A CHRISTMAS COUNT ANALYSIS OF WOODPECKER ABUNDANCE IN THE UNITED STATES

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The science of biogeography ideally includes consideration of both the distribution and density of species. Traditionally, biogeographers have studied only the ranges of species, because of difficulties inherent in measuring population densities over broad geographic areas. On the other hand, animal ecologists (e.g., Andrewartha and Birch 1954, MacArthur 1972) have suggested that those same environmental factors which control the distribution of a species also affect its pattern of abundance within that distribution.

Woodpeckers are among the best known groups of North American birds. Nearly all of the 20 species found north of Mexico have received careful attention. We know where they occur and we know in general what foraging strategies they employ. However, few studies have attempted to determine large-scale patterns of population density.

The National Audubon Society Christmas count data, published as local population censuses, are of varying quality, but collectively are of such magnitude as to reveal continent-wide population phenomena. In this study we have used Christmas count data to analyze some patterns of winter abundance of North American woodpeckers, with a goal of revealing more about the ecology and adaptation of the species than would be possible from simple analyses of their distributional limits.

METHODS

This study represents a continuation of our efforts to use Christmas count data to study large-scale patterns of avian ecology and biogeography in North America. We described details of data storage, retrieval, and analysis previously (Bock and Lepthien 1974).

For this investigation we selected 27 inland regions in the U. S. (Fig. 1), based on the map and descriptions of Küchler (1964). For some areas (especially in the West) we had to combine many of Küchler's vegetation units to form a "region" (Fig. 1, Table 1) which contained even a marginally sufficient number of Christmas counts for meaningful analysis. When possible we combined similar vegetation types, so that each region consisted of generally similar habitats. The regions we analyzed were of varying shapes and sizes—often very complex configurations—designed to correspond when possible with Küchler's units of potential vegetation (see legend of Fig. 1). The 19 woodpecker species included in this analysis are listed in Table 1.

Christmas count data were extracted in groups of counts which fell inside the different regions. The average number of individuals observed per party-hour was computed as a measure of the relative abundance of each woodpecker species within each area. The results of Christmas counts probably are biased in that they underestimate species where

