and 1-m, for females. In spite of the fact that several samples have statistically_different means I cannot successfully determine trends in wing length for both sexes, except that it increases in size along a geographical gradient from south to north and at the western edge of the range in three samples (1, j, k; Table 39). It is possible however to separate this large sample into 4 homogeneous groups on the basis of their wing length from the data of Table 39, as follows: 1) a and b: a long-winged group in the northwestern part of the range; 2) c,d,e,f, and g: a slightly shorter-winged group in the northern part of the range; 3) h,i,j,k, and 1: a medium-length wing group in the central part of the range; and 4) m and n: a short-winged group at the southern extremity of the species range. Differences in the means of those grouped samples are statistically different (P<0.05).

Sexual dimorphism occurs and is reversed in all the samples, females having a longer wing than males. The difference between the means is however not statistically different (P> 0.05) in most cases, such a statistically significant difference having been recorded in only 4 samples only (b,f,k, and n; Table 39).

In summary, the northern Pacific coast sample (pooled) can be separated from the interior and southern coastal samples (pooled) in having statistically different wing length means. Sexual dimorphism occurs in all the coastal samples but is statistically significant in the southern sample only. The Cordillera and southwestern samples

`\\	TAIL	MEASUREMENTS	(in mm)) IN	PICOIDES	PUBESCEN
	, \	ç				ι,

Region Sex SD SE CV I - N Range Mean 0.842 4.505 11 62.00 2.793 Coastal М 58.0-67.0 Alaska F 59,0-69.0 63.44 3.468 1.156 5.466 9 . 57.0-69.0 0.658 26 British М 61.67 3.355 5.441 0.392 F 59.0-63.0 60.91 1.300 2.134 11 Columbia coastal 57.0-64.0 1.664 0.462 2.799 13 М 59.46 Coastal F ¿ 0.569 14 Washington 57.0-66.0 61.07 2.129 3.486 0.523 14 Coastal М 54.0-61.0 58.14 1.956 3.363 F 56.0-63.0 59.89 2.522 0.841 4.211 9 Oregon 2.208 0.637 3.931 12 ** Coastal М 54.0-60.0 56:17 northern -F 54.0-63.5 59.00 2.506 0.607 4.247 14 California 5.467 76 54.0-69.0 59.90 3.275 . 0.375 Pooled М 4.568 57 northern F 54.0-69.0 60.79 2.777 0.367 samples 55 🚯 3.368 Marin Μ 52.0-60.0 1.882 0.432 19 2.349 F 56.86 0.628 4.131 14 County 54.0~61.0 (California) 2.272 0,568 3.706 16 М 56.0-65.0 61.31 Interior 62.00 2.563 0.906 4.135 10 Washington F 57.D-67.D and Oregon 12 3.025 0.873 5.370 Interior 51.0-61.0 56.33 М 15 4:220 .California F 54.0-61.0 56.27 2.374 0.613 0.619 20 Southern ` М 50.0-60.0 55.25 2.770 5.013 California F 53.0-60.0 57.25 2.765 0.977 4.829 10 ĥ 51.0-65.0 58.59 3.487 0.509 5.951 48 Pooled 0.574 5.862 35 southern F 52.0-67.0 57.89 3.394 and interior ÷ samples

Table 40

display a non-significant increase in wing length from north to south and sexual dimorphism is not significantly marked in favor of the males. The means of those samples are statistically different from those of adjacent areas for both sexes. The large sample, east of the Cordillera, displays a marked increase in size along a geographical gradient from south to north, and to lesser extent from east to west. Reversed sexual dimorphism occurs in this sample also but is usually not significant. Four groups with homogeneous wing lengths can be separated from the data of Table 39 and have been detailed above.

II - Variation in tail length

I have followed here the same procedure as that used in the analysis of wing length variation and divided the total sample on the basis of the under parts and dorsal coloration pattern. The rectrices undergo rapid wear as in all woodpeckers and for this reason specimens displaying excessive wear were eliminated. Tail length varies geographically along a gradient from south to north. Sexual dimorphism occurs but appears to be negligible.

The data of the first sample are summarized in Table 40. This character increases along a geographical gradient from south to north and the correlation between tail length and latitude is statistically significant for both sexes (r=0.893, males; r=0.902, for females; df.=7; P < 0.01). In males the mean of the coastal Alaska sample is not significantly different from that of coastal British Columbia whereas the latter is statistically different (P<0.05) from that of

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Region	Sex	¥	Ratte	Mejan	SD	SE	CV	N		
	1				<u>с</u>					
British	М		57.0-68.0	62.03	2.538	0.704	4.091	13		
Columbia,	F		55.0-67.0	62.69	3,627	0.906	5.785	16		
Alberta	1		*	i	·	· ·		X		
E.	M		55.0-67.0	62.03	2.974	0.470	4.794	40		
Washington.	F		56.0-68.0	61.92	2.857	0.583	4.614	24		
E. Oregon.	-		, ,							
Idaho.	٠									
Montana W			• ,							
Wyoming	1	1	•		1					
E'. Nevada.	M-		62.0-67.0	64.43	1.718	0.649	2.666	7		
Utah. W.	F	,	65.0-68.0	66.33				3		
Colorado j	-		\ \			υ	t	ι		
Arizona.	M,		58.0-66.0	62.58	3.088	0.891	4.934	12		
New Mexico, and NW	F		60.0-66.0	62.00			دی هه هم هم _ا ین	4 .		
TEYdo			· -							

TAIL LENGTH (in mm) IN PICOIDES PUBESCENS

M 55.0-68.0 62.35 2.861 0.337 F 55.0-68.0 62.47 3.468 0.464

4.588 72 5.092 .47

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Pooled samples

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Table 41

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coastal Washington, which in turn is inseparable from the coastal Oregon mean. On the other hand the coastal California samples has a statistically different mean when compared to that of coastal Oregon. In females, the means of coastal Alaska and British Columbia only are significantly different (P < 0.05) from each other, all the others are inseparable statistically. Sexual dimorphism was recorded at a significant level (P<0.05) only in the coastal Washington and coastal California samples, where females have longer tails than males. In the other samples, sexual dimorphism is reversed also but does not attain a statistically significant level. In coastal British Columbia, males have longer tails. The Marin County (California) specimens have means (males and females) significantly smaller than those of the pooled northern samples and those of the pooled southern samples. Those means are however not significantly different from those of the interior California and southern California samples. Sexual dimorphism is reversed also in the sub-samples, except in that from interior California (P < 0.05) in which males have longer tails. The means of the pooled samples are significantly different from each other for both sexes. Sexual dimorphism is reversed in the southern pooled sample but the difference between each set of means is not statistically different.

The Cordillera and southwest interior sample (Table 41) is homogeneous. No significant difference was recorded between the means of each sub-sample except for those of Nevada, Utah, and Colorado which are significantly different from both the Washington, Oregon, Idaho, etc., and the Arizona, New Mexico, and Texas samples.



Table 42.

a Alaska and Yukon

b Northwest Territories

c Alberta; Saskatchewan, and Manitoba

d Ontario

e Quebec

f .Newfoundland

g Maritime Provinces and Maine

h New Hampshire, New York, Rhode Island, Massachussetts, and Vermont

i New Jersey, Connecticut, Pennsylvania, Illinois, Ohio, Indiana, Iowa, and Nebraska

j Michigan, Wisconsin, North and South Dakota, and Minnesota

k Maryland, West Virginia, Virginia, D.C., Kentucky, Missouri, and Kansas

1 North Carolina, Tennessee, Arkansas, and Oklahoma,

m South Carolina, Georgia, Alabama, Louisiana, Mississippi, and Texas

Florida

·	c ²	o ²									
Sample	**Sex	Range	Mean	✓ SD	SE	Č CV	N				
··=_···		1.4 • • • •		······································		5 •					
a	M	63.0-69:0	65.14	1.864	0.704	2.861	7				
	F	64.0-73.0	67.67	يتبله سندويه ويود مليه	یسی ریڈی ملک میں جات	 ,	3				
Ъ	M	56.0-69.0	63.00	4.647	1.897´	7.376	6				
	F	64.0-66.0	64.75		/		4				
с	М	58.0-68.0	61.67	2.873	0.563	4.658	26				
	F	57.0-67.0	63.10	3.072	0.602	4.868	26				
ď.	м	53.0-63.0	59.63	2,683	0.460	4.499	34				
	F	55.0-63.0	59.57	2.312	0.482	3.881	23				
е	М	56.0-62.0	58.71	1.677	· 1 0.365	2.856	21				
-	_ F "	55.0-61.0	59.10	2.282	0.721	3.861	10				
f °	M	56.5-64.0	59.82	1 941	0 388	1- 3 244	25				
-	F	58.0-63.0	60.60	1.959	0.427	3.232	21				
Ø	м	57.0-63.0	59" 50	1 057	0.618	. 08.9-4	10				
о	°F	56.0-68.0	60.27	, 2.218	0.572	3.680	15				
b	M	54.0-63.0	57.09	2 376	0 506	4 106	? ?				
••	F	54.0-64.0	58.41	2.785	0.675	4.767	17				
, 1	M	° ' 53.0-61.0	57.42	2,283	0.447		26				
-	·F	53.0-62.0	57.44	2.930	0.586	5.100 ⁵	25				
i	M	56.0-67.0	60.86	2.987	0.651	4. 908	21				
5	F	55.0-64.0	59.50	2.954	0.789	4.964	14				
k	м	51.0-59.0	55.08	2,230	0,328	4.048	46				
	F	52.0-62.0	57.11	2.630	0.392	4.605	45 ⁴⁵				
1 。	r M ⁻	50.0-57.0	·. 53.59	2,217	0.472	4,136	22				
	F	50.0-60.0	55.32	2.809	0.644	5.076	19				
tn	м	50.0-57.0	52.77	2.005	0.321	3.799	30				
•	<u>ج</u>	52.0-58.0	53.75	2.488	0.507	4.628	24				
n	м	50.0-55.0	52.46	1.761	0.488	3.356	12				
	• F	50.0-57.0	53.68	2.262	0.519	4.213	19				

TAIL LENGTH (in mm) IN PICOIDES PUBESCENS

Table 42

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Although sexual dimorphism could be verified in two sub-samples only and in the pooled samples the difference between male and female means are not significant ($\underline{\hat{P}} > 0.05$). When the means of this sample were compared to those of the northern coast and southern and interior samples, they are significantly different ($\underline{P} < 0.05$) in both cases.

The other large sample (Table 42) indicates that variation in tail length takes place along a south-north gradient, the longesttailed individual occuring in the northwestern sector of the species There is a high correlation for both sexes between tail range. length and latitude (r=0.942, males; and r=0.962, females; df.=12; P<0.001). In males, significant mean differences were found between pairs of means (Table 42) as follows: a-b, b-c, c-d, and e-f for males; and g-h for females. Elsewhere no significant differences between means were recorded. The largest sub-samples were tested also for a possible increase in tail length from east to west by breaking them into smaller sub-samples of 5 degrees of longitude. Although a slight increase in size towards the west was recorded in Iowa and Nebraska, the size of the samples analyzed was not sufficient to reach any conclusion. It appears therefore, from the male tail measurements, that a group with longer tails can be delimited in Alaska, Yukon, and the Northwest Territories. Other groups may be segregated on the basis of tail measurements also in the Prairie Provinces, Ontario, and Quebec." Elsewhere, the increase in tail length from south to north is continuous. Sexual dimorphism occurs in all the sub-samples but the difference in means is significant (P < 0.05) only in the following sub-samples: k_{x} 1, m, and n. In
those, females have longer tails. Males with longer tails, but not significantly longer ($\underline{P} > 0.05$), have been found in sub-samples, c, d, and j (Table 42).

In summary, tail length varies geographically with a general increase from south to north. Males usually have longer tails but reversed dimorphism has been recorded in a few instances at a statistically significant level. On the Pacific coast, the northern populations can be isolated from the southern and interior California samples on the basis of their wing length. The Cordillera and southwest interior sample is separable also from adjacent populations on that basis. The very large sample, originating east of the other two groups, displays a continuous increase in tail length from south to north. The populations north of 45° latitude north can be statistically separated among themselves and from all the others found to the south on the basis of their longer tail.

III - Variation in bill length

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The analysis of bill length variation is based on the length of the exposed culmen taken according to prescribed methods. Bill length varies geographically and sexually. The largest means are found in the Cordillera region and in the northwestern parts of the species range, whereas the shortest-billed individuals have been recorded in the southeastern sector. Exposed culmen length ranges from 13.0 to 18.6 mm. The procedure for grouping samples has been described in the previous parts of this study.

In the Pacific coast sample (Table 43), although bill length

EXPOSED	CULMEN	LENGTH	(in	mm)	IN	PICOIDES	PUBESCENS

	Region	Sex	, Range	Mean	SD	SE	CV	N
	Coastal	м	15.0-17.0	15.92	0.862	0.239	5.416	13
	Alaska	F	15.5-17.5	16.30	0.587	0.186	3.601	10
	Coastal	м	13.5-18.0	15.82	1.132	0.214	7.156	28
	British	F	13.5-18.0	14.90	1.350	0.427	9.060	10
υ	Columbia	•		L.				
	Coastal	м	15.0-16.0	15.50	0.408	0.113	2.634	13
	Washington	F	14.0-17.0	15.32	0.890	0.238	5.811	13
	Constal	м	15 0-18 0	16 44	0 946	0.237	5.758	17
	Oregon	F	15.0-18.0	16.56	1.014	0.338	6.124	9
	0	v	16 0 19 0	17 05	0 799	0 227	1 622	11
	Coastal	M	16.0-18.0	17.03	0.760	0.237	4.023	15
	northern California	F	15.0-18.0	10.05	0.741	0.105	4.437	15
	Pooled	м	13.5-18.0	16.07	1.018	0.112	6.333	82
	northern samples	F	13.5-18.0	15.97	1.154	0.152	7.224	57
	Mania	, M	15 5-17 5	16 40	0 503	0 112	3,064	20
	County	F	13.5 = 17.5 14 5 = 17.0	15.64	0.569	0.152	3.639	14
	(California)		14.5 17.0	13104	•••••			
	Interior	м	13.5-17.0	15.00	1.140	0.285	7.601	16
	Washington and Oregon	F	13.5-16.5	14.39	1.112	0.371	7.727	9
	Interior	М	15.5-17.0	16.17	0.880	0.227	5.441	15
	California	F	14.5-18.5	16.03	1.343	0.347	8.373	15
	Southern	м	15.0-18.5	15.60	1.003	0.186	6.431	29
;	California	F	14.5-17.5	15.41	0.970	0.292	6.295	11
	Pooled	м	13.5-18.5	15.68	1.038	0.139	6.617	60
	southern and interior samples	F	13.0-18.5	15.47	1.369	0.238	8.849	35

Table 43

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17(3)

appears to be increasing along a gradient from north to south the data obtained indicate that the correlation between exposed culmen length and latitude is statistically non-significant for both sexes (r=0.265, males; r=0.023, females; df.=7; P>0.05). The means of the sub-samples are not statistically different except for makes of coastal Washington and coastal Oregon. In females, the samples of coastal Alaska and coastal British Columbia, of coastal Washington and coastal Oregon, and interior Washington and Oregon, and interior California are all statistically separable (P < 0.05) from each other. In the Marin County (California) sample the mean is significantly different (P < 0.05) from both that of the northern pooled and southern pooled samples. Female means are not significantly different in those samples. Sexual dimorphism occurs in all the samples, males usually having a longer bill than the females, but the difference is not significant except in the coastal Washington and Marin County samples. Reversed dimorphism was recorded at a non-significant level in the coastal Alaska and coastal Oregon samples.

In the Cordillera and southwest interior sample (Table 44) bill length increases along a north-south gradient but the correlation between the length of the exposed culmen and latitude is not significant for either sex (r=0.695, males; r=0.766, females; df.=2; P>0.05). For males and females the difference between each pair of means is not significant (P>0.05) except for the males of Washington to Wyoming when compared to those of Nevada, Utah, and Colorado. Sexual dimorphism occurs in all the samples and the males have longer bills, although the difference between each set of means

Region	Sex	Range	Mean	SD	⇒ SE	CV	N
British	M	14.5-18.6	15.97	1.322	0.353	8.277	14
Columbia, Alberta	F	13.0-18.5	15.24	1.446	° 0.331	9.490	19
Ε.	м	13.5-18.5	15.60	1.265	0.197	8.110	41
Washington, E. Oregon, Idaho, Montana, W. Wyoming	F	13.0-17.5	15.59	1.293	0.248	8.292	27
E. Nevada,	М	15.5-18.0	16.63	1.187	0.419	7.139	8
Utah, W. Colorado	F	16.0-17.0	16.50	`			4
Arizona,	М	15.0-18.0	16.50	1.140	0.343	6.909	11
New Mexico and NW Texas	F ,	15.0-17.5	16.00			~~~~	5
Pooled	м	13`5-18.6	15:91	1,291	0.150	8,112	74
samples	F	13.0-18.5	15.57	1.306	0.176	8.386	`55

EXPOSED CULMEN LENGTH (in mm) IN PICOIDES PUBESCENS

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Table 44

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is not significant ($\underline{P} > 0.05$). The means of this sample did not prove to be different from those of the northern coastal sample nor from those of the southern coastal and interior sample for both sexes.

In the large sample of the eastern part of the range (Table 45) the difference between the largest and the smallest mean is slight, being 0.97 mm for males and 1.58 mm for females. No variation trend could be detected in the 14 samples analyzed, except that the means of the two southernmost groups (m and n) are significantly different (P < 0.05) from those that occur north of them. The larger samples were tested for a possible size increase along a gradient from east to west but the correlations were statistically non-significant. Exposed culmen length does not therefore appear to vary in any direction in this sample. Sexual dimorphism occurs in all the samples and males usually have longer bills. Significant differences (P < 0.05) were found in the following samples: d,k, and n. Females display longer bills in 4 samples (a,b,e,f,) but significant differences between means (P < 0.05) were recorded only in samples e and f (Table 45). It appears therefore that bill length is a highly stable character in spite of the large geographic area occupied by the sample for which important variation has been noted in other characters.

To summarize, bill length does not vary along geographical gradients to the same extent as the other characters examined, and is relatively stable, particularly in the large sample of eastern North America. Significant differences between means were found in



Table 45.

a Alaska and Yukon

b Northwest Territories

c Alberta, Saskatchewan, and Manitoba $\sqrt{\ell}$

d Ontario

e Quebec

f Newfoundland

g Maritime Provinces and Maine

h New Hampshire, New York, Rhode Island, Massachussetts, and Vermont

i New Jersey, Connecticut, Pennsylvania, Illinois, Ohio, Indiana, Iowa, and Nebraska

j Michigan, Wisconsin, North and South Dakota, and Minnesota

k Maryland, West Virginia, Virginia, D.C., Kentucky, Missouri, and Kansas

1 North Carolina, Tennessee, Arkansas, and Oklahoma

m South Carolina, Georgia, Alabama, Louisiana, Mississippi, and Texas

Florida

n

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EXPOSED CULMEN LENGTH (in mm) IN PICOIDES PUBESCENS

Sample	Sex	Range	Mean	SD	SE	CV	N
a	м	14.5-16.5	15.43	0.731	0.276	4,738	7
	F	15.0-16.5	15.67		, , ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		3
b	м	15.0-17.0	15.79	0.755	0.285	4.783	7
	F	14.5-17.0	16.00	, 			4
с	м	13.5-18.0	16.04	1.088	0 <i>:</i> 205	6.783	28
	F	13.5-18.0	15.58	1.178	0.218	7.561	29
d	М	14.5-18.0	16.01	0.861	0.137	5.377	39
•	F	14.0-17.0	15.52	0.805	0.157	5.187	26
е	м	14.5-17.5	16.05	0.840	0.187	5.233	20
- ,	F	15.0-18.0	16.68	0.782	0.235	4, 687	11
f	M	14.0-16.5	15.66	0.764	0.175	4.879	19
1	F	14.5-17.5	16.34	0.786	0.157	4.810	25
g	м	14.0-18.0	16.29	1.117	0.322	6.856	12
۔ م	F	14.5-18.0	15.97	` 0.93 4	0.241	5.849	15
h	м	15.0-18.0	16.37	0.779	0.149	4.758	27
	F	14.5-18.0	16.10	0.860	0.187	5.343	21
i	М	14.5-17.5	16.05	0.874	0.159	5.445	30
	F	14.0-17.5	15.68	1.029	0.205	6.562	25
j	м	13.5-17.5	16.02	0.934	0.194	5.829	23
	F.	13.5-17.0	15.70	1.048	0,270	6.675	15
k	м	15.0-17.5	16.16	0.692	0.094	4.282	54
	F	14.5-17.5	15.84	0.829	0.117	5.233	50
ľ	M	15.0-18.5	16.00	0.721	0.141	4.506	-26
1	F	14.5-17.5	, 15.90	0.736	-0.164	4.628	20
m -	M	14.0-16.5	`15.4 0	0.595	0.089	3.864	44
	۲.	14.0-16.5	15.09	0.734	0.141	4.863	27
n .	. /м	14.5-17.0	° 15.71 ·	0.662	0.160	4.215	, 17
/	/ F /	14.0-16.5	15.10	0.663	0.144	4.392	`21

Table 45

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two samples along the Pacific Coast. Sexual dimorphism occurs in this character, males having predominantly longer bills than females, but the difference is not always statistically significant. Reversed sexual dimorphism, at a significant level, was recorded in two samples only.

