GEOGRAPHICAL ECOLOGY OF THE COMMON SPECIES OF *BUTEO* AND *PARABUTEO* WINTERING IN NORTH AMERICA

CARL E. BOCK
AND
LARRY W. LEPTHIEN

North American hawks of the subfamily Buteoninae have received considerable attention, mostly with regard to their food habits and breeding biologies (e.g., Errington and Breckenridge 1938, Fitch et al. 1946, Smith and Murphy 1973). Twelve species occur in the New World north of Mexico but only five are widely distributed in winter (A.O.U. 1957). These are the Harris' Hawk (*Parabuteo unicinctus*), Ferruginous Hawk (*Buteo regalis*), Red-shouldered Hawk (*B. lineatus*), Red-tailed Hawk (*B. jamaicensis*), and Rough-legged Hawk (*B. lagopus*). Previously published maps based upon Christmas count data indicate that only the last three of these species are at all common over wide areas (Bystrak 1974).

A number of workers have examined the relationships between locally sympatric populations of two or more *Buteo* species (e.g., Stewart 1949, Orians and Kuhlman 1956, Weller 1964, Schnell 1968). In this study we have compiled data from the 1969–70, 1970–71, and 1971–72 Christmas counts to determine the overall abundance pattern of this genus in the United States and southern Canada. We could then quantify the contributions made by the individual species to that pattern on different parts of the continent. We compared these calculations with certain environmental variables. Results show the degree to which the species' abundance patterns are complementary, and reveal something about the environmental gradients involved.

METHODS

We have found Christmas count data very useful for studying large-scale patterns of avian geographical ecology. Details of computerized data storage, retrieval, and analysis have been described previously (Bock and Lepthien 1974). In this case we retrieved count data by geographic blocks of 5 degrees of latitude and longitude (over 2700 censuses for 1969–70 through 1971–72), and computed mean individuals observed per party-hour of effort for all blocks south of 50° N latitude. Counts are rare farther north.

Field misidentification of these hawks undoubtedly occurs, and maps based upon Christmas count data (fig. 1) should not be taken to represent the exact distributional limits of species. However, we believe they are accurate for depicting overall abundance patterns.

The degree of segregation shown by the three common species (fig. 1) almost certainly is the result of differences in habitat selection (see discussion section). However, it is difficult to accurately quantify the actual abundance of habitat types across the whole continent. Instead, we compared the hawk data with maps of certain climatic variables (U.S. Dept. Agriculture 1941) which should be ultimately responsible for most habitat differences. A contrived "Index of Climate" (I_c) proved the best variable for predicting the relative abundance of the Red-shouldered, Rough-legged, and Red-tailed hawks in a given block of latitude and longitude. This index was calculated for each block as follows:

$$I_c = \sqrt{FFD \times PANN}$$

where *FFD* is the number of frost-free days in the block and *PANN* is the average annual precipitation. Except in montane areas I_c should be roughly proportional to the amount of woodland vs. open habitat in a given area (excluding habitat modification by humans).

RESULTS

Buteonine hawks appear to be rather generally distributed in winter, except in the north (fig. 1a). Christmas count data indicate that highest densities occur on the Pacific slope, the Great Basin, the plains west of the Mississippi River, and along the Gulf Coast.

Red-tailed Hawks accounted for 58.7 percent of all observations in an average latitude-longitude block (table 1). Adding the Rough-legged and Red-shouldered hawks brings the total to 96.9 percent, showing the degree to which these three species dominated Christmas counts of buteos.

Figure 1 shows the abundance patterns of the five most common species, expressed as percent of all buteonine hawks seen in each block. The Red-shouldered Hawk was seen most frequently in the Southeast (fig. 1c), but only in Florida was it the most common *Buteo* observed. The Rough-legged Hawk predominated in the north, the Great Basin, and on the western short-grass prairies. The Red-tailed Hawk was the commonest elsewhere (fig. 1d). The Ferruginous and Harris' hawks were counted in large numbers only in western and southern Texas, respectively (fig. 1e and f).