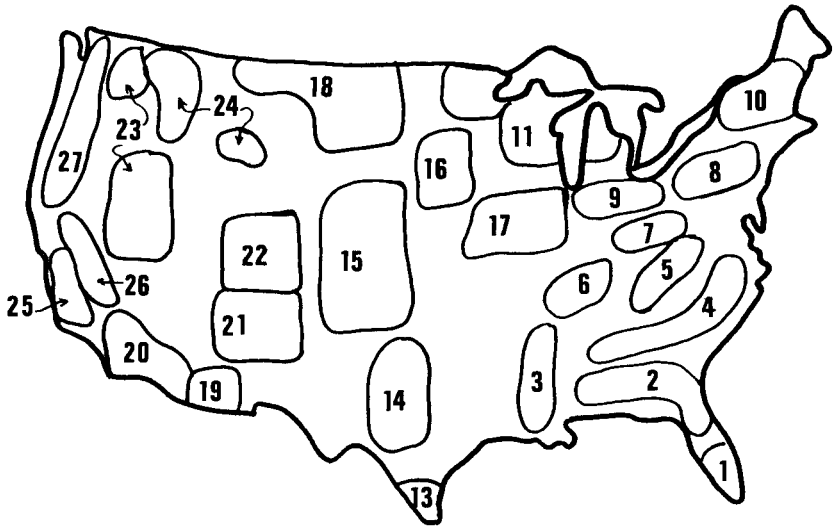

FIG. 1. Locations of vegetation regions used to analyze the winter abundance of woodpeckers in the U.S. 1 = everglades; 2 = southern mixed forest; 3 = southern floodplain; 4 = oak-hickory-pine; 5 = southern Appalachian oak; 6 = oak-hickory; 7 = mixed mesophytic forest; 8 = northern Appalachian oak; 9 = beech-maple; 10 = northeastern mixed forest; 11 = Great Lakes mixed forest; 12 = northern Minnesota coniferous; 13 = mesquite-acacia; 14 = central Texas savannah; 15 = central shortgrass prairie; 16 = bluestem prairie; 17 = ecotone of 16 and 9; 18 = northern shortgrass prairie; 19 = Arizona mixed forest; 20 = warm desert; 21 = southern Rocky Mountain mosaic; 22 = central Rocky Mountain mosaic; 23 = Great Basin; 24 = northern Rocky Mountain coniferous; 25 = interior Calif.; 26 = Sierra Nevada; 27 = northwestern mixed forest. These regions are based as closely as possible upon the classification of Küchler (1964).

they are common and overestimate them where they are rare. We do not feel that this would seriously influence our findings, since these possible biases would minimize real differences and not create artificial ones. However, Christmas count coverage is relatively poor in montane regions of the West; here, rare species may be missed entirely. For example, neither the White-headed Woodpecker nor the Northern Three-toed Woodpecker were observed in region 24, even though both occur there. We feel that the major value of this analysis is to reveal patterns in the more abundant and widespread species.

Avian data were taken from 827 counts published in the Christmas count issues of *American Birds* for the years 1969–70, 1970–71, and 1971–72. Climatological data are 50-year means from U.S.D.A. (1941); primary productivity estimates are from a combination of Whitaker (1970) and Collier et al. (1972).

ABUNDANCE OF SPECIES

Table 1 shows the average number of each woodpecker species divided by total party-hours of effort for counts in the 27 regions. The data suggest that the Common Flicker is the most abundant woodpecker wintering in the

areas we analyzed. It is followed by the Downy, Red-bellied, Hairy, and Acorn woodpeckers. These species are ubiquitous except the Acorn Woodpecker, which had a high average only because it reaches extraordinary densities in California, and the Red-bellied Woodpecker, which is very common throughout much of the eastern half of the U.S. (Table 1).

Habitat preferences of species with restricted distributions are apparent from Table 1. Several widely distributed species require further analysis. Figure 2 shows very generalized maps of their abundances constructed from the data in Table 1. Since our 27 regions did not include all of the U.S., and since Christmas counts may not detect species where they are rare, these maps should not be considered as depicting exact limits of distribution. They do, however, give a picture of relative abundance for the more ubiquitous species. Four degrees of shading were used to indicate increasing densities within each species; they do not represent similar densities between species (see Table 1).

Hairy and Downy woodpeckers.—These resident species are widely distributed, but show a marked concentration in the northeastern quarter of the U.S. (Fig. 2a,b).

Ladder-backed Dendrocopos.—The resident Red-cockaded, Ladder-backed, and Nuttall's woodpeckers occupy the southern and western U.S., and appear to replace their relatives concentrated in the northeastern states (Fig. 2c). However, none of these ladder-backed species reaches the densities of Hairy and Downy woodpeckers (Table 1), a fact which figures significantly in the abundance pattern of the *Dendrocopos—Picoides* group as a whole.

Common Flicker.—More than any group shown in Fig. 2, the Common Flicker concentrates in winter at lower latitudes (Fig. 2d). It is more common in relatively open habitats (Table 1) than would be expected on the basis of latitude alone.

Red-headed Woodpecker.—This species shows greatest winter densities in the Midwest, but also is common in the lower Mississippi Valley and the Southeast (Fig. 2e).

Red-bellied Woodpecker.—This species is abundant in the Midwest, the Mississippi Valley, and the Southeast (Fig. 2f). It and the Yellow-bellied Sapsucker are the only woodpeckers reaching high densities in peninsular Florida.

Pileated Woodpecker.—This species is unusual in that it occurs in both coniferous and broadleaf forests (Fig. 2g, Table 1). Highest densities are found in the same areas as the 2 previous species.