IV - Variation in tarsus length

Tarsus length variation has been analyzed following the procedure described earlier for the other mensural characters. Tarsus length is proportionally much less variable individually or geographically than the wing and tail but is as variable as the exposed culmen. The difference between the greatest and smallest means are 1.26 mm for males and 2.37 mm for females. Sexual dimorphism has been recorded but is not as well marked as in some of the other characters. The low coefficients of variation of the samples indicate a high degree of homogeneity.

In the Pacific coast sample (Table 46) differences between means were found to be significant (P < 0.05) in the coastal Alaska and coastal British Columbia sub-samples and between the latter and the coastal Washington birds, and again between the coastal Oregon and the coastal California sub-samples for males. In females no significant difference (P > 0.05) was observed between the means of the sub-samples. A significant difference (P < 0.05) was obtained upon comparison of the means of males of the northern pooled and southern pooled samples. Although no significant correlation (P > 0.05) was found between size and latitude from south to north in the sub-samples

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Region	Sex	Range	Mean	SD	SE	CV	N
Coastal	м	15.5-16.5	16.00	0.354	0.098	2.210	13
Alaska	F	15.0-16.5	16.00	0, 471	0.149	2.944	10
Coasta1	м	15.5-17.5	16.36	0.525	0.099	3.207	28
British Columbia	F	15.5-16.5	16.00	0.302	0.084	1.884	12
Coastal	М	16.0-18.0	16.73	0.525	0.146	3.138	13
Washington	F	15.0-17.0	16.39	0.561	0.150	3.421	14
Coastal	м	16.0-17.0	16.69	0.443	0.111	2.652	16
Oregon	F	16.0-17.5	16.78	0.507	0.169	3.021	9
Coastal	M	15.0-17.0	16.21	0.497	0.143	3.066	12
northern	F	15.0-17.5	16.26	0.614	0.148	3.775	14
California							
Pooled	м	15.0-18.0	16.45	0.554	0.061	3.368	82
northern	F	15.0-17.5	16:22	0.566	0.073	3.489	59
samples							
Marin °	Μ.	15.5-17.5	16.42	0.575	0.136	3.503	18
County	F	15.5-17.5	16.11	0.487	0.130	3.026	14
(California)	•		- 2 2			•	
Interior	м	15.5-16.5	16.41	0.491	0.123	2.990	16
Washington	F	15.5-16.5	16.22	0.363	0.121	2.239	9
and Oregon					1		
Interior	М	16.0-17.5	16.29	0.508	0.136	3.120	14
California	F	15.0-17.0	16.00	0.632	0.153	3.953	14
Southern	M	15.5-17.0	16.15	0.463	.0.097	2.867	29
California ,	F	15.0-17.0	16.09	0.491	0.148	3.050	11
Pooled	м	15.5-17.5	16.25	0.493	0.067	3.033	59
southern	F	15.0-17.0	16.10	0.519	0.089	3.022	*34 '
and						*	
interior samples		¢					
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TARSUS LENGTH (in mm) IN PICOIDES PUBESCENS

Table 46

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a slight increase in size occurs from south to north. The difference between means of males and females are not significant except in the coastal British Columbia sub-sample and in the pooled coastal sample. In those, the males have longer tarsi than the females, which in turn, have longer tarsi in two sub-samples but at a non-significant level (P > 0.05).

The data from the Cordillera and southwestern interior are summarized in Table 47 and do not indicate any significant variation trend. No size change was recorded along geographical gradients and no significant difference was observed between the means of the various sub-samples, except in one case: the females of British Columbia and Alaska have significantly (P < 0.05) shorter tarsi when compared with those of Washington, Oregon, Idaho, etc. Significant sexual dimorphism was recorded only in the pooled sample, the males having longer tarsi. The pooled Cordillera sample and the pooled northern coastal and southern coastal samples have the same tarsus length (P > 0.05).

The data of the large sample from the eastern part of the species range appear in Table 48 and display a high homogeneity as reflected by their low coefficients of variation. Tarsus length tends to increase slightly from south to north in this large sample but the values obtained are statistically not significant (r=0.278, males; r=0.209, females; df.=12; P > 0.05). No increase in size from east to west was found in any of the samples. Significant differences were observed however between certain pairs of means as follows: for males, j-k, l-m; for females, d-e, e-f, j-k, and l-m.

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Ļ	TARS	US LENGTH	nm) IN <u>PI</u>	COIDES PU	BESCENS		,
Region	Sex	Range	Mean	SD	SE	CV ,~~	N 1
<pre># British Columbia, Alberta</pre>	M F	15.0-17.0 15.0-16.5	16.01 15.85	0.620 0.461	0.165 0.103	3.873 2.908	* 14 20
E. Washington, E. Oregon, Idaho, Montana, W. Wyoming	M F	15.0-17.5 15.5-17.5	16.30 16.28	0.485 [°] 0.423	0.075 0.081	2.974 2.598	41 27
E. Nevada, Utah, W. Colorado	M "F	16.0-17.5 16.0-16.5	16.63 16.33	.0.516	0.182	3.103	'8 3
Arizona, New Mexico, and NW Texas	M F	15.5-17.0 15.5-17.0	,16.33 16.10	0.491	0.141	3.006	12 5
Pooled samples	M F	15.0-17.5 15.0-17.5	16.29 16.11	0.532 0.477	0.061 0.064	3.266 2.961	75 55

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Table 47 👡



Table 48.

a Alaska and Yukon

b Northwest Territories

c Alberta, Saskatchewan, and Manitoba

d Ontario

e Quebec

f Newfoundland

g Maritime Provinces and Maine

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h New Hampshire, New York, Rhode Island, Massachussetts, and Vermont

i New Jersey, Connecticut, Pennsylvania, Illinois, Ohio, Indiana, Iowa, and Nebraska

j Michigan, Wisconsin, North and South Dakota, and Minnesota

k Maryland, West Virginia, Virginia, D.C., Kentucky, Missouri, and Kansas

1 North Carolina, Tennessee, Arkansas, and Oklahoma

m South Carolina, Georgia, Alabama, Louisiana, Mississippi, and Texas

Florida

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Sample	Sex	Range	Mean	SD	SE	ĊV	N
а	м	15.5-16.5	15.93	0.533	0.201	3.346	7
	F	15.5-16.0	15.67				3
Ъ	м	15.5-16.0	15.79	0,266	0.100	1.685	7
	F	15.5-16.0	15.75				4
с	м	15.0-17.0	15.98	0.398	0.072	2.490	30
	F	15.0-16.7	15.81	0.606	0.110	3.830	30
d	м	14.0-17.5	16.19	0.685	0.108	4 . 231	40
-	F	15.0-17.0	15.92	0.541	0.106	3.397	26
۵	м	15 0-17 0	16 02	0 510	0 111	3 182	21
2	F	16.0-17.0	16.36	0.322	0.097	1.967	11
f	м	15.0-16.5	16.02	0.411	0.080	2 - 565	26
-	F	15.0-17.0	15.93	0.576	0.125	3.616	21
Ø	, M	15.5-17.0	16.33	0.577	0.166	3.532	12
U	F	15.5-17.0	16.03	0.480	0.123	2.993	15
h	м	15.0-17.0	16.28	0.486	0.093	2.985	27
	F	15.0-17.0	16.10	0.489	0.106	3.038	21
i	M	15.0-170	16.17	0.562	0.102	3.476	30
	F	15.0-17.0	15.98	0.489	0.094	3.059	27
1	м	15.5-17.0	16:30	0.444	0.092	2.725	23
5	F	15.0-17.0	16.20	0.527	0.136	3.253	15
k	м	15.0-16.5	15.91	0.408	0.055	2.564	55
	F	15.0-17.0	15.85	0.506	0.071	3.192	50
1	М	15.0-16.5	15.87	0.491	0.094	3.093	27
	F	15.5-16.5	15.97	0.423	0.097	2.648	19
m	м	14.5-16.5	15.48	0.504	0.075	3.256	44
	F	15.0-16.0	15.43	0.357	0.068	2.,314	27
n	¢≁ M	15.0-16.0	15.47	0.413	0.100	2.669	17
	F	15.0-16.0	15.41	0.366	0.078	2.375	22

TARSUS LENGTH (in mm) IN PICOIDES PUBESCENS

Table 48

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Sexual dimorphism occurs in all the samples but the difference between means is never significant (P>0.05) and males have longer tarsi in most samples except in samples e and 1.

In summary, tarsus length is not a geographically variable character, although its means were found to be significantly different in a few populations. It is the least geographically variable of the mensural characters. It increases apparently in size from south to north, but the very gradual increase is not statistically significant in that adjacent populations are the same. Sexual dimorphism was observed in all the samples, males usually having longer tarsi than females.

III. TAXONOMY

The study of various characters in the previous sections demonstrates the difficulty of classifying the various populations and individuals examined. Most of the characters display clinal variation and only a few populations can readily be separated from adjacent ones. As a <u>résumé</u> of the situation in <u>Picoides pubescens</u>, the following paragraph, quoted from Oberholser (1896:547) is still applicable: "While the differences assigned are perhaps not such as to positively determine by any single character every given individual, yet the average distinctions are readily appreciated upon comparison, and diagnoses are based upon what may be considered fairly well differentiated averages". Indeed, in a large number of cases it may be difficult to determine the taxonomic status of individual birds. However when series are available it becomes possible to determine

their taxonomic status and assign them to taxa, in using a combination of characters.

Ridgway (1914) recognized 7 subspecies whereas Peters (1948) accepted an additional one. The A.O.U. Check-list, 2nd edition (1957) lists 7 subspecies, basically those recognized by Ridgway (1914). The nomenclatural imbroglio of the subspecies has been untangled by Brewster (1897).

As pointed out in the earlier sections most variation in this species is clinal and affects the color of the under parts, the color pattern of the dorsal regions and of the tail, and various body measurements. It is difficult to interpret this type of variation in terms of the subspecies concept, as mentioned earlier for <u>Picoides</u> <u>villosus</u>. The ranges of certain taxa are difficult to delimit in view of the intergradation that takes places on a large scale. My attempts are based on the weighing of a combination of characters, resulting from the analyses presented in the previous parts, and appear in Figure 23. For measurements or color characteristics, the reader is referred to the sections on variation.

Picoides pubescens glacialis (Grinnell)

Dendrocopos pubescens glacialis (Grinnell)

Although I have currently recognized this taxon, I am not convinced that it is a valid one. I am inclined to think that, in view of the material examined, it is an intermediate form between <u>nelsoni</u>, <u>leucurus</u>, and <u>gairdnerii</u>, occupying the coastal belt of southern Alaska and northern British Columbia (Figure 23). Since no



Figure 23.

Distribution of subspecies of <u>Picoides pubescens</u> recognized in this study based on data provided in previous parts. Intergradation areas are shaded.

- 1. <u>P. p. glacialis</u>
- 2. <u>P. p. nelsoni</u>
- 3. <u>P</u>. <u>p. medianus</u>
- 4. <u>P. p. pubescens</u>
- 5. <u>P. p. leucurus</u>
- 6. P. p. gairdnerii
- 7. <u>P. p. turati</u>



material could be examined from an important area in British Columbia between its range and that of <u>gairdnerii</u> and <u>leucurus</u> I can only speculate about the status of this form. Certainly, it appears to be at the northern end of a color cline in the under parts color, <u>gairdnerii</u> being at the center and the darkest, but gradually becoming slightly lighter along the coast in the Rivers Inlet region. The dorsal and caudal color patterns of some individuals indicate some affinities with <u>leucurus</u> whereas mensural characters are close in some cases to those of <u>nelsoni</u>. Pending the availability of additional material it seems best to retain this taxon.

Picoides pubescens nelsoni (Oberholser)

Dendrocopos pubescens nelsoni (Oberholser)

This large bird with pure white under parts can readily be recognized in series from the northwestern sector of the species range. There is a reduction in the black barring of the rectrices but this character is similar in <u>leucurus</u> with which it intergrades in northern central British Columbia and with <u>medianus</u> in eastern central Alberta, in central Saskatchewan, and in central Manitoba. Its measurements and color characteristics appear in the previous sections and its geographic distribution is detailed on Figure 23.

Picoides pubescens medianus (Swainson)

Dendrocopos pubescens medianus (Swainson)

This taxon comprises birds that are intermediate in size and color of the under parts between nelsoni and pubescens. The under

parts are mainly white, although not as pure as in <u>nelsoni</u> and with less 'buffy' than in <u>pubescens</u>. The coloration pattern of the upper parts does not differ from that of either <u>nelsoni</u> or <u>pubescens</u>. It can therefore be separated from the former by its smaller body measurements, mainly the wings and culmen, and from the latter by its purer white under parts. The form <u>microleucus</u> described by Oberholser (1914) for Newfoundland and Anticosti Island is not recognized here (<u>contra</u> Peters 1948), thus following the A.O.U. Checklist (1957), because these insular populations are not significantly different, in any way, from the mainland populations. The eastern populations tend to have less pure white under parts than the northern and western elements of the population (Figure 23).

Picoides pubescens pubescens (Linnaeus)

Dendrocopos pubescens pubescens (Linnaeus)

The taxon with the smallest body measurements in the large clinal group that occurs east of the Cordillera, has a small range, detailed on Figure 23. It has the smallest measurements (wing, tail, and culmen) recorded in the species. The range outlined on Figure 23 indicates an area occupied by a population with a high incidence of specimens with under parts profusely colored with 'grayish drab'. The northern boundary of the taxon was drawn on that basis and delimits the northern extension of that subspecies.

Picoides pubescens leucurus (Hartlaub)

Dendrocopos pubescens leucurus (Hartlaub)

Upon examination of the material used in this study this taxon is readily recognizable on the basis of a variable reduction of the white areas on the dorsal regions along with a marked reduction in the black barring of the rectrices. It averages larger than adjacent populations for certain mensural characters and its under parts are almost always pure white but sometimes washed with 'drab', particularly near the range of turati. On the basis of the material examined I have outlined and restricted its range to the areas shown on Figure 23. Special attention was given to the birds from Idaho, south central British Columbia, eastern Washington, and northeastern Oregon, which have been described as a different subspecies, parvirostris (Burleigh 1960). I see no valid reason to retain this subspecies which should be considered as a synonym of leucurus. The measurements, color of under parts, and color pattern of the dorsal regions of those birds are in no way significantly different from those of <u>leucurus</u> coming from adjacent parts of the range as determined on Figure 23.

Picoides pubescens gairdnerii (Audubon)

Dendrocopos pubescens gairdnerii (Audubon)

This subspecies in the best marked having very dark under parts and occurring in a limited area with little intergradation with adjacent taxa. Its range is shown on Figure 23. In the north, it intergrades with <u>glacialis</u> (?) which may eventually be considered an intermediate form between it, <u>leucurus</u>, and <u>nelsoni</u>. In the south and

to the west it intergrades with <u>turati</u> over a narrow area. It varies clinally in size from north (larger) to south but its body measurements are significantly longer than those of <u>turati</u>.

Picoides pubescens turati (Malherbe)

Dendrocopos pubescens turati (Malherbe)

Similar to <u>gairdnerii</u> but significantly smaller and much paler on the under parts. It intergrades with that subspecies just south of Mendocino County, California, and the specimens from Marin County, although somewhat darker than typical <u>turati</u>, have body measurements that are not significantly different from those of <u>turati</u>. It intergrades with <u>leucurus</u> to the west and southwest but its small measurements remain characteristic in those areas. Its range is shown on Figure 23.

DISCUSSION

Geographic variation

It has been shown in various studies on species with continentwide distribution ranging across diversified ecological conditions that wing length (and other body measurements to a lesser extent) is influenced by a variety of factors (Gould and Jonshton 1972; Hamilton 1961; James 1970; Jackson 1970; Power 1969, 1970; Selander and Giller 1963; Snow 1954).

In the current study of variation in <u>Picoides villosus</u> and <u>P</u>. <u>pubescens</u> which both have extensive continental ranges, I have selected for analysis several characters and the results have been

presented in the previous parts. Variation in those two species is not limited to wing length but affects other body characters as well, such as weight, bill length, tail length, tarsus length, general color, and color pattern. Sexual dimorphism was found also to vary between populations, at least in <u>P. villosus</u>, and to affect mainly tail length where females were recorded to have longer tails than males. In <u>P. pubescens</u> female wing length was determined to be significantly longer in a few populations. In another section on the comparative ecology of the two species, attempts will be made to interpret variation in terms of the species morphology.

In <u>P</u>. <u>villosus</u> there is a direct relationship between wing length and body weight for both sexes (Figure 24). The same relationship was recorded in that species for culmen length, tail length, and tarsus length. I could not verify if this happens also in <u>P</u>. <u>pubescens</u> because the few body weights available are mainly from the same geographical area, although it appears that the same relationship may exist, at least, for wing length, tail length, and culmen length. Thus the longest-winged birds (or other mensural characters) are the heaviest.

It has been demonstrated previously (Jackson 1970; James 1970) that body weight varies clinally in <u>P</u>. <u>villosus</u> and increases along a south-north geographical gradient (Figure 12) and the other body measurements studied here (Figures 13, 14, 15, 16) follow the same trends, the longest being found in the northern parts of the range. In <u>P</u>. <u>pubescens</u> I have observed similar trends for all the body measurements with the exception of body weight for which a limited 'sample only is available. Those trends resemble those observed in



Figure 24..

Linear regression of mean wing lengths (x-axis) on mean body weights (y-axis) for selected populations of <u>Picoides villosus</u> (choice determined by availability of weight data).

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<u>P. villosus</u> in most populations but are sometimes not as well-marked as it is the case with the tarsus in <u>P. pubescens</u>. In that species the longest-winged individuals occur in the Cordillera sample (Table 38) but the other longest measurements for the other body characters used were found in the northernmost parts of the range. Those data 'are generally in accordance with Bergmann's rule more pertinently redefined by James (1970:387), as follows:

"Intraspecific size variation in homeotherms is related to a combination of climatic variable that includes temperature and moisture. Small size is associated with hot humid conditions, larger size with cooler or drier conditions."

However, how do we account for 'the populations of <u>P</u>. <u>villosus</u> which occur in Central America in humid and temperate (to cool) climatic conditions and which have the smallest body measurements recorded in the species? I cannot answer that but can only suggest that small size in the body characters of <u>P</u>. <u>villosus</u> may be ancestral characteristics retained by the species in that part of the range where climatic and ecological conditions have remained relatively stable over a long period of time in the absence, or near absence, of competition with other congeners. A similar question may be asked with regard to the long-winged population of <u>P</u>. <u>pubescens</u> found in the Cordillera region. In that case, those birds occur at fairly high altitude (1,500-2,000 m) and the altitude effect may tend here to be stronger than some of the other effects as suggested by "Hamilton (1961) and Snow (1954).

James (1970) has recorded trends in the southeastern parts of

the range of <u>P</u>. <u>pubescens</u> which satisfy Bergmann's rule and indicate significant correlation between wing length and several climatic and topographic variables. My data are consistent with those for both species, although on a much larger scale. The situation should be reexamined with regard to topography and climatic factors across the range of <u>P</u>. <u>villosus</u> and <u>P</u>. <u>pubescens</u> in the light of new climatic data when they become available. The most promising areas for such studies would be, in my estimation, in mountainous areas and in adjacent lowlands and coastal regions.