Enderson (1965), Mathisen and Mathisen (1968) and Johnson and Enderson (1972) found the Rough-legged Hawk by far the most common *Buteo* species on Colorado and Nebraska winter roadside censuses. Red-tailed Hawks were even scarcer in these short-grass censuses than indicated by Christmas counts for the same areas. This may be because *B. lagopus* tends to hunt along roadsides on the wing, while *B. jamaicensis* is more likely to be perched in trees near dwellings or water (see Schnell 1968). At the same time, Christmas count results may be biased, because most counts are centered in diverse habitat areas—better *jamaicensis* habitat than open treeless plains.

Figure 2 shows the average proportion of all buteonine hawks contributed by each of the three common species, in blocks grouped by I_c categories.

TABLE 1. Contributions by five species to the total count of buteonine hawks in an average block of latitude and longitude.[a]

Species	Average percent	No. blocks where most common species
Red-tailed Hawk[b]	58.7	35
Rough-legged Hawk	30.8	15
Red-shouldered Hawk	7.4	1
Ferruginous Hawk	1.3	0
Harris' Hawk	1.1	0

[a] Other species contributed less than 0.5 percent each.
[b] Includes "Harlan's Hawk" (*Buteo jamaicensis harlani*).

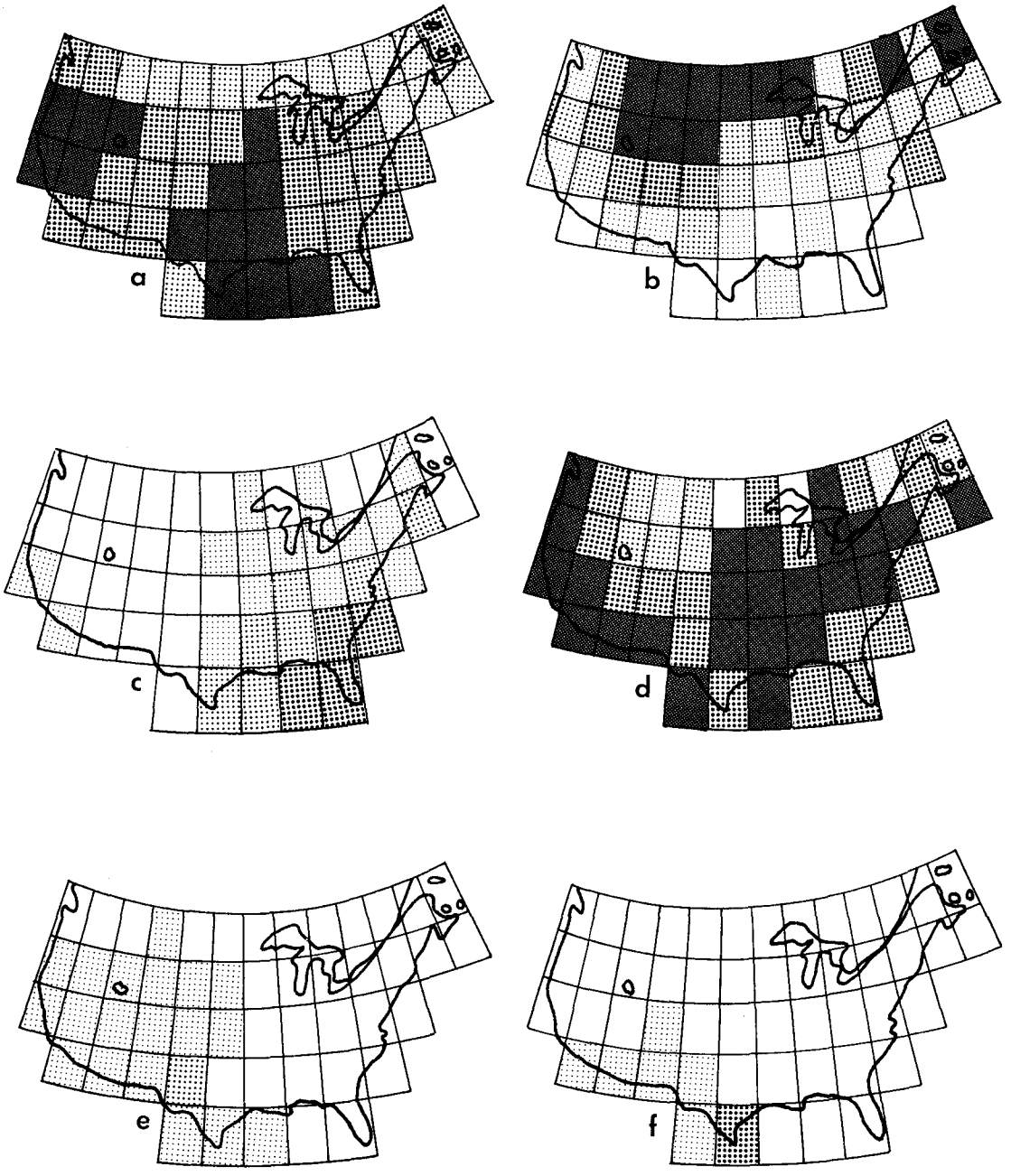

FIGURE 1. (a) Average combined abundance of buteonine hawks in winter in the United States and southern Canada, based upon 1969–70, 1970–71, and 1971–72 Christmas count data. Three degrees of shading represent: less than 0.2, 0.2 to 0.5, and more than 0.5 birds per party-hour. Abundance patterns of the five species, expressed as percent of all buteonine hawks species seen in each latitude-longitude block, are