Yellow-bellied Sapsucker.—This species has migrated from the Great Basin, northern Rocky Mountains, and northern plains by the time Christmas counts are conducted (Fig. 2h). Small numbers remain in the northeastern

TABLE 1

WINTER ABUNDANCE OF WOODPECKERS IN MAJOR VEGETATION REGIONS IN THE U.S. (SEE FIG. 1), BASED ON 827 CHRISTMAS COUNTS.[1]

Species	Region (number of counts)													
	1 (15)	2 (22)	3 (22)	4 (36)	5 (34)	6 (24)	7 (15)	8 (60)	9 (25)	10 (106)	11 (106)	12 (15)	13 (4)	14 (14)
Common Flicker (*Colaptes auratus*)	.21	.88	1.47	.83	.15	.78	.42	.17	.45	.13	.06	.004	–	1.07
Pileated Woodpecker (*Dryocopus pileatus*)	.03	.16	.26	.08	.11	.28	.19	.02	.03	.02	.04	.06	–	–
Red-bellied Woodpecker (*Centurus carolinus*)	.51	.55	1.14	.72	.14	1.02	.35	.09	.44	.001	.24	.008	–	.10
Golden-fronted Woodpecker (*C. aurifrons*)	–	–	–	–	–	–	–	–	–	–	–	–	1.24	.35
Gila Woodpecker (*C. uropygialis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acorn Woodpecker (*Melanerpes formicivorus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Red-headed Woodpecker (*M. erythrocephalus*)	.001	.13	.49	.18	.03	.22	.09	.01	.43	.001	.22	.02	–	.05
Lewis' Woodpecker (*Asyndesmus lewis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	.004
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	.15	.20	.24	.35	.06	.22	.05	.02	.01	.002	.004	.003	.04	.05
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hairy Woodpecker (*Dendrocopos villosus*)	.002	.03	.18	.09	.11	.28	.23	.28	.16	.68	.50	.53	–	.01
Downy Woodpecker (*D. pubescens*)	.01	.08	.61	.48	.40	.97	.99	1.18	1.09	1.09	.88	.93	–	.14
Ladder-backed Woodpecker (*D. scalaris*)	–	–	–	–	–	–	–	–	–	–	–	–	.47	.36
Nuttall's Woodpecker (*D. nuttallii*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Red-cockaded Woodpecker (*D. borealis*)	.001	.03	.03	.06	–	–	–	–	–	–	–	–	–	–
Arizona Woodpecker (*D. arizonae*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
White-headed Woodpecker (*D. albolarvatus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Black-backed Three-toed Woodpecker (*Picoides arcticus*)	–	–	–	–	–	–	–	–	–	.001	–	–	–	–
Northern Three-toed Woodpecker (*P. tridactylus*)	–	–	–	–	–	–	–	–	–	.001	–	.004	–	–

TABLE 1. (*Continued*)