Island populations in <u>P</u>. <u>villosus</u> (eg. Queen Charlotte and Bahama islands) do not display as significant an increase in their body characters as the adjacent mainland populations, particularly where geographical size gradients are involved, as indicated by the data provided (see previous parts).

Concerning Allen's rule, which states that the "tail, ears, bills and other extremities of animals are relatively shorter in cooler parts of a specie's range than in the warmen parts" (Kendeigh 1961), this rule is applicable only partly to birds. My data are inversely proportional to the expected values at least as far as bill and tarsus lengths are concerned. Indeed, these body measurements are much longer in the cooler parts of the species range than in the warmer climates of the range. In both species, they follow the trends observed in the other body measurements (weight, wing, and tail lengths) and increase clinally northward where the largest measurements have been recorded. Heat loss can efficiently be controlled in the legs by regularing blood circulation and by tucking

them under body feathers in cold weather (Irving 1972; personal observation), thus obtaining efficient insulation against cold, whereas heat dissipation is negligible or nil in the bill no matter its size. Thus there seems to be no real advantage in having small bills and small legs in those parts of the range. To the contrary, it is probably advantageous to have long bills in cold areas which may be more efficient tools at obtaining food than a shorter bill. Long tarsi, proportional to a large and heavy body, are probably more advantageous also than small short legs supporting a heavy body. Some of these points will be discussed again in a forthcoming section on the comparative ecology of the two species, particularly with regard to interspecific competition.

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According to Gloger's rule, the races of warm and humid areas are more heavily pigmented than those of cool and dry areas and black pigments are reduced in warm dry areas and brown in cold humid regions (Mayr 1970). This general rule applies to a large number of North American vertebrates, birds in particular. Both species studied here comply in general terms with this statement since the darker populations are generally found in the more humid areas of the range (see sections on under and upper parts color and pattern). However, humidity levels rather than temperature levels may be more important determining factors inasmuch as <u>P</u>. <u>villosus</u> and <u>P</u>. <u>pubescens</u> are concerned because their darker populations occur in the most humid climatic and vegetation areas of North America, north of Mexico, defined by Aldrich (1963) as the Pacific rain forest, where temperatures are not particularly warm but rather cool and stable. On

the other hand, the other darker forms of P. villosus occur in the highlands of Mexico and Middle America where the humidity is' relatively high but where temperature, at least during the night, is not warm but cold, and the day-time temperatures at that altitude, can be considered as temperate. The amount of white in the dorsal 'regions of the Cordillera and Colorado, Plateau populations of both species is also reduced significantly but the humidity and temperature of these regions are low. On the other hand, the Newfoundland population of P. villosus has also reduced white markings dorsally which in this case is compatible with the high humidity levels recorded in that part of the species range but the average temperatures are cool. Further research into this problem using recent and up-to-date climatic data from a large number of localities, particularly localities where those species are known to occur may provide new insights towards a better comprehension of the problem. The physiological basis for this type of variation is not clear and poorly understood and as pointed out by Mayr (1970), there appears to be no genetic evidence for it.

Aberrant specimens

In addition to individual variation recorded within single populations and inter-population geographical variation described in the previous parts for both <u>Picoides villosus</u> and <u>P. pubescens</u>, little abnormal or aberrant variation was detected in those two species.

Among the several thousands specimens examined I have not

recorded totally albinistic specimens in any of those two species. I have however noted partial albinism in variable amounts, usually very small and affecting a few feathers only in areas where those are normally black. These were recorded mainly in the facial pattern or on the dorsal regions, but nevertheless remain a rare phenomenon in both species. Melanism is even rarer and much more difficult to detect having not been reported in P. pubescens. Short (1969) described an apparently melanic individual of P. villosus which displayed many aberrant characters in addition to the extra amount of black in its plumage. It also has a peculiarly colored (ivory) when compared to that of normal individuals (blackish). My measurements of that specimen are somewhat large when compared to that of the population in the area where it was collected but nevertheless do not exceed the expected upper limits. Short (1969) rejected the possibility of hybridization with other species. I concur with his view but cannot offer any additional proposals concerning the origin of the specimen, except that it is probably a very rare mutant.

The black parts of the plumage, under certain conditions turn to brownish, particularly towards the end of the plumage cycle. I have recorded this condition on a few specimens of both species and suspect that these birds were in their first year, judging from the shape of the white markings of the wing coverts. This type of variation appears at random and is seemingly independant of geographic variation. It may be the result of excessive exposure to unusual environmental conditions which have caused an unusually rapid deterioration of the melanin pigments of the plumage. It is equally possible that those

may be birds of the year which missed their first annual molt due to abnormal physiological conditions.

Unusually long claws have been noted in a few specimens of both species but these are nevertheless the exception and may be caused by abnormalities in the toes. This type of variation is not geographical or genetic but is apparently the result of a pathological condition that has occurred in the bird's legs.

Hybridization

No hybrid is known between <u>P</u>. <u>villosus</u> and <u>P</u>. <u>pubescens</u> although the possibility of such hybridization cannot be ruled out entirely. However, I believe that it is very unlikely in view of the great differences observed in the ecology, morphology, and behavior of those two species. Gray (1958) and Short: (1971) have listed the known hydrids between <u>P</u>. <u>pubescens</u> or <u>P</u>. <u>villosus</u> and the other North American species of the genus. The latter recorded and discussed the cases of hybridization between <u>P</u>. <u>pubescens</u> and <u>P</u>. <u>mutallii</u> (3) and between <u>P</u>. <u>villosus</u> and <u>P</u>. <u>scalaris</u> (1). Unfortunately so few hybrids are currently known between the various members of the genus that little information can be derived from the known cases. Hybridization is likely to occur again between other species in other parts of the range of the genus as predicted by Short (1971) when circumstances are suitable for it to take place. To date those cases contribute little information on the relationships of the group.

The subspecies concept

The difficulty of classifying individuals, large segments of populations or whole populations within the subspecies concept criteria as defined by Mayr (1970:210) has led a number of authors (Hagmeier 1958; Jolicoeur 1959; Pimentel 1958; Sokal 1965; Wilson and Brown 1953; and many others) to reexamine critically the practical application of the subspecies concept and even its existence. The newer definition provided by Mayr (1970:210) is acceptable both from a practical biological and theoretical point of view but the practising taxonomist is still often faced with insurmountable difficulties in his attempts to classify organisms at the infraspecific level.

It is usually possible to name populations or even individuals belonging to such populations but it may be difficult or impossible to do so where important overlap between characters occur in adjacent populations, namely where variation is clinal. In island populations, which are often endemic and completely isolated from those of the mainland the problem is usually simpler.

In spite of the attempts that have been made and probably will be made to replace or relinquish this means of describing infraspecific variation, the subspecies remains an acceptable and useful tool for the practising taxonomist in spite of its limitations. It must however be, kept in mind that it is man-made category and not a natural unit of evolution. As far as clinal variation is concerned, in spite of numerous attempts, no satisfactory method has yet been adopted that fulfill the needs or requirements of all taxonomists. Having had much difficulty with this problem, particularly with the

long and wide clines found in <u>Picoides villosus</u> and <u>P. pubescens</u> east of the Rocky Mountains, I found it difficult to differentiate the various subspecies. Even in cases where areas in the range of the cline display a high homogeneity in one or several characters, with broad sectors of intergradation, it may be better to consider the cline as a whole, as a group of populations which vary along gradients but which share some common characters. The following clines have {

- a) <u>Picoides villosus</u>
 - 1. septentrionalis villosus audubonii
 - 2. harrisi monticola hyloscopus
 - 3. monticola orius leucothorectis
 - 4. icastus intermedius jardinii

b) Picóides pubescens

- 1. <u>nelsoni glacialis medianus pubescens</u>
- 2. gairdnerii glacialis turati

3. leucurus - glacialis - gairdnerii - turati

In those cases, in addition to the subspecies identification, where possible, it may be very valuable to indicate the taxon or taxa with which the population identified has the closest relationship or relationships, starting with the enumeration of the subspecies with which it has the greatest affinities. For example specimens of <u>P</u>. <u>villosus</u> from Rivers Inlet, British Columbia could be designated as <u>harrisi (monticola-septentrionalis)</u> or a series of <u>P</u>. <u>pubescens</u> from northwestern Ontario as <u>nelsoni (medianus</u>), the names in parentheses designating the taxa with which the subspecies has close relationships.
This treatment is not new but has the obvious advantage of indicating at once the affinities of the specimens identified. I therefore recommend that it be used as a standard practice when dealing with specimens which do not represent all the characteristics of the taxon to which they are referred.

Historical interpretation

The history of the genus Dendrocopos, heretofore comprising most of the species assigned later to the genus Picoides, except tridactylus and arcticus, has been provided by Voous (1947) who discussed concurrently the process of subspeciation to some extent for villosus and pubescens. The history of the genus Picoides has recently been expanded by Short (1971) and Bock and Bock (1974) and in another part of this study. The views presented here are different from those of Voous (1947). Short's findings (1971) and conclusions are in agreement with my conclusions except for the fact that I place more emphasis on Middle America and Mexico, as well as the southwestern part of the United States as the center of evolution and dispersal of the group into the rest of North America and into South America, after the pre-Picoides (Dendrocopos-like species) ancestors, probably forms closely related to the modern mid-Asiatic Dendrocopos species, had reached North America during the Tertiary. From then on, the various species have evolved and expanded, some occupying vast ranges others being restricted to small areas. It seems that climatic and ecological conditions deteriorated throughout the Tertiary particularly during the Pliocene (Kendeigh 1961).

Upon the glacial advance and retreats of the Pleistocene the vegetation distribution in North America was considerably modified (Dillon 1956). The history of the vegetation in North America since the Tertiary has been summarized by Kendeigh (1961), Mengel (1964), and Hubbard (1969). It is well-accepted that the climatic fluctuations of the period had important effects on vertebrate species primarily in separating populations from parental stocks (Rand 1948). It is probably through this phenomenon that large segments of populations of <u>Picoides villosus</u> and <u>P. pubescens</u> finally gave rise to groups of well-differentiated populations or subspecies.

During the Pleistocene glacial invasions the ranges of the existing populations were probably compressed into small areas south of the ice-cap or in refugia. During the interglacials and after the final last glacial retreat these populations became in contact once more with the reappearance of the continuous transcontinental forests (or nearly so), but many of those population had by then diverged to various degrees from the parental stocks. With <u>P. villosus and P.</u> <u>pubescens</u>, which are essentially forest birds, the taiga, the coniferous forest, and its southern ecotone probably acted as a bridge between a number of populations separated mainly by the Great Plains in the center of the continent (Mengel 1970) and the Cordillera in the north.

Glaciation as an isolating mechanism in speciation has been reviewed by Rand (1948) and Selander (1965) and is widely accepted as such. The existence of refugia during the Pleistocene allowed the survival and differentiation of populations in certain vertebrates.

Various refugia have been proposed (Zeuner 1959; Flint 1971; Calder and Taylor 1968; Heusser 1960; Terasmae 1973; Hopkins 1967; Guthrie 1966) although it is possible that only those found south of the ice sheet could support forest vegetation essential to woodpeckers. The possibility remains however that Beringia (Guthrie 1966) could have supported forest vegetation at that time.

The fact that various populations of Picoides villosus and P. pubescens have been isolated during the Pleistocene either south of the ice-cap or in refugia elsewhere to the northwest (Beringia) is certainly appealing to explain the present distribution of many of the subspecies. For example, assuming that Beringia was a suitable refugium with forest vegetation as the evidence suggest (Guthrie 1966), it would explain the modern day distribution of P. villosus septentrionalis and P. pubescens nelsoni and their expansion to the southeast after the reappearance of forest vegetation and their joining with the populations which occurred south of the ice-cap. The same argument could be invoked to explain the present distribution of several other subspecies, namely along the Pacific Coast and in the Cordillera region. The case of the Queen Islands is more complex although it appears that parts of the islands formed a refugium during the Pleistocene (Calder and Taylor 1968). At that time they could have been colonized by individuals of P. villosus which later may have differentiated markedly from the coastal parental stock the range of which may have fluctuated with the climatic changes of the It is therefore not unreasonable to state that some time. subspeciation took place during the Pleistocene as far as several

populations of these, two woodpeckers are concerned, in the light of Mengel's demonstration (1964) that differentiation of several species of warblers (Parulidae) has taken place during that period through four glacial cycles.

The Middle American races of <u>P</u>. <u>villosus</u> were affected during the process as well, as revealed by the scanty data available and the present knowledge of the subspecies and their present distribution in that part of the range. The current southernmost subspecies, <u>P</u>. <u>villosus extimus</u>, may well have been the forerunner of the other northern taxa! <u>Picoides pubescens</u>, as proposed by Short (1971), was probably prevented from expanding southward into Mexico and Central America as a result of competition with other species. On the other hand the possibility that its range was compressed northward, north of the U.S.A.-Mexico border, by other more successful species must not be dismissed completely. It is possible that the present distribution of <u>P</u>. <u>pubescens</u> is a rather recent phenomenon, due partly to intraspecific competition, but also to ecological changes.

It seems logical to conclude here with Sokal and Rinkel's statement (1963: 469) which sums up my ideas on the subject in an elegant way: "Geographic variation is not likely to be due to adaptation of a few characters to a single environmental variable, but is doubtless a multidimentional process involving the adaptation of many characters to a variety of interdependent environmental factors whose gradients and ranges probably overlap in rather complex fashion".

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PART THREE

Comparative ecology of <u>Picoides villosus</u> (L.)

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and P. pubescens (L.), (Aves:Picidae)

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ABSTRACT

An analysis of the banding recovery data shows that Picoides villosus and P. pubescens are not migratory in most parts of their range but that some wandering occasionally takes place in all geographical directions. Information on the comparative foraging ecology of the two birds indicates little interspecific competition in the areas of sympatry. Preferences for certain tree species for foraging, the utilization of foraging stations of particular sizes, the use of different foraging techniques, nesting habits, and the selection of different insects preys were compared for those two species. The data indicate that interspecific competition is reduced to low levels because each species occupies a different niche or On the Bahama Islands in the absence of P. pubescens, P. habitat. villosus is found in that part of the niche which is occupied by the former in the regions of sympatry, probably as a result of limited food resources. Intersexual differences in body size are associated with differences in foraging techniques and habits in P. villosus whereas such differences are independent of intersexual morphological differences in P. pubescens. Sexual dimorphism varies geographically in P. villosus and appears to be related to the availability of food resources and the presence or absence of other congeners as on the Bahama Islands. Finally the existence of reversed sexual dimorphism in tail length is questioned in those two birds.

RESUME

L'analyse des données de recapture d'oiseaux bagués indique que P. villosus et P. pubescens ne sont pas migrateurs dans la plupart des régions de leur aire de répartition bien qu'il y ait parfois des déplacements d'individus dans toutes les directions géographiques. L'information disponible sur l'écologie comparée du mode d'obtention de la nourriture et de l'écologie générale de ces deux oiseaux indique une faible compétition interspécifique dans les zones de sympatrie. On a comparé le choix des essences d'arbre et les postes utilisés pour la recherche de la nourriture, les modes et les techniques de recherche de la nourriture, la nidification et les insectes utilisés comme proies. A la lumière de ces données on en déduit que la compétition interspécifique est réduite à de faibles niveaux du fait que chaque espèce occupe une niche distincte ou un habitat particulier. Aux îles Bahamas, en l'absence de P. pubescens, P. villosus occupe la portion de la niche ordinairement occupée par P. pubescens et ce, probablement à cause de ressources alimentaires restreintes. On a noté des différences intersexuelles dans les dimensions corporelles qui semblent associées à des différences écologiques chez P. villosus tandis que ces différences ne correspondent pas à des modifications morphologiques chez P. pubescens. Le degré de dimorphisme sexuel varie géographiquement chez P. villosus et peut être associé à la disponibilité de la nourriture et/ou à la présence de congénères, comme aux îles Bahamas. Enfin on met en doute l'existènce du dimorphisme sexuel inversé dans la longueur de la queue chez ces deux oiseaux.

INTRODUCTION

It is widely accepted that two species of animals cannot occupy the same area unless they differ ecologically. \checkmark According to Lack (1971) who has compiled a large volume of information on the subject in a brilliant synthesis this important biological factor was first enounced informally as a principle by J.B. Steere (1894, in Lack 1971). Independantly Joseph Grinnell, in a series of papers from 1904 to 1943, reached similar conclusions and coined for the first time the term "ecological niche" to define the ecological area occupied by each animal. The term is still widely used and its definition has recently been restated (Whittaker et al. 1973). Grinnell also stated the principle of competitive exclusion. Concurrently, Gause (in Lack 1971), on the basis of the mathematical equations of Lotka and Volterra, demonstrated the principle which states that an ecological niche can only be occupied completely by stabilized populations of a single species. This became known as "Gause's Principle" or "Gause's Rule".

In the following sections I will attempt to verify how Gause's Principle is applicable to two sympatric (over most of their respective range) woodpecker species (<u>Picoides villosus</u> and <u>P</u>. <u>pubescens</u>) with similar color and color pattern but with marked differences in their body size and other body measurements.

Aspects of their ecology will be examined by comparing ecological data recorded for each species from direct field observations to determine the extent of niche divergence. I have followed a similar procedure for the data recorded for each sex

within each species in order to obtain additional information on niche partitioning within each species as indicated by a few authors for woodpeckers and as recorded in a number of other bird species (Lack 1971).

METHODS

The main study area was located at Mont St. Hilaire, in southwestern Quebec, at the Gault Estate of McGill University, and adjacent areas (1965-1970). The flora and its ecological aspects have been described by Maycock (1961). Additional information were obtained in similar areas in the Great Lakes-St. Lawrence Forest Region, in other parts of Quebec and in Ontario from 1966 to 1975. Elsewhere, observations were made in other life regions, in March and April 1968, in Washington, Oregon, California, New Mexico, and Arizona. In March 1966 detailed records were obtained for <u>Picoides</u> <u>villosus</u> in the pine forests of some of the Bahama Islands (New Providence and Great Abaco), an area of allopatry, <u>P. pubescens</u> being unknown on those islands. Further information was noted in the boreal forest region and its southern ecotone in the Upper St. Maurice River and Abitibi regions of Quebec (1967, 1968, 1972).

Observations were made intensively from mid-September 1964 to mid-November 1965, from May through July 1966, and irregularly thereafter until December 1975. Data were recorded variously from daybreak to sunset, under various weather conditions. Birds were followed when foraging as long as possible and when they moved to a branch or a trunk, no matter what the number of times was, each was counted as a sighting. Each activity session, provided it lasted more than 30 seconds, was recorded as a separate sighting. Binoculars (7x35) were used when necessary.

Observations comprised quantitative data as follows: species of woodpecker, sex, locality, date, species of trees and number of trees utilized, diameter of trunk or branch (number of times on each noting size), height of tree, foraging activity (gleaning, pecking, excavating, fly-catching, sap-drinking), behavior activities, foraging height, time spent on the tree, and time of day.

The frequencies of occurrence in each category were tested by means of the G statistic (Sokal and Rohlf 1973), a test of independance (or association) which has general theoretical advantages over the conventional Chi-square test and is computationally simpler. The significance level accepted here is P=0.01.

MIGRATION

Most of the species in the genus <u>Picoides</u> are resident throughout the year in their breeding range (A.O.U. Checklist 1957; Schauensee 1966; Miller 1957) although irruptive and unpredicted movements have been observed in certain species namely <u>P. arcticus</u> and <u>P. tridactylus</u>. Wandering off the breeding range has been reported also in a few subspecies of <u>P. villosus</u> and <u>P. pubescens</u> although the majority are resident (op. cit.). In addition there are contradictory reports concerning the status of certain populations of those two species.

For P. villosus Bent (1939) quotes several reports from observers

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who mention that some wandering, sometimes extensive, has taken place in parts of the range particularly in the fall. Those movements appear to affect particularly the populations of the northern and northeastern parts of the range as well as those from the northern mountainous areas. The subspecies <u>villosus</u> and <u>septentrionalis</u> are listed as wanderers (A.O.U. 1957). The results obtained by Lawrence (1967) in northern Ontario concur with the published reports mentioned above.