shown in: (b) *B. lagopus*; (c) *B. lineatus*; (d) *B. jamaicensis*; (e) *B. regalis*; and (f) *Parabuteo unicinctus*. White areas indicate no birds present; four degrees of shading represent: $\leqslant 10$, 11–30, 31–70, and > 70 percent, respectively.

The widths of the histogram bars vary in proportion to the number of latitude-longitude blocks falling in each I_e category. The Red-tailed Hawk occupies an intermediate position along the climatic gradient, just as it does geographically across the continent. While *B. lineatus* and *B. lagopus* occupy areas with largely dissimilar climatic regimes, *B. jamaicensis* overlaps both species extensively.

DISCUSSION AND CONCLUSIONS

It is very unlikely that differences in food habits among Red-tailed, Rough-legged, and Red-shouldered hawks are sufficient to permit extensive winter sympatry. Errington and Breckenridge (1938:121) studied *Buteo* species in the Midwest and concluded: "We have little reason to believe that preference for some type of prey influences the food habits of the species

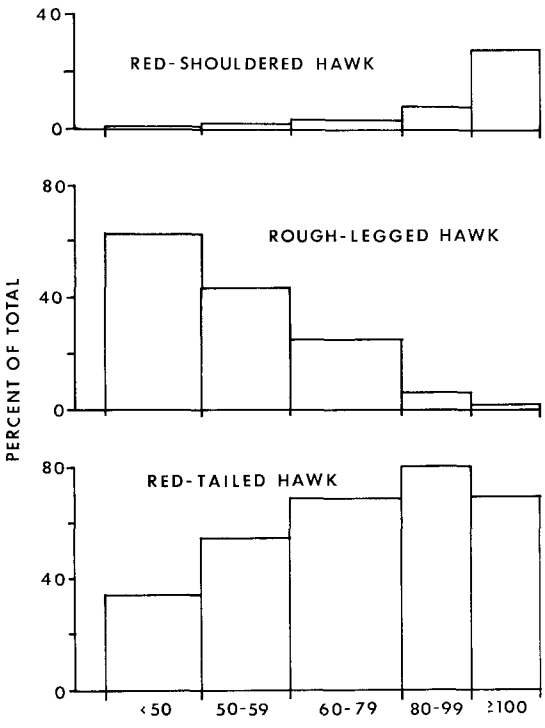

FIGURE 2. Contribution of the three most common species to the total *Buteo* count in latitude-longitude blocks grouped by Climatic Index (I_c) categories (see text). Widths of histogram bars vary in proportion to the number of blocks falling in each category.

herein discussed to any conspicuous extent; . . . What a redtail or any other *Buteo* eats is largely a matter of what is to be had without too much trouble." Smith and Murphy (1973:64) observed that "raptors are considerably opportunistic in their predatory habits and take a variety of prey throughout different parts of their ranges."