Species	Region (number of counts)													
	15 (21)	16 (23)	17 (98)	18 (25)	19 (5)	20 (23)	21 (18)	22 (29)	23 (12)	24 (6)	25 (14)	26 (9)	27 (13)	$\bar{X}$
Common Flicker (*Colaptes auratus*)	1.04	.22	.70	.03	.80	.61	.49	.27	1.73	.33	1.32	1.60	1.10	.62
Pileated Woodpecker (*Dryocopus pileatus*)	–	.005	.03	–	–	–	–	–	–	.02	–	.02	.03	.05
Red-bellied Woodpecker (*Centurus carolinus*)	.07	.04	.81	–	–	–	–	–	–	–	–	–	–	.23
Golden-fronted Woodpecker (*C. aurifrons*)	–	–	–	–	–	–	–	–	–	–	–	–	–	.06
Gila Woodpecker (*C. uropygialis*)	–	–	–	–	.30	.40	–	–	–	–	–	–	–	.03
Acorn Woodpecker (*Melanerpes formicivorus*)	–	–	–	–	.17	–	.08	–	–	–	.55	3.14	.30	.16
Red-headed Woodpecker (*M. erythrocephalus*)	–	–	.56	–	–	–	–	–	–	–	–	–	–	.09
Lewis' Woodpecker (*Asyndesmus lewis*)	–	–	–	–	–	.001	.05	.05	–	–	.02	.33	.26	.03
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	.008	.001	.03	–	.05	.03	.03	–	–	–	.04	.06	.08	.06
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	–	–	–	–	.003	–	.003	–	–	–	–	.01	–	<.01
Hairy Woodpecker (*Dendrocopos villosus*)	.06	.33	.25	.22	.003	.03	.16	.08	.002	.11	.01	.04	.07	.16
Downy Woodpecker (*D. pubescens*)	.22	.81	1.42	.30	–	.002	.004	.09	.01	.19	.06	.15	.28	.46
Ladder-backed Woodpecker (*D. scalaris*)	.03	–	–	–	.33	.08	.02	–	–	–	–	–	–	.05
Nuttall's Woodpecker (*D. nuttallii*)	–	–	–	–	–	–	–	–	–	–	.17	.16	.006	.01
Red-cockaded Woodpecker (*D. borealis*)	–	–	–	–	–	–	–	–	–	–	–	–	–	.01
Arizona Woodpecker (*D. arizonae*)	–	–	–	–	.02	–	–	–	–	–	–	–	–	<.01
White-headed Woodpecker (*D. albolarvatus*)	–	–	–	–	–	–	–	–	–	–	–	.10	.002	.01
Black-backed Three-toed Woodpecker (*Picoides arcticus*)	–	–	–	–	–	–	–	–	–	–	–	–	–	<.01
Northern Three-toed Woodpecker (*P. tridactylus*)	–	–	–	–	–	–	–	.01	–	–	–	–	–	<.01

[1] Data are expressed as the average number of birds observed per party-hour of effort.