With regard to <u>P</u>. <u>pubescens</u> Bent (1939) considers it a non-migratory species but mentions that local movements and wandering have been recorded mainly in the northern and mountain populations. Lawrence (1967) considers it a migratory species with only 16 per cent of the banded local population being resident. Smith (1973) suggests that some wandering takes places in South Dakota as well. The A.O.U. Check-list (1957) reports wandering in <u>P. pubescens nelsoni</u> and <u>P. p. medianus</u>. Extralimital records from England are listed also but the bird collected in Gloucestershire does not appear to have reached England by its own means (Smallcombe 1909: 382; editor's comments). This record would be very surprising in view of the analysis of recovery data of banded birds which follows.

The records of the official recovery data of banded birds provided by the Canadian Wildlife Service and the United States Banding Office have been summarized in Table 1. They indicate that wandering occurs in both species to a small degree but such movements affect less than 3 per cent of the birds banded and recovered. No

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· .	Distribution of recovery data in relation to distance from banding station					
	25 + miles (40 + km)	50 + miles (80 + km)	100 + miles (160 km)	- 25 miles (-40 km)	Total	
Picoides villosus	8. (0.98%)	8 (0,98%)	5 (0.62%)	792 (97.42%)	813	
Picoides pubescens	43 (1.17%)	26 (0.71%)	33 (0.90%)	3572 (97.22%)	3674	

<u>x</u>²=11.345; d.f.=3; G=1.530; <u>P</u>>0.01

Table 1

significant difference was observed between the distance travelled and the recovered number of birds between the two species $(X^2=11.345;$ d.f.=3; G=1.530; P>0.01). The data of Tables 2 and 3 Indicate no directional pattern or that one sex or an age group is more prone to wandering than the others. In P. villosus only females were found. to have travelled more than 100 miles. In view of the small size of the sample I think that those results are purely fortuitous. In P. pubescens, both sexes, adults and immatures, were recorded 100 miles (160 km) or more from the banding point. It must be pointed out that with both species the time elapsed between banding and recovery (Tables 2 and 3) varies from a few weeks to more than 6 years. It is not possible with those data to demonstrate that any type of migration takes place at a given time, in a given direction. They, however, provide information on the wandering that takes place in some individuals irrespective of their sex or age. This kind of wandering is not directional and sometimes takes place over considerable distances (800 + miles (1287 + km); Tables 1, 2, 3; possible records in England, from A.O.U. Check-list 1957).

An additional argument against migration in those two birds resides in the fact that no pre-migratory accumulation of subcutaneous fat occurs in them during the fall as expected from true migratory woodpecker species, such as <u>Sphyrapicus varius</u>.

The results of my banding and marking at Mont St. Hilaire (Quebec) indicate also that both species are not migratory (at least the largest segment of the local populations) in that part of their range and that local movements do not take place on a large scale.

نامانىمانىمىرىي بالاراتىمانىمىرىي	3	Ban	ding Data	Recov	ery Data	
Sex	Age	Date	Latitude Longitude	Date 🕔	Latitude Longitude	Distance* Dir.
F.	ad	12 Jan. 1935	51.1 - 099.3	15 Aug. 1938	51.9 - 102.9	165m.(265km) NW
F	ađ.	28 Apr. 1963	45.1 - 092.4	19 Oct. 1963	45.3 - 094.1	100m.(161km) NW
F	ad.	18 Jul. 1961	43.3 - 072.0	,16 Nov. 1961	42.2 - 071.1	105m.(169km) SE
/ F	\	1 Nov. 1964	47.2 - 094.5	[*] 12 Feb. 1967	49.0 - 097.0	175m.(282km) WNW
F	imm.	25 June 1965	43.5 - 069.2	6 Mar. 1966	44.2 - 073.0	230m.(371km) NW

RECOVERY DATA IN PICOIDES VILLOSUS

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* Minimum estimated distance between banding and recovery stations.

Table 2

RECOVERY DATA OF PICOIDES PUBESCENS

		Bandi	ng Data	Recov	very Data		
Sex	Age	Date	Latitude-Longitude	Date	Latitude-Longitude	Distance*	Direction
м		-12 Feb. 1961	42.2 - 089.0	16 Feb. 1962	44.5 - 091.0	240m (387km)	NW
F	ad.	18 June 1962	43.4 - 070.2	Nov. 1962	42.0 - 073.1	200m (322km)	SW
М	ad.	2 Oct. 1958	41.2 - 070.3	11 Nov. 1960	41.0 - 073.4	140m (226km)	W
F	ad.	22 Nov: 1959	41.2 - 070.3	6 Nov. 1960	41.0 - 073.4	150m (241km)	W
F	ad.	26 Sept.1959	41.2 - 070.3	5 Sept.1960	41.0 - 073.4	150m (241km)	W
F	imm.	8 June 1941	42.2 - 083.5	4 Oct. 1941	41.1 - 082.5	125m (201km)	SE
F	ad.	12 Mar. 1959	44.0 - 092.4	18 May 1959	45.4 - 094.3	135m (217km)	NW
F	ad.	12 Dec. 1948	38.2 - 092.2	27 Mar. 1955	38.2 - 092.1	100m (161km)	W
-	imm.	5 Sept.1961	39.5 - 074.0	Feb. 1964	35.0 - 076.4	325m (523km)	S
м		18 Oct. 1956	42.2 - 076.3	27 May 1959	33.0 - 086.4	800m (1,287km)	SW
м		15 Oct. 1956	42.2 - 076.3	3 Oct. 1961	33.3 - 086.4	800m (1,287km)	SW
M	ad.	23 Oct. 1957	40.4 - 073.3	26 Feb. 1958	40.5 - 074.0	100m (161km)	SW
F	imm.	13 July 1963	32.5	Apr. 1964	35.1 - 082.1	125m (201km)	NW
F	imm.	13 Jan. 1951	32.5 - 080.0	July 1952	35.1 - 082.1	125m (201km)	NW
F	imm.	1 Feb. 1953	43.5 - 088.3	23 Jan. 1954	47.1 - 095.5	300m (483km)	NW
_	ad.	10 May 1958	44.5 - 091.2	23 June 1959	47.2 - 087.5	125m (201km)	NE
F	ad.	29 June 1963	42.5 - 088.0	12 Dec. 1963	41.0 - 088.4	150m (241km)	SW
F	imm.	27 July 1964	41.5 - 080.4	26 Nov. 1964	34.2 - 088.4	600m (965km)	SW
F		2 Feb. 1925	42.5 - 091.2	25 Oct. 1925	45.2 - 092.2	185m (298km)	S
M	ad.	15 Jan. 1958	41.4 - 087.5	3 May 1956	43.0 - 087.5	150m (241km)	S
F	ad.	1 Oct. 1961	40.5 - 079.4	25 Nov. 1961	39.1 - 080.4	100m (161km)	S
M		12 Feb. 1961	42.2 - 089.0	16 Feb. 1962	44.5 - 091.0	190m (306km)	NW
-	ad.	5 Sept.1961	39.5 - 074.0	Feb. 1964	35.0 - 076.4	375m (603km)	S
F	ad.	18 June 1962	43-4 - 070.2	Oct. 1962	42.0 - 073.1	200m (322km)	SW
7	ad.	29 June 1963	42.5 - 088.0	12 Dec. 1963	41.0 - 088.4	100m (161km)	S
F	imm.	13 July 1963	32.5 - 080.0	Apr. 1964	35.1 - 082.1	200m (322km)	NW
-		24 Oct. 1963	41.5 - 080.4	Feb. 1964	39.5 - 083.0	175m (282km)	SW
F	imm.	27 July 1964	41.5 - 080.4	26 Nov. 1964	34.2 - 088.4	650m (1,046km)	S
- F	ad.	2 June 1965	41.0 - 075.1	13 Oct. 1965	42.5 - 073.1	150m (241km)	NE
F	ad.	3 July 1965	41.0 - 075.1	9 Mar. 1966	43.1 - 079.1	- 175m (282km)	NW
- F	1 mm	9 Oct. 1967	38.2 - 075.0	1 June 1968	44.1 - 076.0	450m (724km)	N
м.	1 mm.	29 Sept.1968	39.5 - 074.0	11 June 1969	41.2 - 075.4	135m (217km)	NW
' F	imm.	10 Aug. 1968	40.1 - 074.0	1 Apr. 1969	39.0 - 076.0	100m (161km)	S

* Minimum estimated distance between banding and recovery stations.

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Most of the birds banded and recovered by me from the fall of 1964 to the fall of 1966 were seen throughout the winter and following nesting season, although a few only could be recaptured for checking the band numbers.

With the exception of one male, all banded and color-marked <u>Picoides villosus</u> were irregularly observed until the end of July 1965 and all are assumed to have nested in a radius of 5 miles (8.1 km) from the banding location, although nests were not found in all cases. With regard to <u>P. pubescens</u> 12 birds were banded and colormarked (8 males, 4 females) during the same period, all of which, one male and one female excepted, were irregularly seen until the end of July 1965. Those data therefore indicate that the two species are primarily permanent resident in that region and probably in most of the general area as well. Those data concur with the information derived from the banding-recovery results provided above.

To sum up, the information currently available indicates that both <u>Picoides.villosus</u> and <u>P. pubescens</u> are equally non-migratory in most of their range and that some individuals, irrespective of their sex or age, occasionally wander in any direction from their regular range. The longest distance travelled by <u>P. pubescens</u> exceeds 800 (1,287 km) miles from the point of banding whereas in <u>P. villosus</u>, it barely exceeds 230 miles (371 km).

FORAGING ECOLOGY

1. Habitat selection

Picoides villosus occurs throughout most of the forested parts

of North and Central America (A.O.U. 1957; Peters 1948) whereas \underline{P} . <u>pubescens</u> occupies forested areas also but its distribution southward stops near the international U.S.A.-Mexico border (A.O.U. 1957). The habitat preferences of species vary geographically to a great extent as pointed out by several authors.

The southernmost population of P. villosus, in Panama and Costa Rica, occupies the central highlands between 1,200 and 2,100 metres to tree line, in the Sub-tropical and Temperate Life Zones (Slud 1964:194; Wetmore 1968:574). In Guatemala and Honduras the species is mainly found in the interior highlands also but from 600 to 2,900 metres in pine and oak forests (Land 1970:185; Monroe 1968:218). In Mexico it has been recorded in the wooded highlands also mainly in pine and oak forests (Blake 1953:300; Lowery and Dalquest 1951: 600). In the western part of the United States, P. villosus occurs mainly in coniferous and oak forests, although it has been recorded frequently in other forest associations (Grinnell and Miller 1944: 238-241; Short 1974). Its habitats in Arizona are similar (Phillips et al. 1964:74). In the northwestern states (Washington, Oregon, and Alaska) and in British Columbia it is essentially a bird of the coniferous forests which vary from the humid coastal forests to the dryer sub-alpine and montane forests (Jewett et al. 1953:408-410; Gabrielson and Jewett 1970:318-383; Munro and Cowan 1947:142-146). To the east it is found in almost any type of forest, even suitable small woods but may vary locally in abundance. Oberholser (1974:521) recorded it in the "secluded timberlands" of Texas whereas it occurs in the "extensive tracts of bottomlands and upland deciduous forest

	Picoides villosus (23,284)*		Picoides (18)	<u>pubescens</u> 457)*
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
Fagus grandifolia	5,647	4,864	3,21 <u>,</u> 6	3,001
Acer saccharum and other Acer sp.	3,361	2,943	1,750	1,194
Ulmus americana, mostly dead	1,974	2,359	2,819	2,744
<u>Quercus</u> <u>rubra</u> and other <u>Quercus</u> sp.	237	201	177	139
Populus sp.	19 5	116	872	461
Pinus sp.	148	223	18	14
Others (including <u>Alnus</u> and Salix sp.)	453	563	934	1,128
Total 、	12,015	11,269	9,786	8,681

Comparative number of sightings throughout the year, by species and sex, on trees used for foraging in Great Lakes-St. Lawrence forest region of Canada.

* Total number of sightings

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Table 4

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of North Dakota (Stewart 1975:168). Bird (1961:16) found it in the aspen parklands of the Prairie Provinces of Canada, between the extensive North American grasslands and boreal forest. In the east, it occupies almost all the forest types recorded (Godfrey 1966; Bent 1939; this study).

At Mont St. Hilaire and in the adjacent areas in the Great Lakes-St. Lawrence Forest Region (Rowe 1972) where I have recorded observations for several years Picoides villosus is well-distributed in the forests, wood stands, woods, and woodlots of various ages at all times of the year. It displays a marked preference for Fagus grandifolia and other hardwood species (Table 4). The fact that Ulmus americana rates highly on the list is probably a recent. phenomenon resulting from the serious damage caused to that tree by the Dutch elm disease. It would be expected that tree species with a coarse bark such as most Acer sp. and Quercus sp. should provide more foraging surface area than a species with a smoother bark like Fagus grandifolia. Consequently those would be expected to be selected first but my data indicate clearly that those species rank second and fourth in the list. The difference between the various tree species selected by males against those chosen by females proved to be highly significant as indicated in Table 4, the females favoring mainly dead Ulmus americana (X²=18.545; d.f.=6; G=146.918; P<0.005).

My observations in the boreal forest of Quebec and Ontario, recorded mainly from May through July, with a few records in August and during the fall are summarized in Table 5. Populus tremuloides

/	Picoides villosus (223)*		Picoides pubescens (226)*	
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
Populus tremuloides	47	, 42	28	33
Betula sp.	27	× 37	38	34
Picea sp., Abies balsamea	8	11	12	° 19
Alnus and Salix sp.	4	10	16	23
Dead and burnt trees	20	17	1 8	7
Total	106	117	110	116
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Table 5

Comparative number of sightings, by species and sex, on trees used for foraging in the boreal forest region of Quebec and Ontario, from May through July (1967-1969).

* Total number of sightings

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and other <u>Populus</u> species, along with <u>Betula</u> species are the preferred trees used by <u>P</u>. <u>villosus</u> for foraging whereas the coniferous trees are not used as often. Dead and burnt trees are frequently used where they occur and there appears to be no distinction as to their species, which in most instances could be identified as coniferous species. In several <u>Pinus banksiana</u> stands, often very extensive, in the Abitibi and Upper St. Maurice River regions of Quebec, I have seldom recorded <u>P</u>. <u>villosus</u>. On the 'rare occasions when it was observed in those stands, it was near clumps of <u>Populus</u> or <u>Betula</u> species. It therefore appears that pure stands of Jack Pines are not attractive to <u>P</u>. <u>villosus</u>. I found no selective difference between males and females for particular species of trees used as foraging sites (\underline{X}^2 =13.277; d.f.=3; G=4.683, P>0.01) in the boreal forest.

In the humid coastal forest of Washington State, during March 1968, no difference was observed between the tree species selected by males when compared with those selected by females (\underline{X}^2 =9.201; d.f.=2; G=0.830, P>0.01). The sightings summarized in Table 6 indicate a preference for conifers and large deciduous trees, whereas alders and willows were used only occasionally for foraging. Elsewhere in the interior of the western part of the range (California, New Mexico, and Arizona), in the montane woodland (Table 7), no significant difference between sexes with regard to tree species selection for foraging was observed during March and April 1968 (\underline{x}^2 =13.277; d.f.=4; G=1.551; P>0.01). Both sexes used Pinus and Quercus species more frequently than any other tree 1

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,	Picoides villosus P (73)*		<u>Picoide</u> (B pubescens 89)*
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
Conifers	19	15	2	` 1 ý
Large deciduous	13	14	18	23
Alnus, Salix, and Populus sp.	5	7	21	24
Total ,	37	36	41	48

Comparative number of sightings, by species and sex, on trees used for foraging in coastal forest of Washington State, March 1968.

* Total number of sightings

Table 6

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Comparative number of sightings, by species and sex, on trees used for foraging in interior California, New Mexico, and Arizona, March and April 1968.

	<u>Picoide</u> (20	<u>s villosus</u> 08)*	Picoides pubescens (131)*	
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
/ - / - / / / / / / / / / / / / / / / /	37	31	9	, 6
Quercus sp.	33	29	· 3	1
Other conifers	. 8	11	6	3
Other hardwood sp.	· 9	" 7	11	_. 15
Populus, Salix, and Alnus	20	23	37	40
Total	107	101	66	65

* Total number of sightings

Table 7

species on which they were observed. In certain situations, mainly along rivers, they were noted a few times in willows, aspens, and cottonwoods.

In the Bahama Islands, during March 1966, only six sightings were recorded on deciduous trees (<u>Casuarina</u> sp.; 4 for males, and 2 for females) from a total of 1,991 sightings (1,055 for males, and 936 for females). All the other sightings were recorded on pines (<u>Pinus caribaea</u>), which appeared to be in good condition. <u>Picoides</u> <u>villosus</u> therefore appears to be very specific to pines on the Bahama Islands. This is strengthened further by the fact that where deciduous trees are found among pines, mainly at the edges of stands or near areas of regeneration, only six sightings of <u>P</u>. <u>villosus</u> were recorded in those trees. Those sightings were all made at the edge of a highly disturbed area where only a small clump of pines had been left, near Nassau. One live-shelled <u>Casuarina</u> sp. was being used for nesting.

<u>Picoides pubescens</u> displays great geographic variation in its choice of habitats as indicated by Bent (1939) and more recent observations provided by several other authors. In the eastern part of its range <u>P</u>. <u>pubescens</u> occurs in a variety of wooded habitats ranging from wet thickets to mature forest stands. In the western part of its range it is often restricted to different habitats. In California, it is more often found in riparian growths and tracts of deciduous trees, and more rarely in oak belts and tracts of conifers (Grinnell and Miller 1944:241-244; this study). In Arizona it is limited primarily to deciduous trees of the Transition and

Canadian Life Zones (Phillips <u>et al</u>. 1964: 74-75). In Oregon and Washington, it usually occurs in coniferous trees in riparian situations and infrequently in conifers (Gabrielson and Jewett 1970: 383; Jewett <u>et al</u>. 1953:411; this study). In British Columbia and Alaska it is mainly a bird of riparian thickets (Munro and Cowan 1947:142-146; Gabrielson and Lincoln 1959:571-572). Stewart (1975: 167-168) recorded it in "tracts of bottomland and upland deciduous trees" in North Dakota whereas Bird (1961:16) found it in the aspen Parkland of the Canadian Prairie Provinces. In Texas Oberholser (1974:523) reported it from "humid woodlands, wooded and bushy streamsides". Elsewhere in the United States its habitat preferences have been summed up by several authors in regional works and in Canada by Godfrey (1966:245).

In the Great Lakes-St. Lawrence Forest Region of eastern Canada, mainly in the relatively undisturbed forest stands of Mont St. Hilaire, Quebec, <u>P. pubescens</u> displays a marked preference for <u>Fagus</u> <u>grandifolia</u> and dead <u>Ulmus americana</u>, the latter sightings having been recorded mainly during the fall and winter months (Table 4). <u>Acer saccharum</u> comes third on the list of trees used for foraging whereas <u>Quercus</u> and <u>Pinus</u> species are used the least for foraging by <u>P. pubescens</u>. Miscellaneous species such as <u>Alnus</u>, <u>Salix</u>, <u>Amelanchier</u>, etc. rate high in the list and are followed by <u>Populus</u>^{*} species. It is surprising to find <u>Fagus grandifolia</u> to be the most frequently used tree in foraging in that forest type because its relatively smooth bark does not appear to offer as <u>large</u> a foraging surface area as the other species with rougher bark but the softer

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· bark of those trees may provide a higher density of preys, due to its softness. Beech trees used by pubescens for foraging usually have a smaller diameter $(D.B. \cancel{A}.)$ when compared with those used by P. villosus. However, the numerous small knot holes, cracks, and shallow crevasses of the bark of beech trees may yield a high percentage of preys more attractive to P. pubescens than the prey species found on other trees. Those may be easier to obtain on beech. A similar situation was noted in P. villosus, which forages. however on larger trees. A significant difference was found in the frequency of trees on which sightings were observed for male pubescens when compared to female sightings (X²=19.545; d.f.=6; G=200.100; P < 0.005). This difference can be accounted for partly by the fact that females (13%) were observed more frequently than males (9.5%) in Alnus and Salix species and that males (8.9%) forage more frequently in Populus species than females (5.3%). In that part of the range, the combined frequencies of Picoides villosus, when compared to those of P. pubescens are different at a highly significant level (X²=18.545; d.f.=6; G=3,362.059; P<0.005). Picoides villosus utilizes Fagus grandifolia and Acer species to a significantly greater extent than P. pubescens. On the other hand the latter made more frequent use of dead Ulmus americana (particularly during winter months), Populus species, Salix and Alnus species than P. villosus. It is therefore evident from the data of Table 4 that Fagues grandifolia (45.1%) is selected for foraging more frequently by P. villosus than the other tree species in the deciduous, relatively undisturbed forests of the Great Lakes-St.