We conclude that the species in question are opportunistic hunters, and that the primary niche dimension separating them in winter is position along a climatic (fig. 2) or habitat gradient. Orians and Kuhlman (1956), Weller (1964), and Schnell (1968) worked in separate parts of the Midwest; all found that in a mosaic of woodland and grassland-agricultural habitats, the Rough-legged Hawk preferred open areas while the Red-tailed Hawk more often was associated with woodland edge situations. Stewart (1949:26) found that "on the Coastal Plain of Maryland a combination of fairly extensive floodplain forests with adjacent clearings appear to meet the major ecological requirements of the Red-shouldered Hawk during the nesting season." Adjacent upland areas, even though extensively wooded, were occupied by Red-tailed Hawks. Christmas count data strongly support these sorts of observations and indicate that factors operating on a local scale also are responsible for continent-wide abundance patterns. Along a habitat-climate gradient from areas with short growing season and low precipitation (treeless prairies and shrub-steppe communities) to those with relatively long growing season and high precipitation (moist woodlands and the Florida peninsula generally), the species appear and replace each other in the order: *Buteo lagopus*, *B. jamaicensis*, and *B. lineatus*.

Many observers have noted the behavioral flexibility and agressiveness of the Red-tailed Hawk (e.g., Johnson and Peeters 1963, Brown and Amadon 1968, Luttich et al. 1970). These attributes no doubt account for much of its success. In addition, the recent activities of European people have created new habitat for this species. As dense forests were cleared and treeless plains were planted, *B. jamaicensis* must have increased in numbers while other species, especially *B. lineatus*, declined drastically (Henny et al. 1973).

MacArthur (1970, 1972) argued mathematically that a species "trapped" between two close competitors along a resource gradient is in a potentially disastrous ecological position. The Red-tailed Hawk occupies such a position and yet thrives, at least in terms of population size. It could be argued that Rough-legged, Red-tailed, and Red-shouldered hawks simply select different habitats, that the Red-tailed Hawk occupies the most abundant of these, and that no interspecific competition is involved. This is possible; our evidence for competition is only circumstantial. But, in fact, we are dealing with only two fundamentally different habitat types which mix together forming a continuous gradient from pure woodland to open treeless prairie or shrub-steppe. It seems highly likely that the Red-tailed Hawk evolved behavioral and ecological plasticity, an ability to occupy "edge" habitats, and perhaps its aggressive behavior, as adaptive responses to interspecific competition from more specialized species on both sides of the habitat gradient. These characteristics and ecological position could have pre-adapted it for the tree-grassland mosaic imposed by agriculture over most of the United States and southern Canada.

We are grateful to the University of Colorado Computer Center and Taximetrics Laboratory, to the many students who have helped to build the Christmas count data banks, and to Monte Kirven for his advice and assistance. This project was supported by grant GB 36860 from the National Science Foundation.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds. Fifth ed. Am. Ornithol. Union, Baltimore.

BOCK, C. E., AND L. W. LEPTHIEN. 1974. Winter patterns of bird species diversity and abundance in the United States and southern Canada. Am. Birds 28:556–562.

BROWN, L., AND D. AMADON. 1968. Eagles, hawks and falcons of the world. 2 vols. McGraw-Hill Book Co., New York.

BYSTRAK, D., [ed.] 1974. Wintering areas of bird species potentially hazardous to aircraft. Natl. Audubon Soc., New York.

ENDERSON, J. H. 1965. Roadside raptor count in Colorado. Wilson Bull. 77:82–83.

ERRINGTON, P. L., AND W. J. BRECKENRIDGE. 1938. Food habits of *Buteo* hawks in north-central United States. Wilson Bull. 50:113–121.

FITCH, H. S., F. SWENSON, AND D. F. TILLOTSON. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48:205–237.

HENNY, C. J., F. C. SCHMID, E. M. MARTIN, AND L. L. HOOD. 1973. Territorial behavior, pesticides, and the population ecology of Red-shouldered Hawks in central Maryland, 1943–1971. Ecology 54:545–554.

JOHNSON, D. H., AND J. H. ENDERSON. 1972. Road-

side raptor census in Colorado—winter 1971–72. Wilson Bull. 84:489–490.

JOHNSON, N. K., AND H. J. PEETERS. 1963. The systematic position of certain hawks in the genus *Buteo*. Auk 80:417–446.

LUTTICH, S., D. H. RUSCH, E. C. MESLOW, AND L. B. KEITH. 1970. Ecology of Red-tailed Hawk predation in Alberta. Ecology 51:190–203.

MACARTHUR, R. H. 1970. Species packing and competitive equilibrium among many species. Theoret. Pop. Biol. 1:1–11.