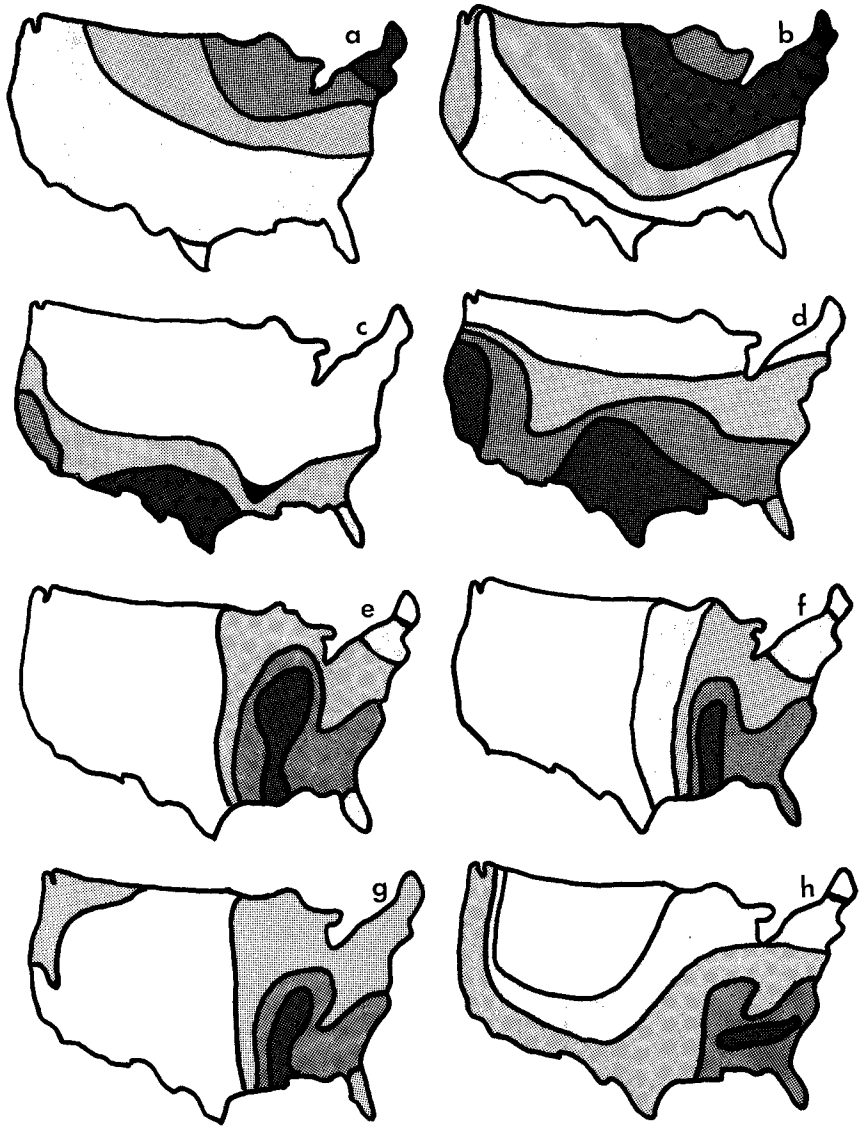

FIG. 2. Winter abundance patterns of common woodpecker species. White areas = no birds observed; the darker shadings indicate increasing densities within species, but are not comparable between species (see Table 1). a = Hairy Woodpecker; b = Downy Woodpecker; c = ladder-backed *Dendrocopos*; d = Common Flicker; e = Red-headed Woodpecker; f = Red-bellied Woodpecker; g = Pileated Woodpecker; h = Yellow-bellied Sapsucker.

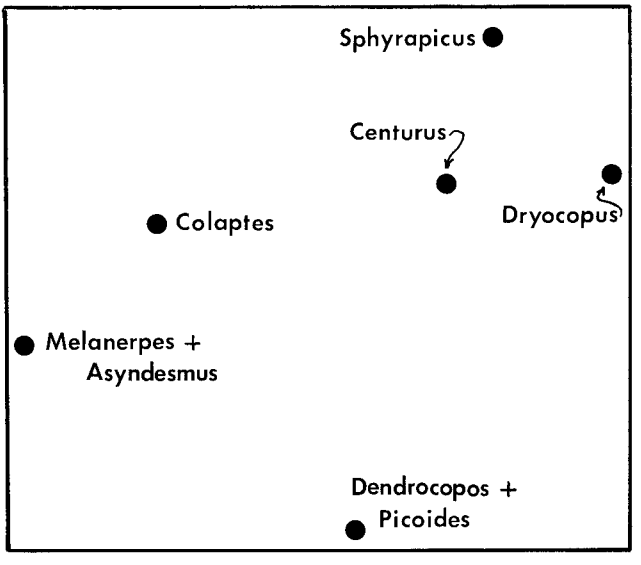

FIG. 3. Two-dimensional ordination of 6 woodpecker taxonomic groups, based on similarities of distribution and abundance in winter in the U.S. The axes have no specific meaning, but the distances between points are inversely proportional to the similarities of distribution and abundance patterns (see Beals 1960).

states and the Midwest (see Tate 1973), but the greatest concentrations are, again, the Mississippi Valley and especially the Southeast—including peninsular Florida. Of course many sapsuckers winter south of the U.S. (Howell 1952, 1953). *Sphyrapicus varius ruber* of the Pacific Northwest is a resident subspecies, and *S. v. daggeti* winters along the Pacific Coast. Our data suggest that these sapsuckers are less abundant than the eastern *S. v. varius*.

SIMILARITY OF TAXONOMIC GROUPS

Data on woodpecker species were combined to provide information on the distribution and abundance patterns of 6 woodpecker taxonomic groups; *Dendrocopos* and *Picoides* were treated as one group, because of their general similarity, as were *Melanerpes* and *Asyndesmus*. The other four groups were *Colaptes, Sphyrapicus, Dryocopus,* and *Centurus*. We carried out a similarity analysis and 2-dimensional ordination of the groups, based upon similarities of their abundance patterns in the 27 regions analyzed (see Beals 1960 for techniques). The closer the groups are shown in the ordination (Fig. 3), the greater the similarity of their abundance patterns. Results of this analysis show that: (1) *Centurus* is most nearly intermediate to all of the other groups in terms of its abundance pattern. (2) *Dendrocopos—Picoides* as a