Lawrence Forest Region (Mont St. Hilaire; Gatineau Park) where most of my observations were recorded.

In the coniferous forest, the sightings of P. pubescens in relation to the tree species utilized in foraging are shown in Table No significant difference was observed between the tree species 5. selected by males against those chosen by females (\underline{x}^2 =13.277; d.f.=4; G=6.949, P>0.01). Betula species are used extensively and rank first (31.9%) followed by Populus species (27.0%), and Alnus and Salix species (17.3%). Foraging on other trees amounts to 13.7 per cent on conifers and to 10.2 per cent on dead or burnt trees. When the combined frequencies of trees chosen by P. villosus are compared with those used by P. pubescens the difference in choice by the two birds is highly significant (x^2 =14.860; d.f.=4; G=1,332.953; P<0.005). The principle difference is that P. villosus uses more frequently the Populus species and the dead or burnt trees than P. pubescens. On the other hand, the latter species forages more frequently on Betula, Alnus, and Salix species, as shown in Table 5.

In the Pacific Rain Forest, for <u>P</u>. <u>pubescens</u>, the proportions of trees selected by males for foraging do not differ significantly from those selected by females as shown in Table 5 ($\underline{X}^2=9.210$; d.f.=2; G=0.600; <u>P</u>>0.01). Those birds forage primarily on <u>Salix</u> and <u>Alnus</u> species as well as on other large deciduous trees. They rarely go on conifers. When those data are compared with those obtained for <u>P. villosus</u>, the difference is highly significant ($\underline{X}^2=10.597$; d.f.=2; G=52.138; <u>P</u><0.005), although both birds frequently select large deciduous trees for foraging (<u>P. villosus</u>, 37.0%; <u>P. pubescens</u>
46.1%). However, little overlap occurs between the two birds as far as the most frequently selected trees are concerned, which indicates a good degree of segregation in the foraging substratum in that part of the range.

In the interior of the western part of the range of <u>P</u>. <u>pubescens</u> (California, New Mexico, and Arizona) primarily in montane woodland, the difference in the choice of trees selected by males versus females (Table 7) is not significant (\underline{X}^2 =13.277; d.f.=4; G=3.397; <u>P</u>>0.01), and softwood deciduous trees are chosen in preference to hardwood trees. Upon comparison of those data with those recorded for <u>P</u>. <u>villosus</u>, the difference in trees selected by one bird against the other is highly significant with little overlap between the main trees (\underline{X}^2 =14.860; d.f.=4; G=96.124; <u>P</u><0.005). Thus <u>P</u>. <u>villosus</u> forages primarily in pines and oaks whereas <u>P</u>. <u>pubescens</u> selects mainly softwood deciduous trees like <u>Populus</u>, <u>Alnus</u>, and <u>Salix</u> species.

2. Time spent foraging

A considerable amount of time during the active period in a bird's day is spent searching for food. It was not possible to determine the amount of time devoted to this essential activity in comparison with other equally essential activities during a 24-hour period, because I could not follow a given individual for more than a few hours at a time, except at the nest.

However, for a number of birds, which spent more than 30 seconds foraging, I recorded the time to the nearest 0.5 minute, devoted to

that activity by means of stop-watch in the Mont St. Hilaire area. It proved to be difficult to record with greater accuracy this type of information. My compiled data appear in Table 8, where the number of sightings, the mean of the time spent foraging, and the range of the recorded values are shown. Those data show little variation between sex and species, except on the Bahama Islands where the birds spend more time, on an average, in each foraging session. Furthermore the range of the observed values is not as wide.

This type of information, although interesting is not informative due to the particular mode of feeding of woodpeckers (to be discussed more fully later). For example, a bird may appear on a tree, explore it for 1.5 minutes, feeding in the meantime or carrying various other behavioral activities. Then it moves to another tree where it spends 10 seconds only locating an appropriate source of food at which it may spend a considerable amount of time, up to 18 minutes as recorded in a male <u>P</u>. <u>villosus</u>, on an aspen in the Abitibi region of Quebec, in June 1969.

3. Foraging height

Foraging height is highly variable in woodpeckers as indicated in some of the published data (Selander 1966; Jackson 1970). Jackson (1970) found a tendency for male <u>Picoides pubescens</u> to forage lower than females although there is overlap between the two sexes. In my experience, I never found a satisfactory way of recording foraging height, other than recording the height at which a bird starts foraging and the height at which the activity stops

Average time, in minutes, spent foraging in various populations of woodpeckers.

	Picoides villosus				- <u>Picoides</u> pubescens							
		MALE	S		FEMAL	ES		MALE	S		FEMALE	S
LOCALITY	N	mean	range	N	mean	range	N	mean	range	N	mean	range
Eastern Canada	174	1.6	0.5-18.0	168	1.9	0.5-16.0	191	"1. 7	0.5-13.0	177	1.9	0.5-16.5
Western rain forest	41	1.7	0.5-13.0	25	1.6	0.5-11.0	34	1.8	0.5- 9.0	27	1.7	0.5- 8.0
Western interior forest	17	1:4	0.5- 4.5 *	23	1.7	0.5- 6.0	29	1.9	0.5- 8.5	33	· 1.8	0.5-10.5
Bahama Islands	87	2.4	1.5- 4.0	49	2.1	1.0- 3.5						, B

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Table 8 '

or where it leaves the tree. No difference in landing heights were recorded between sexes. My reservations concerning the significance of time spent foraging are applicable here as well. Indeed, woodpeckers of both sexes, often start low on a tree (P. villosus) or on a lateral branch near the trunk (P. pubescens) and proceed upwards or outwards until they locate a point of interest, where a more specific activity takes place. A single bird may thus land, forage upwards, outwards, around the trunk, on the limbs of a single tree from a few feet above the ground (or snow) to the top of the tree in a few seconds without engaging in any specific activity. It then moves to another tree, or several other trees, where it repeats the same procedure, until it finds an area of interest on one tree or limb. Then a specific activity takes place. Since these activityrelated areas occur totally at random on trees and are found as a result the birds' search, not as a result of selection for a particular foraging height, this factor is thus probably highly dependent on chance and does not appear to be related to the sex of the birds. I can only conclude that height is independent of the foraging activity and that it has little importance with regard to the general ecology of those birds.

4. Foraging stations

The selection of foraging stations or sites in <u>Picoides</u> <u>villosus</u> and <u>P. pubescens</u> has been discussed recently by a few authors (Kilham 1961, 1965, 1970, 1973; Lawrence 1967; Jackson 1970; Kisiel 1972) and for the other woodpeckers (Ligon 1968a, 1968b;

Selander 1966; Wallace 1974; Williams 1975; Hogstad 1970, 1971, 1976). Those authors found temporal and spatial differences between species and between sexes of the same species, which are in general greement with my results.

a. Choice of foraging stations

My data are summarized in Table 9 and indicate highly significant differences between the foraging sites selected by the two sexes within a species and between the two species. In <u>Picoides villosus</u> both sexes forage on the trunk as well as on the limbs but males display a marked preference for trunks whereas females have been observed more frequently on branches. Both sexes infrequently forage on the ground or on trees, or branches lying on the ground. The difference between the frequencies recorded for females foraging on branches compared with those against trunks is not well-marked, but the choice of foraging stations by females compared with the frequencies obtained for males is highly significant (\underline{X}^2 =10.597; d.f.=5; C=676.136; P<0.005).

In <u>Picoides pubescens</u> (Table 9) the difference between the frequencies observed for males and females is highly significant $(\underline{X}^2=10.597; d.f.=2; G=341.365; P<0.005)$. Females forage significantly more often on branches than males whereas the latter forage equally (or nearly so) on branches and trunks. Females go more frequently to the ground than males but the difference is not significant.

When the combined data (both sexes) of both species (Table 9)

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Number of sightings in relation to foraging stations, by species and sex.

	<u>Picoides</u> vill	Picoides pubescens (17,848)*			
Sightings on	MALES	FEMALES	MALES	FEMALES	
Tree trunks	`7,764 (65.1)*	* 5,253 (48.1)	4,731 (49.4)	2,969 (35.9)	
Branches	4,014 (33.6)	5,498 (50.3)	4,619 (48.3)	4,996 (60.4)	
Ground ,	155 (1.3)	172 (1.6)	223 (2.3)	310 (3.7)	
Total	11,,933	10,923	9,573	8,275	

* Total number of sightings ** Percentage

Table 9 4

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are compared the difference between the foraging stations selected by <u>P. villosus</u> and <u>P. pubescens</u> is highly significant ($\underline{X}^2=10.597$; d.f.=2; G=812 655; <u>P</u><0.005). <u>Picoides villosus</u> is found more frequently on trunks than on branches and <u>P. pubescens</u> forages more frequently on branches and on the ground.

b. Live versus dead trees

Jackson (1970) and Kisiel (1972) found differences in the choice of trees (dead versus live) for foraging in both species studied here. I have collected data, mainly in the Great Lakes-St. Lawrence Forest Region on this topic and found no significant difference in the choice of live trees versus dead trees between the sexes of both species, especially in <u>P. villosus</u> (50.9% - 49.1%), although females <u>P. pubescens</u> show a slight preference for dead trees even in summer (47.3% - 52.7%). My data appear in Table 10 and indicate that <u>P. villosus</u> does not show any preference for the type of trees used for foraging throughout the year (\underline{X}^2 =6.635; d.f.=1; G=4.337; <u>P>0.01</u>). On the other hand, <u>P. pubescens</u> displays a marked **pre**ference during the summer months for live trees and for dead trees during the rest of the year (\underline{X}^2 =6.635; d.f.=1; G=7.629; P>0.01). Those results are consistent with Jackson's (1970) in Kansas.

No significant preference appears for one type of tree against the other when the combined data of <u>P</u>. <u>villosus</u> are compared with those of <u>P</u>. <u>pubescens</u> (X^2 =6.635; d.f.=1; G=5.839; <u>P</u>>0.01). It is therefore evident that the condition of the trees used for foraging

Selection of live versus dead trees for foraging in eastern Canada (Great Lakes-St. Lawrence, Forest Region)

. ′ .	Picoides villos	<u>us</u> (9,684)*	Picoides pubescens (6,729)*			
<u>></u>	DEAD TREES	LIVE TREES	DEAD TREES	LIVE TREES		
May through October	2,308 (47.8)**	2,513 (52.1)	1,891 (48.4)	2,012 (51.6)		
November through April	2,431 (50.0)	2,432 (50.0)	1,273 (45.0)	1,553 (55.0)		
All year	4,739 (48.9)	4,945 (51.1)	3,164 (47.0)	3,565 (53.0)		

* Total number of sightings for both sexes . ** Percentage

Table 10

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has some significance only with <u>P. pubescens</u> particularly during the winter months when dead trees (<u>Ulmus americana</u>) are selected (and for live trees in summer) more frequently.

5. Diameter of foraging stations

Some selection takes place between sexes in <u>P</u>. <u>villosus</u> and <u>P</u>. <u>pubescens</u> in the choice of the foraging substratum, mainly with regard to the species of trees used and certain parts of the trees. (trunk versus branches). It appears that further selection exist between sexes of one species and between species as to the size of the foraging medium. Both woodpecker species use extensively the branches and trunks of trees for foraging. The extent to which the 'niche' is partitioned between the sexes in a given species and between the two species (diameter foraging substratum) is dealt with below.

a. Diameter of trunks and branches - Eastern Canada

In the Great Lakes-St. Lawrence Forest and Boreal Forest regions, my data, recorded throughout the year (Table 11), indicate some significant trends with regard to the size of the foraging stations.

In <u>Picoides villosus</u> females tend to use more frequently (47.2%) than males (32.6%) trunks larger than 12 inches (30 cm) in diameter whereas males show a marked preference for trees in the 4-8 inches (10-20 cm) DBH range, and again females prefer trunks in the 2-4 inches (5-10 cm) class, and males, trunks of 2 inches (5cm) or smaller. The difference between the various frequencies is highly

	<u>P1</u>	coides vi (19,062	2)*	Picoides pubescens (10,227)*			
TREE DBH	MALES		FEMALES	MAĻES	FEMALES		
2 in. (5cm) or less	['] 146	(1.6)**	78 (0.8)	1,812 (31.	.7) 1,428 (31.7)		
2 - 4 in. (5-10cm)	139	(1.5)	299 (3.0)	1,427 (24.	.9) 1,728 (38.4)		
4 - 8 in. (10-20cm)	1,131	(12.3)	657°(6.7)	880 (15.	4) 341 (7.6)		
8 - 12 in. (20-30cm)	3,880	(42.0)	4,149 (42.2)	1,239 (21.	6) 851 (18,9)		
12 - 16 in. (30-40cm)	3,002	(32.5)	4,279 (43.5)	169 (3.0)) 75 (1.7)		
16 in. (40cm) or more	"93 4	(10.1)	368 (3.7)	196 (3.4	81 (1.8)		
Total	9,232	54 	9,830	5,723	• 4 , 504 [°]		
	,	<u>,</u> , ,	λ		· · · · · · · · · · · · · · · · · · ·		

DIAMETER OF FORAGING STATIONS - TRUNKS (Eastern Canada, all year)

** , Percentage

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Table 11

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significant (\underline{x}^2 =16.750; d.f.=5; G=677.802; <u>P</u><0.005).

In <u>Picoides pubescens</u> males and females use more frequently trunks of 4 inches (10 cm) or less in DBH than <u>P. villosus</u> but females use whose much more often than the males. Males tend to forage more frequently on trunks larger than 4 inches (10 cm) DBH, with a marked preference for the 4-8 inches (10-20 cm) DBH class. Comparison of all the frequencies shows a highly significant difference between the size of the trunks used by males compared with those used by females (\underline{x}^2 =16.750; d.f.=5; G=333.910; <u>P</u><0.005).

The difference between the two species are more striking, with <u>P</u>. <u>pubescens</u> foraging significantly more frequently on trunks with a 4 inch (10 cm) or less DBH, whereas <u>P</u>. <u>villosus</u> shows a marked preference for those with a DBH of 8 inches (20 cm) or more. Some overlap occurs however in the 4-8 inches (10-20 cm) class. Nevertheless the comparison of the frequencies obtained for each species on each trunk class is highly significant (\underline{X}^2 =16.750; d.f.=5; G=15,580.546; <u>P</u><0.005). Those data indicate a well-marked niche partioning between the two species with regard to the size of the tree trunks selected for foraging.

In the same geographical area, my data on the selection of certain sizes of branches for foraging by both sexes of both species are summarized in Table 12. For <u>Picoides villosus</u> they indicate no significant difference between the sexes (\underline{X}^2 =9.210; d.f.=3; G=1.220; <u>P</u>>0.01). Both birds forage more frequently (70%-) on branches with a 4-inch (10 cm) diameter or more, whereas branches with a 2-inch (5 cm) diameter or less are used the least (11.8%). Both sexes of <u>P</u>. <u>pubescens</u> display almost similar foraging

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DIAMETER OF FORAGING STATIONS - BRANCHES (Eastern Canada, all year)

	Picoides vi , (5,467	<u>110šus</u>)*	Picoides pubescens -(7,088)*			
DIAMETER	MALES	FEMALES	MALES	FEMALES		
2 in. (5cm) or less	294 (11.5)**	352 (12.1)	1,495 (41.2)	1,363 (39.4)		
2 - 4 in. (5-10cm)	443 (17.4)	.533 (18.2)	1,397 (38.5)	1,460 (42.2)		
4 - 6 in. (10-15cm)	612 (24.0)	694 (2 3.8)	477 (13 <u>.2</u>)	525 (15.2)		
6 in. (15cm) or more	1,197 (47.0)	1,342 (45.8)	258 (7.1)	<u>,</u> 113 (3.3)		

* Total number of sightings ** Percentage

Table 12

frequencies on branches with a 6-inch (15 cm) diameter or less, but males were observed foraging significantly more often than females $(7.1\frac{1}{3}/3.3\%)$ on branches with a 6-inch (15 cm) diameter or more. This is probably the factor which accounts for the significant difference recorded in the frequencies of foraging sites obtained for the two sexes of that species ($X^2=12.838$; d.f.=3; G=64.110; <u>P</u><0.005). The frequencies observed for each species for each branch class show a highly significant difference obtained (X²=12.838; d.f.=3; G=5,115.945, P<0.005). Those data indicate that P. villosus selects significantly larger branches than pubescens and that there is little overlap between species and branch class, particularly in the branches over 6 inches (15 cm) in diameter. Thus niche partioning existing here also in a well-marked manner. Each species and the two sexes of P. pubescens (to a lesser extent) select a well-defined range of branch sizes for foraging. Although tests of significance were not performed, there appears to be no seasonal variation in this group of data.

b. Diameter of trunks and branches - Pacific Rain Forest

In that part of the range no significant difference in the selection of a particular size of foraging medium was observed between the sexes of <u>Picoides villosus</u> and <u>P. pubescens</u> (X^2 =15.086; d.f.=5; G=4.456, <u>P. villosus</u> and 4.524, <u>P. pubescens; P>0.01</u>) as shown by the data in Table 13. On the other hand, a significant difference was obtained upon comparison of the combined frequencies recorded in each species (X^2 =16.750; d.f.=5; G=53.757; P<0.005).

	Picoides vil (73)*	losus	(89)*		
DIAMETER	MALES	FEMALES	MALES	FEMALES	
2 in. (5cm) or less	• 3 (8.1)**	5 (13.9)	11 (26.8)	17 (35.4)	
2 - 4 în. (5-10cm)		2 (5.6)	9 (22.0)	6 (12.5)	
4 - 8 in. (10-20cm)	3 (8.1)	2 (5.6)	9 (22.0)	11 (22.9)	
8 - 12 in. (20-30cm)	8 (21.6)	9 (25.0)	8 (19.5)	9 (18.8)	
12 - 16 in. (30-40cm)	16 (43.2).	11 (30.6)	4 (9.8)	3 (6.3)	
16 in. (40cm) or more	7。(18.9)	7 (19.4)	- -	2 (4.2) -	

DIAMETÉR OF FORAGING STATIONS - TRUNKS AND BRANCHES (Pacific Rain Forest)

Total number of sightings

** Percentage

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Thus <u>P</u>. <u>villosus</u> forages more frequently on trunks and branches with an 8-inch (20 cm) diameter or more while <u>P</u>. <u>pubescens</u> was observed more frequently on branches and trunks with an 8-inch (20 cm) diameter or less. There is some overlap in the 8-12 inch (20-30 cm) diameter class but not sufficiently to affect the overall results. The fact that <u>P</u>. <u>villosus</u> has a high percentage in the 2-inch (5 cm) class or less is due to its presence on smaller branches, particularly on the large conifers of the Pacific Rain Forest. In spite of entirely different general ecological conditions, niche partioning is evident again here.

c. Diameter of trunks and branches - Western Montane Woodland.

In that region the two species forage on different trees (Table 7) which are mainly conifers and oaks for <u>P. villosus</u>, and willows, alders, and cottonwoods for <u>P. pubescens</u>. In spite of those general differences no marked-differences were found between the sexes of both species (Table 14) with regard to selection of one size of foraging medium against another (\underline{X}^2 =15.086; d.f.=5; G=8.703, <u>P.</u> <u>villosus</u> and 3.607, <u>P. pubescens</u>; <u>P</u>>0.01). A significant difference was however obtained upon comparison of the combined frequencies recorded in both species (\underline{X}^2 =16.750; d.f.=5; G=159.831; <u>P</u><0.005). Again <u>P. villosus</u> selects the larger foraging sites and <u>P. pubescens</u> the smaller ones. Niche partioning is thus expressed here in two ways: in the selection of foraging sites of different sizes by each species and in the selection of different tree species for foraging by each bird.