MACARTHUR, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York.

MATHISEN, J. E., AND A. MATHISEN. 1968. Species and abundance of diurnal raptors in the panhandle of Nebraska. Wilson Bull. 80:479–486.

ORIANS, G., AND F. KUHLMAN. 1956. Red-tailed Hawk and Horned Owl populations in Wisconsin. Condor 58:371–385.

SCHNELL, G. D. 1968. Differential habitat utilization of wintering Rough-legged and Red-tailed hawks. Condor 70:373–377.

SMITH, D. G., AND J. R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young Univ., Sci. Bull. 18:1–76.

STEWART, R. E. 1949. Ecology of a nesting Red-shouldered Hawk population. Wilson Bull. 61: 26–35.

U. S. DEPARTMENT OF AGRICULTURE. 1941. Climate and man. Yearbook of agriculture. U. S. Dept. Agr., Washington, D.C.

WELLER, M. W. 1964. Habitat utilization of two species of buteos wintering in central Iowa. Iowa Bird Life 34:58–62.

Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80302. Accepted for publication 13 September 1975.

GROWTH OF THE SWAINSON'S HAWK

JAMES W. PARKER

The growth of naturally-raised birds of prey is inadequately documented. When analyzing the growth patterns of 105 bird species, Ricklefs (1968) had to calculate growth statistics from single broods or individuals of many bird species, and for North American species of *Buteo* he could discuss only the Red-tailed Hawk (*B. jamaicensis*). Ricklefs' (1968, 1973) emphasis on the importance of growth rates in avian reproductive biology illustrates the need for continued fieldwork on bird growth and prompts me to report the growth of a brood of Swainson's Hawks (*B. swainsoni*). No published data describe the growth of wild-raised Swainson's Hawks, although Olendorff (1971) studied captive juveniles and tabulated all references of growth studies of raptors then available.

In 1970 I studied the nesting of a pair of Swainson's Hawks 6.4 km east of Arnett, Ellis County, Oklahoma. The nest was a mass of sticks typical for this species, about six dm in diameter and four m up in a 6-m osage orange tree (*Maclura pomifera*) on the south side of a shelterbelt woodlot. A colony (six nesting attempts) of Mississippi Kites (*Ictinia misisippiensis*) used the same group of trees. When found, the hawk nest held two nestlings and one egg that did not hatch and eventually disappeared. The ages of the two nestlings were estimated at three and five days on the basis of my experience and comparison with Olendorff's (1971: 234, 243) data for weight and tarsal length.

Weight and several body dimensions of the nestlings were measured at irregular intervals (table 1). Tarsal length was measured as the distance along the posterior surface of the tarsus from the base of the first digit to the posterior side of the distal head of the tibiotarsus at the heel; the tarsometatarsus was held perpendicular to the tibiotarsus. I measured the culmen as the chord from the anterior dorsal edge of the cere to the tip. The third-toe claw measurement was the chord from the tip of the claw to the proximal-most ventral surface of the claw at the toe pad. The greatest weights of the juveniles were estimates because the tares for a triple-beam balance were not available, and a spring scale graduated in English units was used to weigh the nestlings. Feather length was the distance from the point where the shaft exited the skin to the tip of the rachis minus natal down. The seventh primary remex and the longer of the two central rectrices were used.

The younger nestling was recently dead in the nest when it would have been 32 days old. Its condition did not indicate malnutrition; rather, it died of injuries suggesting either intentional or unintentional

TABLE 1. Growth data for two sibling Swainson's Hawks. The italicized days of age indicate the older nestling.

Days of age	Weight (gm)	Tarsal length (mm)	Culmen (mm)	Third toe-claw (mm)	Seventh primary (mm)	Longer central rectrix (mm)
3	49	17.9	8.7	2.6		
5	72	20.8	8.8	3.4		
10	226	35.5	12.4	6.1	1	
12	322	39.4	13.3	6.8	6	
15	328	47.2	15.3	8.5	20	
17	470	56.3	15.9	9.5	35	11
21	530	54.5	16.4	11.8	63	27
23	595	64.5	18.0	11.4	83	42
32	680	69.6	19.4	13.2	111	79
34	610	72.0	20.8	13.9	169	112
40	–	75.4	21.1	14.4	209	133