TABLE 2

CORRELATION COEFFICIENTS BETWEEN WOODPECKER ABUNDANCE AND ENVIRONMENTAL CHARACTERISTICS[1]

	Average temp.	Maximum temp.	Minimum temp.	Summer precip.	Winter precip.	Primary productivity
Dendrocopos + *Picoides*	−0.41	−0.22	−0.50	0.42	−0.03	0.18
Melanerpes + *Asyndesmus*	−0.07	−0.10	0.00	−0.21	0.45	−0.07
Colaptes	0.23	0.24	0.36	−0.23	0.40	−0.10
Dryocopus	0.19	−0.04	0.16	0.40	0.35	0.60
Sphyrapicus	0.50	0.10	0.50	0.45	0.46	0.63
Centurus	0.65	0.36	0.53	0.41	0.06	0.50

[1] See methods for data sources. $N = 27$ for all calculations; r values $\geqslant 0.33$ are significant at the 0.05 level of probability.

group has by far the most distinctive abundance pattern. (3) *Sphyrapicus*, *Dryocopus*, and *Centurus* (because of the abundant Red-bellied Woodpecker) form a cluster, although all 6 groups are rather well spread. (4) *Melanerpes*—*Asyndesmus* is widely separated from all other groups except *Colaptes*.

We next measured a number of environmental parameters for each of the 27 regions, and computed correlation coefficients between these and the winter abundances of the 6 woodpecker groups (Table 2). These data may shed some light upon the ultimate causes of the configuration of abundance similarities shown in Fig. 3.

Dendrocopos—*Picoides* is the only group strongly negatively correlated with temperature regime. Northeastern populations of the Hairy and Downy woodpeckers are so large that they give the entire group a northern abundance pattern. This could be a reflection of the common circumboreal distribution and evolutionary history of these genera (see Short 1971).

Centurus, *Sphyrapicus*, and *Dryocopus* all are positively correlated with areas of higher temperatures, precipitation, and especially primary productivity. These are birds of wet, warm climates.

Colaptes and *Melanerpes* (plus *Asyndesmus*) winter in regions which are relatively unproductive, and where winter precipitation exceeds summer precipitation (Table 2).

DISCUSSION AND CONCLUSIONS

There appears to be a strong correlation between patterns of woodpecker abundance described in this study and published information on the feeding ecology of the species. Some of the major relationships of common species are discussed in the following paragraphs.

Dendrocopos.—The Hairy and Downy woodpeckers forage in winter largely by excavation (Kilham 1966, Lawrence 1967, Jackson 1970), and are so-adapted morphologically (Spring 1965). This explains their ability to live in areas where winters are severe and tree-surface insects scarce. By contrast, the ladder-backed *Dendrocopos* are more generalized foragers, relying to a greater degree in winter upon free-living insects (Ligon 1971, Short 1971, Miller and Bock 1972). These are species restricted to areas of warmer climate, where surface insects would persist in greater numbers all year.

Melanerpes—Asyndesmus.—The Acorn, Lewis', and Red-headed woodpeckers to varying degrees are dependent upon stored mast in winter (Kilham 1958a,b; Bock 1970; MacRoberts 1970). Red-headed Woodpeckers are most common in the Midwest (Fig. 2e), undoubtedly because of the abundance of oaks and corn in this region. Acorn Woodpeckers are more common in California than in the Southwest (Table 1), probably because acorn crops are larger and more predictable in California (Bock and Bock 1974a). Tables 1 and 2 indicate that *Melanerpes* and *Asyndesmus* winter most abundantly in areas which are relatively open and lacking in summer rains. This undoubtedly is related to the fact that all 3 species forage extensively in summer by flycatching. Summer requirements should have little to do with winter abundance patterns, but the Acorn Woodpecker is resident and the Lewis' and Red-headed woodpeckers, while often migratory, are highly opportunistic and will remain on or near breeding grounds if it is possible (e.g., Hadow 1973). Also, these species will flycatch on warm winter days.