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× .	<u>Picoides vil</u> (208)*	Picoides pubescens (128)*			
DIAMETER	MALES	FEMALES	MALES	FEMALES	
2 in. (5cm) or less	15 (14.0)**	14 (13.9)	20 (30.3)	22 (35.5) "	
2 - 4 in. (5-10cm)	8 (7.5)	14 (13. [`] 9)∘ ·	9 (13.6)	9 (14.5)	
4 - 8 in. (10-20cm)	10 (9.3)	13 (12.9)	16 (24.2)	15-(24.2)	
8 - 12 in. (20-30cm)	23 (21.5)	30 (29.7)	17 (25.8)	14 (22.6)	
12 - 16 in. (30-40cm)	36 (33.6)	23 (22.8)	4 (6.1)	1 (1.6)	
16 in. (40cm) or more	15 (14.0) ⁴ / ₇ / ₁	7 (6.9)	0	1 (1.6)	

DIAMETER OF FORAGING STATIONS - TRUNKS AND BRANCHES (Western Montane Woodland)

* Total number of sightings ** Percentage

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Table 14

d. Diameter of trunks and branches - Bahama Islands

The frequencies in the choice of foraging sites of different diameters between males and females of <u>Picoides villosus</u> in the pine forests of the Bahama Islands are summarized in Table 15. The difference between the frequencies recorded for each sex is highly significant (\underline{X}^2 =14.860; d.f.=4; G=1,224.77; <u>P</u><0.005). Thus males forage more frequently on trees with a 4-inch (10 cm) diameter or more whereas females were observed more frequently on smaller trunks and on branches, although males do not avoid the latter (17.6%). It thus appears that females <u>P</u>. <u>villosus</u> occupy a niche which could be occupied by <u>P</u>. <u>pubescens</u> but which is left unoccupied in its absence. There are no other woodpecker species in the pine forests of those islands.

6. Foraging activities

Kilham (1965) and Jackson (1970) described various activities related to foraging for both <u>Picoides villosus</u> and <u>P. pubescens</u>. I have used here a slightly different terminology in describing and comparing the foraging activities of both species. Based on my field observations the foraging activities of the two species can be divided into three main groups and two marginal categories which are described as follows:

<u>Gleaning</u> - this activity refers to any type of foraging that takes place at the surface of the bark or in crevasses, with the exclusion of the activities described below. It comprises "percussion", "peering and poking", and "scanning from a distance" as described by

	Picoides villosus (1,983)*					
DIAMETER	<u></u>	* MALES	FEMALES			
,2 in. (5cm) or less	ę	185 (17.6)**	379 (40.7)			
2 - 4 in. (5-10cm)		158 (15.0) ·	232 (24.9)			
4 - 8 in. (10-20cm)		279 (26.5)	178 (19.1)			
8 - 12 in. (20-30cm)		352 (33.5)	115 (12.3)			
12 in. (30cm) or more	*	(77, (7.3)	28 (3.0)			

DIAMETER OF FORAGING STATIONS - TRUNKS AND BRANCHES (Bahama Island)

* Total number of sightings ** Percentage



Kilham (1965). It includes also the birds' movements on the surface of the trunk (with or without bark) or on the branches in search of food and the actual taking of preys at the surface.

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Pecking - this activity combines the "pecking" and "scaling" of Kilham (1965) and the "scaling" of Jackson (1970). It consists in the removal of surficial bits of bark to reach preys by means of a few blows or by placing the bill under or on the side of poorly secured pieces of bark. I combined under this heading the two definitions of Kilham (1965), since "pecking", contrary to Jackson's definition (1970) is a more general and comprehensive, and less specialized term than "scaling" to describe a variety of foraging activities. Furthermore, I found it difficult, unless conditions ⁰ were ideal, to distinguish between "scaling" and "pecking" (<u>sensu</u>) Kilham 1965).

Excavating - this is a common activity observed in both species. It excludes here all excavating activities associated with nesting and is restricted to foraging for food. It consists in the extraction of preys in the bark, under the bark on the cambium, or in the wood of a tree or a branch, live or dead, by actually digging into those substances with the bill. Depths of more than 2 inches in digging for wood-boring larvae have been occasionally recorded. In this manner, sizeable chunks or splinters of wood are removed by means of sharp blows with the bill and then seized to be tossed aside if they have not already fallen off to the ground.

Flycatching - this foraging activity is rare and was seldom recorded in Picoides villosus but was slightly more frequent in P.

pubescens. It was observed mainly on warm, calm days. Woodpeckers do it in two ways, by sitting on a dead limb, in the open, and by waiting for an insect to fly by. Then it captures it in a typical flycatcher fashion, including bill-snapping. It is done also by capturing flying insects on the wing when a bird is foraging in some other fashion.

<u>Sap-drinking</u> - this activity is unusual in that genus and was consequently observed only in <u>Picoides pubescens</u> during May, at the sap-holes excavated by <u>Sphyrapicus varius</u> in <u>Acer</u> and <u>Populus</u> trees at Mont St. Hilaire, Quebec. Few encounters were recorded between the two species. This behavior pattern does not appear to have been reported previously for <u>P. pubescens</u> although Kilham (1965:140-141) observed it in <u>P. villosus</u>.

Kilham (1965), Selander (1966), Jackson (1970), Kisiel (1972), Ligon (1968a and b), and several other authors have recorded marked differences in the foraging ecology of various woodpecker species and even between the sexes of a same species. My data on foraging behavior were recorded to see if similar results could be obtained in other parts of the range of <u>Picoides villosus</u> and <u>P. pubescens</u> and to determine any change in behavior in an area of allopatry. In the latter case, field studies were conducted in the Bahama Islands, where <u>Picoides pubescens</u> does not occur. In addition to <u>Pillosus</u> the only other two woodpeckers found on those islands are <u>Centurus (Melanerpes?) superciliaris</u>, an uncommon resident, and <u>Sphyrapicus varius</u>, a winter resident. Both species, however, occupy different habitats from that of P. villosus (Bond 1956;



Table 16

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Legend of Roman symbols:

I: Eastern Canada, Great Lakes-St. Lawrence Forest Region and boreal forest, all year.

II: Great Lakes-St.Lawrence Forest Region, mainly at Mont St. Hilaire (Quebec), nesting season.

III: Bahama Islands, March.

IV: Pacific Rain Forest, March.

V: Western Montane Woodland, March and April.

	1	0	-		<u> </u>				*		· · · · · · · · · · · · · · · · · · ·
	٠. ١	م ۹		Gleani	.ng	Peckin	g	Excava	ting	Flycatching	Sap-drinkin
	•		з	, 			·····				
	P. villosus	(20,121)*	Ň	469	(4-3)**	4,409	(40.1)	6,110	, (55.6)	3 (0.03)	
I		6	F	418	(4.6)	3,884	(42.5)	4,827	(52.9)	1 (0.01)	
	P. pubescens	(17,725)	M	4,818	(53.0)	3,721	(40.9)	442	(4.9)	29 (0.3)	81 (0.9)
		1	F	4,533	(52.5)	3,681	(42.6)	304	(3.5)	43 (0.6)	73 (0.8)
	· · · · · · · · · · · · · · · · · · ·	·····			(0, 0)	r	·····		(77 5)		-
•	P. villosus	(5,895) .	M	63	(2.0)	642	(20.4)	2,430	$(// \cdot 2)$	2 (0.1)	
II -	`		F	• 84	(3,1)	793	(28.7)	1,874	(68.1)	1(0.04)	
٠	P. pubescens	(9,804)	M	2,343	(48.6)	2,206	(45.7)	211	(4.4)	64 (1.3)	
;			F.	2,467	(49.5)	2,314	(46.5)	110	(2.3)	·83 (1./,)	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
~~~~~		(1 095)	<u>м</u> ,		(44 9)	/ 02	(46.8)	87	. (8 3)		
III-	<u>r. viilosus</u>	(1,90J) 	F	481	(51.5)	°406	(43.5)	47	(5.0)		,
°											,
-	P. villosus	(71)	M	7	(19.4)	10	(27.8)	19	(5,2.8)		
IV	-		F	9	(25.7)	9	(25.7)	17	(48.6)		
`	P. pubescens	(86)	M	16	(41.0)	15	(38.5)	' 8	(20.5)		
-	<u> </u>	· ·	F	22	(46.8) 、	. 17	(36.2)	8	(17.0)		
	· · · · · · · · · · · · · · · · · · ·	· · · · · · · · · · · · · · · · · · ·		· · · · · · · · · · · · · · · · · · ·	1	·····				<u></u>	·
	P. víllosus	(201)	М	27	(26.0)	42	(40.4)	35	(33.7)	الله في عند عند عن جه مي عن -	
· v		· -	F	30	(30.9)	39	(40.2)	63	(28.9)		
2	P. pubescens	(123)	M	29	(47.5)	23	(37.7)	9	(14.8)		,
٠.			F	33	(53.2)	.26	(41.9)	3	(4.8)	وہ او بلن نیڈ جہ نیا ہے ہے	· · · · · · · · · · · · · · · · · · ·
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FORAGING ACTIVITIES

* Total number of sightings ** Percentage

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Table 16

Brudenell-Bruce 1975; this study). My data appear in Table 16.

Foraging activities: Eastern Canada

A highly significant difference was found between the frequencies of foraging activities of males <u>Picoides villosus</u> when compared to those of females ( $\underline{x}^2$ =12.838; d.f.=3; G=97.788; <u>P</u><0.005). Thus males "excavate" more frequently than females which in turn "peck" more frequently than males. Little difference between the sexes was observed in "gleaning" which is not a frequent foraging activity in that species. "Flycatching" is not usual either but was observed more frequently in males than in females and coincides with warm and windless days (Table 16, I). During the nesting season, the relative proportions recorded for the various foraging activities shift and most of the food is obtained, by both sexes, by "excavating" (Table 16, II). "Gleaning" has diminished and "flycatching" remains unimportant at that time of the year. Then, the difference between male and female frequencies for those activities is highly significant ( $\underline{x}^2$ =12.838; d.f.=3; G=66.806, <u>P</u><0.005).

In <u>Picoides pubescens</u> males and females exhibit significant differences in their mode of foraging ( $\underline{X}^2$ =14.860; d.f.=4; G=25.951; <u>P</u><0.005) throughout the year (Table 16, I). Males obtained higher frequencies while "gleaning" and "excavating" whereas females have been observed more often "pecking" and "flycatching". "Sap-drinking" is a marginal and opportunistic activity that has probably arisen in areas where <u>P</u>. <u>pubescens</u> is sympatric with <u>Sphyrapicus varius</u> and little difference was recorded between males and females in this

foraging pattern. During the nesting season, the difference in the overall modes of foraging between males and females (Table 16, II) remains highly significant ( $\underline{X}^2$ =12.838; d.f.=3; G=20.177; P<0.005). During that part of the life cycle the frequencies obtained for "pecking" increase whereas "gleaning" diminishes when compared to the annual values.

The modes of foraging of both species are very different as indicated by the data of Table 16 (I,II) throughout the year (X²=14.860; d.f.=4; G=18,993.164; <u>P</u><0.005) and during the nesting season (X²=12.838; d.f.=3; G=10,479.755; P<0.005). Picoides villosus can thus be characterized by its "excavating" activity in foraging, whereas P. pubescens is primarily a "gleaner". Overlap occurs between the two species in "pecking" but the diameter of the foraging stations used by each species is different as démonstrated earlier. The overlap is considerably reduced during the nesting season because P. villosus shifts to excavating more frequently. 'Therefore competition between the two species is reduced to a minimum at'a critical period in the life of those birds. Sap-drinking in P. pubescens was not recorded during the nesting season, probably because little sap runs at the holes in the bark at that time of the year, but "flycatching" was observed more often in P. pubescens than at any other time of the year because it is unlikely that this attivity could take place unless the weather is

warm enough to allow insects to fly.

## b. Foraging activities: Bahama Islands

Two subspecies of <u>Picoides villosus</u> are recognizable in the Bahama Islands (<u>P. v. maynardi</u> and <u>piger</u>) and no difference was found in their foraging activity. Those birds, as shown previously in this study occur mainly in the coniferous forest of <u>Pinus caribeae</u>, on which they forage almost exclusively. A significant difference was however obtained upon comparison of the frequencies recorded for males and females (Table 16, III) with regard to the three modes of foraging recognized in this study ( $\underline{X}^2$ =10.597; d.f.=2; G=13.558; <u>P</u><0.005). Males "peck" and "excavate" more frequently than females, whereas the latter "glean" proportionally more often than males. The foraging behavior of those insular birds is reminiscent of that P. pubescens in eastern Canada.

### c. Foraging activities: Pacific Rain Forest

It has been shown in previous parts of this study that both species utilize to a great extent different species of trees for foraging in that part of their range. In both <u>Picoides villosus</u> and <u>P. pubescens</u> (Table 16, IV) no significant difference was observed in the mode of foraging of males upon comparison with females  $(\underline{X}^2=9.270; d.f.=2; G=0.400; \underline{P}>0.01)$ . In <u>P. villosus</u> males "excavate" and "peck" more frequently than females but the latter "glean" more often. In <u>P. pubescens</u> the situation is reversed, males and females were found "gleaning" and "pecking" more frequently than "excavating". However, when the combined data of both species are compared, a significant difference was obtained in the foraging activities of

the two species ( $\underline{x}^2$ =10.597; d.f.=2; G=19.038; <u>P</u><0.005). <u>P</u>. <u>villosus</u> thus "excavates" more frequently than <u>P</u>. <u>pubescens</u> whereas the latter "gleans" and "pecks" more often than <u>P</u>. <u>villosus</u>. In spite of the overlap recorded in "pecking", competition between the "two species is attenuated by the fact that each woodpecker forages to a great extent on different species of trees in that region as indicated earlier in this study.

## d. Foraging activities: Western Montane Woodland

In that diversified ecological region (Table 16, V) no significant difference in the foraging activities of males and females were found in Picoides villosus ( $\chi^2$ =9.210; d.f.=2; G=0.803; P>0.01) and in P. pubescens (X²=9.210; d.f.=2; G=3.573; P>0.01). However, when the foraging activities of the two species are compared against each other a highly significant difference is obtained  $(X^2=10.597;$ d.f.=2; G=27.227; P<0.005). For P. villosus the frequencies observed in "excavating" are significantly higher than those obtained in P. pubescens and the latter species was recorded more frequently while it engaged in "gleaning". There is a significant overlap in absolute frequencies in "pecking" between the two species but, as pointed out earlier, those two woodpeckers, in that part of their range, forage mainly on different species of trees (Table 7) and each bird selects foraging substrata of different sizes (Table 4). Thus intrasperfic competition is reduced considerably and allows both species to coexist in the same geographical area, provided habitats, peculiar to each species, are available.

In summary, the two species of birds dealt with here have evolved complex foraging strategies that allow them to coexist. in the same habitat. Picoides villosus selects tree species that are different from those chosen by P. pubescens with regard to their size and the type of foraging substratum. P. villosus forages more, frequently on subtrate with a larger diameter than those on which P. pubescens has been observed. The mode of foraging of P. villosus is different from that of P. pubescens in that it "excavates" more 'frequently. The latter on the other hand "gleans" more often and the overlap in "pecking" is usually reduced by the selection of different foraging sites. In the absence of P. pubescens (Bahama Islands), P. villosus occupies those parts of the tree on which its, smaller congener is expected to be found and its foraging behavior resembles in that manner that of P. pubescens, as recorded in the areas of sympatry, by making more frequent use of the foraging techniques peculiar to P. pubescens.

## 7. Weather-dependent foraging activities

Climatic variables in relation to foraging behavior in birds have been ignored for the most part as recently pointed out by Grubb (1975). I have no quantitative data on the subject but will nevertheless attempt to demonstrate how, from my own observations, climatic factors affect foraging activities.

In the Great Lakes-St.Lawrence Forest Region, where most of my data were recorded throughout the year, winter is a very critical period and implies marked ecological changes which affect the

resident birds. With regard to Picoides villosus and P. pubescens I noticed little change in the foraging behavior during that season, except that both species were seen more frequently on dead Ulmus americana than at any other time of the year. On windy days (estimated at 25 m.p.h. -40 km - or more) both birds tend to forage lower on the substratum and select bigger foraging stations. In order to avoid the direct effects of wind, often combined with low temperatures, they tend to stay on the lee side of trees or branches. Snow reduces also foraging activities to a great extent, especially if it is accompanied by strong winds. Then birds were seen seeking shelter in crevasses and cracks on the lee side of trees, and even to enter holes for several minutes. Cold alone appears to have little effect on the foraging behavior of both woodpeckers if it is not accompanied by strong winds. When the sky is clear, those birds appear to seek the side of trunks or branches exposed to the sun for foraging. The most intense periods of foraging during December and January take place from about 08:30 to 11:00 and from about 15:30 until shortly before sunset. I have recorded intense foraging and behavior activities (drumming and courtship calls) in P. villosus on very cold (around -25° Celsius), but calm and sunny days, in January more than once. Those activities are regular in the cold sunny days of February when temperatures do not exceed -15 Celsius. It appears therefore that low temperatures alone do not affect the foraging activities of those birds (at least P. villosus), but that strong winds and snow are inhibiting factors in my study area. This aspect deserves further investigation.

In summer most of the foraging (intense) takes place about an hour after sunrise until mid-morning and resumes intensely again in the afternoon some three hours before sunset to stop at dark. In mid-day there is little foraging except during the period when the young are attended assiduously by the parents. Strong winds tend to keep the birds lower and on the lee side of trunks or branches, and rain appears to have little effect unless it is driven by strong winds. High temperatures,  $\pm 25^{\circ}$  Celsius or more, slow down the foraging activity to some extent but those high temperatures are unusual during the part of the day when the most intensive foraging occurs. It is on those hot windless days that I have recorded "flycatching" in both species. This behavior is probably the result of a high insect activity caused by the heat in the vicinity of foraging or resting birds.

In spring and fall I observed that high winds have the same effects as in winter or summer and tend to keep the foraging birds at a lower level than usual, <u>i.e.</u> keeping them off the smaller high branches of grees. Rain reduces foraging also when it is driven by strong winds as it does in summer and the birds seek shelter on the lee side of trees. On warm and calm sunny days there is more activity both in foraging and other behavior patterns such as displaying, drumning, calling, etc.

In spite of a lack of quantitative data on climatic variables in relation to foraging activity, it appears that low temperatures alone tend to have little effect on the foraging activities of both species. However, strong wind, snow, rain, and high temperatures 'tend to reduce or modify the expected foraging patterns to some extent

## NESTING ECOLOGY

The general nesting ecology of <u>Picoides villosus</u> and <u>p. pubescens</u> has been summarized in Bent (1939) and additional information has been provided more recently by Lawrence (1967). I have recorded various data on the nesting ecology of those two birds but I will consider here only those aspects which pertain more directly to the coexistence of the two species in the same habitat.

1. Trees and nest cavities

Bent (1939) has listed a few of the species of trees used by both species for excavating their nesting cavity. Lawrence (1967) is more specific and shows that P. villosus and P. pubescens use exclusively Populus tremuloides (11 nests of each species) in central Ontario for nesting. However, the trees utilized by P. pubescens are dead trees (100%) whereas P. villosus usually selects live trees (90.9%). My data, combined with those obtained by various observers through the Quebec Nest Record Card Program, where obtained in the Great Lakes-St.Lawrence and Boreal Forest regions and appear in Table 17. They indicate a far greater selection of tree species used as nesting sites than previously reported. Those observations show in addition that one bird is more selective than the other towards certain species of trees. The difference in frequencies between both birds for the selected nesting tree species is highly significant (<u>x</u>²=20.278; G=48.438; d.f.=7; <u>P</u><0.005). <u>P</u>. <u>villosus</u> in southern Quebec and adjacent parts of Ontario, selects Fagus grandifolia more frequently than any other species (43.5%). Farther north, in

	Picoi	des villosus	Picoides pubescent			
Fagus grandifolia	30**	(43.5)***	<b>b16</b>	(10.9)	,	
Åcer sp.	7	(10.1)	48	(32.7)		
Populus sp.	18	(26.1)	26	(17.7)		
<u>Betula</u> sp.	4	( 5.8)	18	(12.2)		
Ulmus americana			15	(10.2)	ſ	
Quercus sp.	1	( 1.4)	3	( 2.0)		

(13.1)

TREE SPECIES SELECTED FOR NESTING CAVITY *

* Origin of nests is from eastern Canada in the Boreal and Great Lakes-St.Lawrence Forest regions.

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** Number of nests

Dead or burnt conifers

Wooden post

Total

*** Perc'entage



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20 (13.6)

1 ( 0.7)

the coniferous forest, Populus species are preferred (26.1%) but dead or burnt conifers are used as well. (13.1%) where available. P. pubescens uses frequently the Acer (32.7%) and Populus species (17.7%). Betula species are used more frequently by the smaller woodpecker (12.2%) than by P. villosus (5.8%). Ulmus americana is not used by P. villosus, but P. pubescens often builds its nest in dead trees of that species (10.2%). This can partly be explained by the fact that P. pubescens is not as retiring a species as P. . villosus and will readily nest in the more open areas where elms grow commonly. Elsewhere, I found a single nest on the Bahama Islands, near Nassau, in a Casuarina sp. tree. My data, although superficially different from Lawrence's are however consistent with hers, when the comparison is made on a geographical basis. The main difference is due to the larger sample size and the larger geographical area covered by my data. It must be kept in mind also that the availability of trees species suitable for nesting is of prime importance no matter where the geographical area is located. Upon comparison of my data with the results of Conner et al. (1975) it appears clear that the species of trees selected in that part of the range are very different. The flora of southwestern Virginia is indeed different from that of southern Quebec.

2. Tree condition and nesting cavities

Bent (1939) reports that <u>P</u>. <u>villosus</u> and <u>P</u>. <u>pubescens</u> use both live and dead trees for nesting. Lawrence (1967) found that <u>P</u>. villosus selects significantly more often (90.9%) live trees

compared with dead trees for nesting. In <u>P. pubescens</u> she writes that dead trees are always used. Conner <u>et al</u>. (1975) reported that <u>P. villosus</u> uses equally dead and live trees in southwestern Virginia and that <u>P. pubescens</u> nests more often in dead trees (73.7%) than its congener.

In recording my data I have divided the sites used for excavating the nesting cavities into 3 categories based on the condition of the trees, inasmuch as it could be determined. The live tree category comprises all the trees thought to be "live" and those which were "live-shelled". The latter trees appear to be healthy but have a rotten core and only a solid outer shell. Many of the trees classified as "live" probably. would have been classified as "liveshelled" if it had been possible to verify their condition. For this reason those two types of trees were joined in the same group. "Dead trees" comprise all the dry trees without leaves or the burnt trees left standing, including stumps. "Dead limb", although selfdescriptive, comprises all the live trees with a dead limb used for nesting. From those data (Table 18), P. villosus selects "live or live-shelled" trees for nesting in preference to any other type of trees, but in the Boreal Forest Region, it uses frequently dead or burnt trees also, particularly in burnt or cut-over areas. In contrast P. pubescens nests more frequently in dead trees (59.4%) and dead limbs (37.5%). The difference between the two birds for the choice of a nesting site is thus highly significant  $(\chi^2 = 10.597;$ ,G=113.822; d.f.=2; P<0.005).

TREE CONDITION	Picoides villosus	<u>Picoides</u> pubescens		
Live or live-shelled	46 (80.7)*	3 (3.1)		
Dead or burnt	· `10 (17.5)	ِ 57 (59.4) ُ		
Dead limb only	1 (1.8)	36 (37.5)		
Total	57	96		

* Percentage

. Table 18

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3. Location of nest entrance

This aspect has been discussed only briefly by Bent (1939) but Lawrence (1967) and Conner (1975) provide more information on the subject. In central Ontario, Lawrence (1967) found in a small sample of 22 nests that the entrance of most nests, in <u>P. villosus</u> and <u>P. pubescens</u>, faced east and south. Conner (1975) recorded that most of his nests opened in a northeasterly direction, contrary to Lawrence's findings.

My own results combined with Lawrence's (1967:66), because they were collected in the same general geographical area, appear in Table 19. P. villosus displays a marked preference for nest holes oriented to the south (30.4%) and to the east (27.5%) as originally found by Lawrence. Upon comparison of my data with Lawrence's no significant difference was obtained. Nest openings facing a southwesterly (22%) or a westerly (21.1%) direction predominate in P. pubescens. No nest of either species was found to face north. The difference in orientation of the nesting cavity entrance between the two birds is highly significant  $(\underline{X}^2=20.278;$ d.f.=7; G=350.867; P>0.005). Those data are different from Conner's (1975) who suggests that the slope of the trunk may be "the most important factor in nest orientation". Although I have no detailed information on the slope of the trees where the nests were found, most of the nests examined by me were on vertical trunks or limbs, or a few degrees only off from the vertical. I do not believe this to be an important factor in nesting site selection and/or in determing the orientation of the nest entrance.
· - 	ORIENTATION OF NEST OPENING					·			
•	N	NE	E	SE	S	ัรพ	W	, NW	Total*
<u>Picoides</u> villosus	0.	3 (4.3)**	19 (27.5) 12	(17.4)	21 (30.4)	4 (5.8)	7 (10.1)	3 (4.3)	69
Picoides pubescens	0	1 (0.9)	14 (12.8) 19	(17.4)	17 (15.6)	24 (22.0)	23 (21.1)	11 (10.1)	109

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* including data provided by Lawrence (1967:66)

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** Percentage

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Table 19

The fact that the highest proportion of the nests of both species (89.9%) examined in eastern Canada face in a general southerly direction, from east to west, and that only 6.2 per cent face NW, 2.3 per cent NE, and none N, indicates a selective value for those orientations, irrespective of the regional topographic or geographical influences. My data, including Lawrence's (1967), indicate clearly that the orientation of the nest entrance is selected as a function of the amount of sunlight falling on the entrance, particularly in P. villosus, which is an early nesting species in the spring when temperatures are still relatively low. Even in a wooded area, it is advantageous to have the entrance of the nest facing in those directions, because, by the time the leaves filter the amount of sunlight, incubation is advanced in P. villosus. A good amount of sunlight on the nesting cavity entrance in the early part of the incubation can thus provide light and warmth as suggested by Lawrence. This is not as important in P. pubescens because it nests a few weeks later than P. villosus, when temperatures are usually several degrees higher. This factor seems to account for the different orientation of the nesting cavity entrance at least under this latitude. Thus the orientation of the nest entrance, as suggested by the evidence provided above, appears to be determined by the amount of sunlight available and probably has a survival value to be determined in future studies.

4. Characteristics of nest trees

Bent (1939) reported in general terms only on the size of the

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trees used for nesting and the heights of the nesting cavities. Lawrence (1967) and Conner <u>et al</u>. (1975) provided more detailed information on those topics. The data summarized in Table 20 are derived from my own observations and from the information compiled from the Quebec Nest Record Card Program. They are comparable with Lawrence's (1967:65) but they are different from Conner's <u>et</u> <u>al</u>. (1975:146). The difference, as pointed out earlier, can be explained mainly by the different general ecological conditions of the forests in southwestern Virginia as compared with those of southern Quebec and central-southern Ontario where most of my observations were made.

As pointed out by various authors, both species of an excavate the nest entrance under a protusion which may offer protection against rain. This is particularly frequent in <u>P</u>. <u>villosus</u>. In <u>P</u>. <u>pubescens</u> the nesting cavity is more often excavated near the top of a broken trunk or near the end of a limb where there is no protection. I therefore conclude that the presence of a protuberance above the nest entrance is more coincidental than a result of selection for such a site.

The means of the diameter of the trees or limbs used by both species as nesting sites (Table 20) are different. But this factor is not very important as far as I could determine it and as indicated by the range in diameters observed for each species. Furthermore, irrespective of the size of the trees selected for nesting, other factors appear to be more important as shown in . previous sections. In addition, the time of nesting is different.

DBH **				He	leight of nest (in feet)			
	N .	Range	Mean	N	Range	Mean	SD	
Picoides villosus	59	7 - 18	13.9	63	7.5 - 78	30.43	20.543	
Picoides pubescens	109	5 - 18	9.4	154	4.0 -085	28.91	19.840	

MEASUREMENTS OF NEST TREES * AND HEIGHT OF NEST

* Including limbs and trunks

** Diameter of tree at breast height, in inches

Table 20

in each species, being much earlier in P. villosus which would contribute to reduce competition between it and P. pubescens for nesting sites. Those data indicate also that the upper limit of the diameter of the trees or limbs is not important but that the lower kimit of the diameter is probably a limiting factor in the selection of the nesting sites. In this respect my results are more comparable with Conner's et al. (1975) than with Lawrence's (1967), who found her nests primarily in Populus tremuloides. A smaller diameter in a hardwood species may accommodate better a nest cavity than a softwood species of similar size. Thus the hardness and rigidity of the wood in the former species may allow thin walls around the nest cavity and yet be able to support the part of the trunk or limb above the nest, which could not be prevented from breaking in soft wood species, particularly in strong winds. This applies particularly to P. villosus since pubescens often builds its nests near the top of a stump.

The data on the height of nest entrance appear also in Table 20. My results are comparable with Lawrence's (1967:65) but average somewhat higher than those recorded by Conner <u>et al</u>. (1975:146). The local ecological conditions of the flora in those three areas probably account for that difference. On the other hand, the difference in height selected by the two woodpecker species is not significant ( $\underline{t} = 0.537$ ;  $\underline{P} > 0.05$ ). The heights recorded are extremely variable as indicated by the ranges of Table 20. In view of those results and of the evidence presented in the other parts, the height of the nest is not a significant competition factor between two birds.

To sum up, the evidence presented above on the species of trees selected as nesting sites, the condition of the trees used for nesting, the location of the nest entrance, the general characteristics of the nesting sites, and the time of nesting makes it possible to conclude that little interspecific competition exists between the two birds at that critical time of the year.

## FOOD

Beal (1911) and McAtee (1911) provided detailed information on the food habits of <u>Picoides villosus</u> and <u>P. pubescens</u> from the analysis of a large number of stomach contents obtained across the species ranges and other data are given in Walbauer <u>et al</u>. (1970).

I have reexamined Beal's data in search of differences in the food habits of the two species purely upon comparing the insect species taken by each bird. I have summarized the results in Table 21. They clearly indicate that little overlap occurs in the species of insects preyed upon by each bird. Stomach contents collected by me and recently identified by the Entomology Research Institute (Canada) agree with Beal's earlier findings although only 3 stomach contents of each bird were examined. In addition to the insects known to be eaten by <u>P. villosus</u> I have recorded 3 cases where a male has eaten slugs (<u>Philomycus carolinensis</u>) taken on a dead trunk lying on the ground at Mont St. Hilaire, Quebec. I have observed the same species (females) taking earthworms twice, under leaves in the same area in June 1965. The insects captured on the wing by <u>P</u>.

Order	Picoides villosus	Picoides pubescens	Overlap *
Coleoptera	17	.25	3 (7.1)
Hymenoptera	1	2	0
Diptera	1	0	0
Hemiptera	2	6	1 (12.5)
Lepidoptera	0	. 3	0
Total	21	36	4 (7.0)

NUMBER OF INSECT SPECIES EATEN ACROSS THE RESPECTIVE RANGES

* As indicated by the number of insect species recorded in the stomach contents of both species of woodpeckers. Percentage of overlap appears in parentheses.

Table 21

1965 at the study area.

Beal (2911:10) provides also information on the amounts of vegetable matter eaten by each species, as follows: <u>P. villosus</u> 22.33%, <u>P. pubescens</u> 23.95%. Otvos (1967) reported a high insect contents (95%) in the stomach of a bird from Costa Rica. Upon comparison of the list of materials ingested by each species there is a considerable overlap, mainly in the fruits and seeds eaten. In this instance, interspecific competition is probably minimal in spite of the appearances, because those food items are usually available in good quantities, assuming that they were taken in the fall.

In summary, in spite of the overlap recorded in the vegetable items eaten by each species, there is little competition for animal food between those two woodpeckers, as predicted from the analysis of their foraging habits.

# INTERSPECIFIC CONFLICTS

Interactions between <u>Picoides villosus</u> and <u>P. pubescens</u> are few and of low intensity in the study areas. Lawrence's findings (1967) on this matter are comparable with my results.

Interspecific contacts between <u>P. villosus</u> and <u>P. pubescens</u> and other vertebrate species have been dealt with to some extent in an abundant literature on woodpecker ecology (Bent 1939; Lawrence 1967; Kilham 1962, 1965, 1966a and b, 1969, 1970, 1974; Ligon 1968a and b, 1970, 1973; Foster and Tate 1966; Morse 1972; Davis 1965) and in many shorter less important articles and notes.

I will report here only on my most significant observations. On 2 May 1965, at Mont St. Hildire, Quebec, I watched a Starling (Sturnus vulgaris) attempting to dislodge a female P. villosus from her nesting cavity for several hours (16:40 to 19:23). The Starling was apparently not successful because it was not seen in the vicinity of the nest again. This was an unusual nesting situation; in an open àrea, with only a'few tall Fagus grandifolia left standing. Usually P. villosus selects a nesting site deep in the forest which is not attractive to Starlings.» In the same area on 24 May 1965, I watched a pair of P. pubescens being chased away from a nearly finishe nest cavity by a pair of Sphyrapicus varius which occupied it after having enlarged the entrance. The latter successfully raised a brood in that cavity? Over a period of several years I observed a number of encounters between P. pubescens and Tree Swallows (Iridoprocne bicolor) for the possession of cavities, particularly, in open areas and in sectors where dead trees are standing in water. To my knowledge swallows were never successful in their attempts at taking over nest cavities. On a few occasions, I observed aggressive behavior between both P. villosus and P. pubescens and the Great Crested Flycatcher (Myiarchus crinitus) but I could not determine the motive of the encounters.

A pair of <u>P</u>. <u>pubescens</u> was dislodged from a freshly excavated nest cavity by a Northern Flying Squirrel (<u>Glaucomys sabrinus</u>) at Mont St. Hilaire in late May 1966. The squirrel was thereafter regularly seen in the cavity throughout June and early July, and later from September to November, when it disappeared from the area.

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In the meantime, the dislodged pair of <u>P</u>. <u>pubescens</u> had successfully raised a brood in another tree some 10 metres away from the original nest.

No aggressive interactions were observed in the study area between <u>P</u>. <u>villosus</u> and <u>P</u>. <u>pubescens</u> and the other nesting woodpeckers such as <u>Dryocopus pileatus</u> and <u>Colaptes</u> auratus, or with other cavity nesting species such as <u>Sitta carolinensis</u>.