Colaptes.—Flickers concentrate at lower latitudes in winter, and apparently prefer relatively open habitats (Table 1, Fig. 2d). Very likely this is due to their decided preference for ants which they take on open ground (Bent 1939, Dennis 1969). Areas of dense forest, and especially areas where snow often covers the ground, would be relatively unsuitable flicker habitat.

Dryocopus.—The Pileated Woodpecker is more restricted to mature, dense, and productive forests than any other considered here. In winter it relies heavily on carpenter ants excavated from partially decayed trees (Hoyt 1957). It is easy to see why it is most common in the moist forests of the Mississippi Valley and Southeast, where the maturation-decay process is relatively rapid. The virtual absence of Pileated Woodpeckers from the central and southern Rocky Mountains no doubt is due to the scarcity of dense highly productive forests in these regions compared to the Northwest or the Southeast (see Bock and Bock 1974b).

Sphyrapicus.—Tate (1973) recently reviewed the foraging ecology of the eastern Yellow-bellied Sapsucker. He made the significant observation that (p. 854) "northern wintering birds subsist on a diet of arthropods (mostly insects) obtained from the bark of trees, frozen fruit, and very little sap,"

whereas ". . . sapsuckers in the middle latitudes feed on local sap flow from many tree species." This specialized woodpecker clearly would be best suited to areas with milder winters and extensive, productive woodlands, where sap would be available all year. This conclusion is strongly supported by our data (Tables 1 and 2, Fig. 2h).

Centurus.—The 3 species of *Centurus* in the U.S. form no clear ecological pattern, perhaps because they are part of a much more diverse group of species occurring to the south (Selander and Giller 1963). *Centurus* woodpeckers are very generalized foragers, and also showed the most intermediate pattern of abundance of the genera studied (Fig. 3). The widespread *C. carolinus* appears to be particularly generalized among North American species. It does relatively little excavating (Cruz, in press), takes considerable vegetable material in winter (Bent 1939), and concentrates in winter in productive, warm areas (Table 2). It may store mast (Kilham 1963), but it does not appear to be nearly as specialized in this regard as *Melanerpes* or *Asyndesmus*.

SUMMARY

Analysis of Christmas count data for 27 inland regions in the U.S. revealed major patterns of woodpecker abundance. Data for 6 woodpecker taxonomic groups were subjected to ordination analysis. In general, abundance patterns correlated well with information on the foraging ecology of the species and genera.

Dendrocopos (plus *Picoides*) showed a strong northeastern abundance pattern due to the high densities of Hairy and Downy woodpeckers in that region. The Common Flicker is very abundant at lower latitudes and in relatively open habitats. The Yellow-bellied Sapsucker was concentrated in the Mississippi Valley and the Southeast. *Sphyrapicus varius varius* appeared much more abundant than the western subspecies. The Pileated Woodpecker was most abundant in forests of the Midwest and Southeast, and relatively rare in the West. The Acorn, Lewis', and Red-headed woodpeckers wintered where mast crops are available. Acorn Woodpeckers were much more common in California than in the Southwest; Red-headed Woodpeckers were abundant in the Midwest, where oaks and corn are available. *Melanerpes* and *Asyndesmus* forage extensively by flycatching, and are most abundant in open habitats, even in winter.

ACKNOWLEDGMENTS

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NEW LIFE MEMBER

John P. Ryder has recently become a life member of the Wilson Ornithological Society. Dr. Ryder is an Associate Professor in the Department of Biology at the Lakehead University, Thunder Bay, Ontario. He is interested in the breeding behavior and ecology of colonial birds and in age-specific differences in larid behavior and reproductive success. He has published nearly 20 papers resulting from his research activities. Dr. Ryder is presently Director of the Federation of Ontario Naturalists. In addition to his professional interests, Dr. Ryder enjoys snowshoeing and photography.