Elsewhere, particularly in the burnt over areas of the boreal forest, encounters may be expected between <u>P. villosus</u>, <u>P.</u> <u>tridactylus</u>, and <u>P. arcticus</u> which in those areas appear to prefer dry trees in similar ecological situations for nesting. Short (1974) has reported upon such an encounter between <u>P. villosus</u> and <u>P.</u> <u>arcticus</u> in a relatively undisturbed region of New York State, and Gibbon (1966) between <u>P. villosus</u> and <u>P. tridactylus</u> in a disturbed area in New Brunswick.

In summary, the information available from the literature and from my observations show few aggressive interspecific contacts between <u>P. villosus</u> and <u>P. pubescens</u>, as a result of their different ecological preferences, as demonstrated earlier. Aggressive encounters are however more frequent with other birds (mainly unsuccessful) and infrequent with cavity-dwelling mammals (one successful case in the study area).

### SEXUAL DIMORPHISM

Several recent studies have dealt with aspects of the complex problem of sexual dimorphism in vertebrates. In birds there is an abundant literature on the subject and a number of papers treat of this problem in woodpeckers in relation to sexual differences in foraging habits (Kilham 1965; Selander 1966; Ligon 168b, 1973; Koch et al. 1970; Short 1970; Jackson 1971; Wallace 1974; Hogstad 1976) or in relation with more general theoretical aspects (Yom-Tov and Ollason 1976).

I have examined here the extent to which sexual dimorphism occurs in various body characters in the subspecies recognized in the previous parts of this study for Picoides villosus and P. pubescens. My results appear in Tables 22 and 23. Those are derived from the various body measurements used elsewhere in a study of geographic variation. For body weight the percentage of dimorphism varies in P. villosus from 0.00 to 15.99 with a mean of 11.41 in a sample of 89 individuals (52 males, 37 females). Those data indicate strong general dimorphism in body weight, males being substantially heavier than females. The percentage varies also as indicated by those limited data, from population to population. This would require further testing however. In P. pubescens, from a sample of 38 specimens (20 males, 18 females) from various populations, the mean of males is not statistically different from that of females (P>0.05) and the percentage dimorphism recorded is very small, 1.67. Little can be said about geographic variation in this parameter for P.' pubescens because of the small size of the sample. In spite of those deficiencies it can be concluded from the examination of those data that sexual dimorphism in body weight is strong in most populations of P. villosus and that it is nearly nonexistent in

			in subspecies		villosus
	,	Wing	Tail	Culmen	Tarsus
1.	: septentrionalis	2.43*	2.28*	13.15*	3.28*
~ <del>2</del> ŋ	terraenovae	1.03	**-0.94	8 48*	0.40
з.	<u>villosus</u>	2.35*	-0.25	9.82	2.46
4.	audubonii	1.04	1.34	9.74*	1.37
5.	piger	2.33*	2.50	12.97*	6.71*
6.	maynardi	2.94*		11.43*	5.80*
7.	picoideus -	2.32*	• 1.67 •	9.75*.	3.48*
8.	harrisi	2.02*	0.49	10.47*	3.40*
9.	hyloscopus	1.83*	-0.44	11.42*	4,.02*
10.	orius	2.67*	-0.11	11.94*	3.88*
11.	monticola	2.52*	<b>、1.73</b>	11.99*	3.40*.
12.	leucothorectis	2.62*	1.63	12.67*	5.25*
13.	icastus	2.43*	0.15	11.99* .	3.02
14.	intermedius	2.31*	-0.21	<b>`11.20*</b>	1.96
15.	jardinii	1.44*	2.20*	12.48*	3.62
16.	sanctorum	2.15*	1.90	11.98*	2.81
17.	extimus	2.24*	1.20	12.67*	2.76

* indicates a significant difference between means ( $\underline{P} < 0.05$ ) ** minus sign indicates reversed sexual dimorphism

Percentage sexual dimorphism = <u>Mean male - Mean female</u> x 100

Table 22

				,			
		- d Wing	<b>Tail</b>	Culmen	Tarsus		
1.	glacialis	**-0.50	-2.32	-2.39	0.00		
2.	nelsoni	-0.40	-2.22	-0.01	0.98		
3.	medianus	-0.81	-1.29	0.28 [.]	0.37		
4.	pubescens	-0.80	-2.09	2.95	0.36		
5.	leucurus	0.41	-0.19	2.14	1.10*		
6.	<u>gairdnerii</u>	-0.86	-1.49	0.62	1.40* *		
7.	<u>turati</u>	-1.91*	1.19	1.34	0.92		

Percentage sexual dimorphism in subspecies of Picoides pubescens

*' indicates a significant difference between means ( $\underline{P} < 0.05$ ) ** minus sign indicates reversed sexual dimorphism

Percentage sexual dimorphism = <u>Mean male - Mean female</u> x 100 Mean male

Table 23

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### P. pubescens.

Table 22 provides a summary of sexual dimorphism percentages calculated for 17 subspecies of <u>P</u>. <u>villosus</u> previously recognized in another study on the basis of the data obtained as a result of an extensive analysis of geographic variation. Wing length in that species is only slightly dimorphic but males have consistently longer wings than females. The difference between means is not significant (<u>P</u>>0.05) in two populations only (<u>terraenovae</u> and <u>audubonii</u>). In all the others it is significant (<u>P</u><0.05) but the percentages are small and highly consistent from population to population.

Tail length displays some dimorphism in all the subspecies of <u>P. villosus</u> but it is usually slight and a significant difference (P < 0.05) between means was recorded in two subspecies only (<u>septentrionalis</u> and <u>jardinii</u>). Tail length is a highly variable character that must be used with the greatest caution owing to the rapid and extensive wear undergone by the rectrices as soon as they are sufficiently developed to support the bird after the molt. Although, reversed sexual dimorphism (females having longer tails than males) has been observed in six populations at a very slight level (Table 22) the means of males are not significantly (P > 0.05) different from those of females in those populations. In spite of the fact that this phenomenon can apparently occur in <u>P. villosus</u>, as pointed out by a few authors, I am not at all certain that it really exists. I am currently inclined to think that it is the result of a strong bias in the measuring procedure (use of worn specimens) although ecological evidence could support such a theory (see previous sections). To solve this imbroglio, once and for all, it will be necessary to measure adequate samples in several populations soon after the molt. This could be done by capturing the birds alive in nets or traps and releasing them later if one is not inclined to collect large samples of specimens. Until this is done, it will not be possible to resolve the problem one way, or the other because museum specimens with unabraded tails are currently too few to represent an adequate sample for each subspecies for their purpose.

Bill size dimorphism is strong in the various populations of P. villosus (Table 22), males having consistantly and significantly (P < 0.05) longer bills than females. The percentage is smaller in the eastern populations but not markedly so. On the other hand it is high in the Middle America populations and in certain insular populations (piger, maynardi). My data are thus in accordance with Selander and Giller's (1963) results which ind#cate that sexual dimorphism in bill length is greater on islands in certain woodpeckers. This does not appear, however, to apply to the northern islands. The northern insular populations, terraenovae and picoideus, display a relatively low dimorphism percentage. Dimorphism in this character can be correlated to a great extent in most populations studied with the results obtained in the ecological analysis where it was demonstrated that females forage in a different way from males, except in the Pacific Rain Forest and Montane Woodland ecological regions. The data at my disposal from those areas are not extensive and we're recorded during a short

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period of the year only. For this reason more thorough information on the foraging ecology throughout the year in those regions may prove otherwise, particularly in areas of sympatry with other congeners.

Dimorphism in tarsus length is present in all populations and is strongest in the two Bahama Islands subspecies and in the U.S.A. southwest. It is smallest in the insular taxon of Newfoundland, terraevovae. I have no data on the foraging ecology of those birds in Newfoundland, but the Bahama Islands ecological data clearly indicates a significant difference in the mode of foraging between the two sexes and between those two subspecies when compared to mainland population. Longer tarsi in males "could thus be correlated with different foraging habits in insular populations. My results are comparable with those of Grant (1965, 1966, 1968) for Passeriformes, although the tarsi of male P. villosus alone are significantly longer than those of females from adjacent mainland Those data (Table 22) thus indicate that longer tarsi in areas. males are correlated with different foraging habits and with the selection of a different foraging niche when compared to females of the two subspecies in the Bahama Islands. A similar situation prevails in the subspecies leucothorectis in which this effect may be the result of greater selective pressures from closely related Picoides species (Short 1971). Thus additional niche partioning between the sexes in villosus may be an advantageous strategy. My ecological data on this aspect are insufficient and do not support that hypothesis. Additional field observations, recorded throughout

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the year, may, however, yield different results.

In <u>Picoides pubescens</u> females have consistently longer wings than males (Table 23) except in one subspecies (<u>leucurus</u>) but the difference in each set of means is not statistically different (P > 0.05), except in <u>turati</u>. The current results are somewhat different from the preliminary data presented by Short (1970) who found also that females tend to have longer wings than males in a number of populations in <u>P</u>. <u>pubescens</u>, using the measurements provided by Ridgway (1914), which are often based on very small samples. In all cases my samples are sufficiently large to verify the significance of the difference observed and it can be concluded that such a difference in wing length is significant only in <u>turati</u> (P < 0.05). In spite of the fact that females often have longer wings than males the difference observed is not statistically different. In <u>leucurus</u>, males have longer wings than females but the difference between the two means is not statistically different (P > 0.05).

With regard to <u>turati</u> it is difficult to offer an explanation for that situation. It is not unlikely that females <u>P</u>. <u>pubescens</u> in that part of their range have evolved longer wings than males, possibly as a result of competition and pressures from other sympatric and closely related species of the genus <u>Picoides</u> with which interactions have been reported (Davis 1965; Ligon 1968a, b; Short 1971). My ecological data on this complex problem are not extensive but indicate no significant difference in the foraging ecology of the two sexes in that area.

With regard to tail measurements (Table 23), reversed sexual

dimorphism was observed in this character as well, as pointed out earlier by Short (1970). Males of <u>turati</u> have longer tails than females. The difference in tail measurements between males and females is not significant (P > 0.05) in any of the subspecies of P. <u>pubescens</u>. The remarks made earlier concerning tail dimorphism in <u>P. villosus</u> are applicable here as well and a new investigation of. the problem is warranted when fresh material from various populations becomes available.

Light dimorphism occurs in bill length and males tend to have slightly longer bills than females. The percentage (Table 23) vary somewhat between populations but the difference between the means in each subspecies is not significant (P > 0.05). Those results are surprising in view of the significant differences observed in foraging between sexes in certain populations (<u>nelsoni</u> and <u>medianus</u>).

Dimorphism in tarsal length varies little in <u>P</u>. <u>pubescens</u> (Table 23) and males tend to have longer tarsi than females. Significant differences between the means of each sex (<u>P</u><0.05) were obtained for this character in two subspecies only, <u>leucurus</u> and <u>gairdnerii</u>. It is difficult to explain this difference due to my limited data on the foraging ecology of the species in that part of the range. For two subspecies no significant difference was obtained between the foraging activities of males when compared to those of females. More extensive field data may provide new insights on the problem.

In summary, strong sexual dimorphism in bill size in <u>P</u>. <u>villosus</u> - males having longer bills than females - corresponds to significant

differences in the mode of foraging in the two sexes. There is little evidence for reversed sexual dimorphism in tail length although the data on foraging ecology may support this contention. Dimorphism occurs to some extent in wing and tarsus lengths but is not as strong as in bill length. The morphological data Correspond for the most part to the expected foraging patterns. In Picoides pubescens sexual dimorphism is poorly marked and the difference between male and female measurements is significant in a few cases only. Significant sexual dimorphism occurs in wing length in one. population, turati. This may be interpreted as a strategy evolved to cope with intense competition pressures in an area of sympatry with other congeneric species of similar size and similar color pattern. Tarsus length is significantly but not strongly dimorphic in two subspecies, leucurus and gairdnerii. The explanation provided for dimorphism in wing length is not applicable in this case owing to the absence of other congeneric species of small size in that part of the species range.

#### DISCUSSION

Competition between sympatric species occupying a similar habitat has been the object of numerous papers and several books which have provided useful compilations of data and various interpretations of the information (Cody 1974; Lack 1967, 1968, 1971; Mayr 1970; MacArthur 1958, 1972; Wynne-Edwards 1972). In order to coexist in the same habitat sympatric congeneric species, particularly those with similar color patterns, have evolved strategies which allow

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them to occupy particular 'niches' as shown in several recent studies on birds.

With regard to <u>Picoides villosus</u> and <u>P. pubescens</u>, two similarly color-patterned congeneric woodpeckers, sympatric over most of their respective ranges, it has been demonstrated in the previous parts of this study how each species has evolved its own strategies. These allow them to coexist sympatrically. In addition, in certain parts of their range they coexist with other congeneric species as well.

Both species have not evolved migratory habits in their mutual zone of sympatry and over the area of sympatry with other congeners as a means of reducing interspecific competition particularly in winter, a time of the year when resources are more limited and at a greater premium than during the milder seasons of the year. Obviously other adaptations must have been evolved by each species to cope with the problem of year-round coexistence in the same habitat.

The information presented in the section on habitat selection indicates that each woodpecker, in several parts of its range, favors one type of habitat over another. The main differences in niche selection, however, have been observed in areas where the two species occupy similar habitats. In those areas, the niche preferences of each species have been found to be different in the choice of trees utilized for foraging. Those data indicate selections at two levels: a) in the choice of a peculiar general habitat by each species in certain parts of its range and, b) in the choice of a specific niche by each species where both species occur concurrently in similar habitats. Those results are in general agreement with the

findings of most authors who reported on woodpeckers and other bird species as well.

Contrary to the findings of a few authors (Jackson 1970; Kisiel 1972) the time spent foraging and the foraging height 'determined' for each woodpecker were found in the present study to have little importance in reducing interspecific competition between Picoides villosus and P. pubescens. The amount of time spent foraging may equally prove to be a factor of relatively little importance in foraging studies of other species of birds because the time spent at each foraging activity is greatly dependent on the opportunities encountered by the foraging birds to engage in a particular activity. Foraging height is important in other species as demonstrated by Several authors, notably MacArthur (1968) with wood warblers. This parameter, insofar as P. villosus and P. pubescens are concerned, is the result, like foraging time, of the opportunistic aspect of the foraging behavior of each species. Thus foraging height and/or time spent foraging should not be considered as ecological adaptations to reduce interspecific competition between those two species. Indeed those two birds spend more time at particular foraging activities and at particular heights, i.e. where food has been found. Elsewhere, irrespective of height, if no food is available, they continue their search until they find something of interest. Then, and only then, some specific activity takes place.

The information presented in the previous parts shows how <u>Picoides villosus</u> selects more frequently tree trunks and <u>P. pubescens</u> branches and the ground for foraging. This in itself could be

considered a significant partioning of the niche sufficient to permit the coexistence of two congeneric species, all, year, in the same habitat. On the other hand, my results, contrary to those presented by Jackson (1970) and Kisiel (1972) do not indicate that live trees are favored over dead trees by one bird when compared with the other, except for females P. pubescens in winter, which favor dead elms. A selection in favor of dead trees, which should provide more insect resources than live or live-shelled trees, would, however, be ' expected. But the bark of mature trees such as Fagus grandifolia and other favored species may provide a more abundant surface or sub-surface insect fauna than dead trees, due to its more tender bark. In dead trees more energy may be required to reach the deep woodboring larvae. It may thus be more advantageous to those two woodpeckers, especially in winter when the gub-surface parts are frozen hard, to search for insects on the surface (P. pubescens) or just below the surface of the bark (P. villosus) using foraging techniques that require a relatively lesser expenditure of energy compared with excavating deeply in a hard substratum for insect prey. In the areas of sympatry it has been shown here that the two species have evolved additional foraging strategies to reduce interspecific The selection by each species of foraging substrata of competition. different diameters appears to be very important in this respect. On the other hand, on the Bahama Islands, occupied allopatically by P. villosus, both sexes of that species tend to forage on smaller tree trunks and branches than what would be expected in that species in a similar habitat where it occurs sympatrically with P. pubescens.

The divergence in the choice of foraging stations of different sizes by the two birds is amplified by the information obtained on their respective modes of foraging as illustrated in the previous parts of this study. My findings are in general agreement with the observations reported by other workers (Jackson 1970; Short 1971; Kisiel 1972) in other parts of the range. They provide additional behavioral-ecological information in support of Gause's Principle and add to the data compiled by Lack (1971) with regard to the selection of a particular niche by sympatric ecologically similar species, the mode of foraging peculiar to each species, their nesting ecology, and the reduction in the competition for food resources by the selection of different prey species.

Differences in body size have been shown to be associated with differences in foraging habits for a number of birds both at the interspecific and at the intraspecific levels for several non-woodpecker species (Lack 1971; Grant 1965, 1966, 1968) and for a few woodpeckers (Kilham 1965; Ligon 1968b; Selander 1966; Wallace 1974; Kisiel 1972; Jackson 1970; this study). Those differences are in addition associated with the size of the foraging substratum and probably also, as suggested by Lack (1971) with the size of the preys. The difference in prey species is very significant between <u>P. villosus</u> and <u>P. pubescens</u>. Thus the intense selection for a particular type of foraging substratum by a given species, especially in areas of sympatry with one or several congeners of similar size and color pattern, may have given rise to sexual dimorphism. The principal purpose of this evolutionary feature is probably to lessen intersexual

competItion in the niche occupied by each species. A few authors have dealt with this problem (Rand 1952; Amadon 1959), particularly in woodpeckers and obtained for the most parts results comparable to those presented in this study (Selander and Giller 1963; Selander 1966; Kilham 1965; Ligon 1968b; Short 1970; Hogstad 1976).

In Picoides villosus the marked intersexual differences in body 1 weight, bill length, and, to a lesser extent, in wing length are associated with marked intersexual differences in the foraging ecology of each sex as shown elsewhere in this study. The intersexual morphological differences analyzed in another study (body weight; wing, bill, and tarsus lengths) vary geographically. Two allopatric insular populations of P. villosus (Bahama Islands, piger and maynardi) have a slightly higher dimorphism percentage in bill and tarsus lengths than most mainland and other insular populations. This can be correlated with the marked intersexual differences observed in the foraging ecology recorded in those two populations. The intersexual morphological differences are more pronounced on those islands than in the areas of sympatry with P. pubescens or other congeners, in spite of the fact that interspecific competition is reduced there as a result of the absence of other woodpeckers in the Bahamian pine forests. The other insular populations have not diverged morphologically (intersexually only) to the same extent because the colonization of the islands is probably too recent as it may be the case with P. villosus terraenovae, or because abundant food resources did not exert selective pressures in favor of very strong sexual dimorphism, as perhaps with P. v. picoideus. On the

Bahama Islands, where food resources appear to be limited in the pine stands my data suggest that strong intersexual partioning of the niche may be advantageous to the species in reducing competition for food between sexes.

The problem of reversed sexual dimorphism in tail length remains unresolved because of a lack of pertinent specimen material. The hypothesis, however, remains attractive but neither my morphological (insufficient) nor my ecological data can support Short's (1970) contentions or Jackson's (1971) proposal on the importance of this alleged phenomenon.

For <u>Picoides pubescens</u> most of what I have mentioned for <u>P</u>. <u>villosus</u> is applicable as well with regard to sexual dimorphism. However, 'reversed sexual dimorphism in wing length (<u>turati</u>) and regular sexual dimorphism in tarsus length (<u>leucurus</u> and <u>gairdnerii</u>) have been observed at a statistically significant level. In the first instance, the intersexual difference in wing length is probably the result of strong interspecific competition with sympatric congeners (Short 1971) of similar size and color pattern. In such cases it may be to some, yet unknown, advantage for females to have longer wings than males. This hypothesis, however, cannot be correlated with my limited ecological data which indicate no intersexual difference in the mode of foraging of the species in that part of its range.

On the other hand, I find it difficult to explain the significantly longer tarsi of the males in two populations. This intersexual difference may favor males and reduce competition with

females in allowing them to forage more efficiently on larger trunks or branches on which locomotion may be easier with longer tarsi. My ecological data, although insufficient in that part of the range, do not indicate the expected intersexual differences in foraging. It thus appears that certain ecological intersexual differences do not always correspond to expected morphological differences (sexual dimorphism) as illustrated by P. pubescens.

It is not unlikely that some intersexual morphological differences are the result of unknown selective forces which may be uncovered only after more ecological and morphological data have become available. Furthermore it seems appropriate to point out here that some of the intersexual differences, both ecological and morphological, are probably due to chance entirely, and the challenge of future studies will be to discover what is due to chance and what is the result of selective pressures.

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### GENERAL DISCUSSION

The information analyzed in the first part of this study shows that the three-toed woodpeckers of the genus <u>Picoides</u> are closely related to the Hairy and Downy woodpeckers and consequently to all the other Nearctic species of the genus <u>Dendrocopos</u>. For nomenclatural reasons the latter species have been assigned to the genus <u>Picoides</u> and this treatment is in partial agreement with certain proposals (Delacour 1951; Goodwin 1968; Short 1971; A.O.U. 1976). On the basis of marked morphological, behavioural, and ecological differences the genus <u>Dendrocopos</u> is thus restricted to the Palaearctic and Asiatic species conventionally referred to it with the exception of <u>obsoletus</u> which is best classified in the genus <u>Dendropicos</u>, as suggested earlier by Goodwin (1968).

The modern <u>Picoides</u> and <u>Dendrocopos</u> species have probably evolved from a common mid-Asiatic ancestor. After having reached North America extensive divergence presumably took place and eventually gave rise to the modern <u>Picoides</u> species. Among those, <u>Picoides</u> <u>villosus</u> and <u>P. pubescens</u> which now occupy vast ranges across diversified ecological conditions have evolved concurrently with present-day congeners in the southwestern part of the United States and in Mexico, and possibly also in Middle America. As a result of selective pressures from sympatric congeners their ranges shifted , and their ecological preferences changed. Under the Pleistocene climatic fluctuations caused by glacial advances and retreats (Dillon 1956), segments of populations became isolated and gave rise to strong variation in several body characters and contributed to an

increase in the variability in the general ecology of each species, as demonstrated in the third part of this study.

Variation in body characters (color, color patterns, body weight, and length of wing, tail,culmen, and tarsus) is treated in the second part. It follows similar trends in the two species although it is not as well-marked for certain characters in <u>P</u>. <u>pubescens</u>. Most of the variation is clinal, except in insular populations and appears to be associated with climatic factors as reported by other authors (James 1970). It is in general agreement with the well-known ecogeographic rules (Bergmann's, Allen's, and Gloger's). However, the small size of the Middle American populations of <u>P</u>. <u>villosus</u>, which are found in humid and cold climatic conditions, may in part be explained by the fact that those populations are probably derived from the colonizing stock and have retained their ancestral characters apparently in the absence of other sympatric congeners.

The current subspecies concept makes it difficult for the practising taxonomist to classify populations in which variation is clinal. In spite of its shortcomings, that concept nevertheless remains an acceptable and useful infra-specific category. In the case of <u>P</u>. <u>villosus</u> and <u>P</u>. <u>pubescens</u> the situation is particularly acute because variation in several characters is clinal over vast geographical sectors. However, when areas of uniformity or stability in one character or in sets of characters can be identified within clines those can be used to delimit the ranges of various populations with their associated broad areas of intergradation. This procedure allows for a reevaluation of the subspecies after a thorough analysis
of variation in morphological characters for both species has been made. Consideration has been given here to historical factors such as the effects of the Pleistocene glaciation on present-day distribution and its role in isolating populations, as found in other species (Mengel 1964, 1970; Hubbard 1969).

Concurrently those two sympatric congeners have diverged significantly in their ecology. Competition between congeneric species found in the same habitat has been treated recently by a number of authors (Cody 1974; Lack 1967, 1968, 1971; MacArthur 1958, 1972; Wynne-Edwards 1972) and it has been demonstrated that sympatric congeneric species coexisting in the same habitat have evolved strategies peculiar to each.

Picoides villosus and P. pubescens which are non-migratory congeneric species sympatric over vast areas of their respective ranges have similar color patterns but differ significantly in size in the areas of sympatry. The data presented in this study indicate how each bird has evolved particular strategies to reduce interspecific competition thus permitting their sympatric coexistence. Each species occupies a different habitat in several areas of their ranges but where they both occur in the same habitat each is found in a specific niche. The data presented here complement the information obtained by other authors on the subject in other parts of the species ranges (Kisiel 1970; Jackson 1970; Short 1971; Conner 1975; Conner <u>et al</u>. 1975). Time spent foraging and foraging heights as proposed by Jackson (1970) and Kisiel (1972) to be important factors in reducing interspecific competition appear to have little effect due to the

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opportunistic foraging behavior of those two birds. On the other hand, other aspects of the foraging ecology of the two birds such as the choice of foraging stations (trunks vs branches), the species and condition of trees used for foraging, the size of the foraging stations, the differences in nesting sites, the selection of different prey species by each bird, and the mode of foraging peculiar to each bird, provide strong evidence in support of Gause's Principle. Furthermore, marked intersexual differences in body size exist in Picoides villosus which correspond to strong differences in foraging ecology as demonstrated previously. It was not, however, possible to ascertain the existence of reversed sexual dimorphism in tail length in that species. The degree of sexual dimorphism varies geographically and appears to be lower in areas of sympatry with other congeners. In Picoides pubescens sexual dimorphism in body dimensions is not strong and generally nonexistent but marked intersexual differences in the foraging ecology have been observed. This information therefore suggests that, in addition to niche partioning to reduce interspecific competition, further partioning of the niche takes place possibly to minimize intersexual competition. Finally the evidence presented here indicates that morphological intersexual differences generally correspond to expected ecological differences in foraging such as in P. villosus (Selander 1966) but such differences are not always related to intersexual morphological differences as shown in P. pubescens.

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