PARTITIONING OF FOOD AND NICHE CHARACTERISTICS OF COEXISTING *ACCIPITER* DURING BREEDING[1]

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ABSTRACT.—The abundance of resources and their use by *Accipiter* in two areas within Oregon from 1969 through 1974 are presented. In the coastal mountains of northwestern Oregon only Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) nested. In the remainder of the state, *A. striatus*, *A. cooperii*, and Northern Goshawks (*A. gentilis*) were syntopic during the nesting season. The number of species and the total density of birds in eastern Oregon were about one-half those in northwestern Oregon. Mean prey size of *A. striatus* in northwestern Oregon (12.8 g) was significantly smaller than that of the same species in eastern Oregon (28.4 g). *Accipiter striatus* diets in both areas were composed almost entirely of birds (<5% mammals). Mean prey size of *A. cooperii* in both areas was nearly the same (134.7 g vs. 136.3 g) and was significantly larger than mean prey size of *A. striatus*. The frequency of occurrence and the size of prey taxa in *A. cooperii* diets, however, varied between areas: 74% birds ($\bar{x}$ = 79.2 g) and 25% mammals ($\bar{x}$ = 296.4 g) in northwestern Oregon versus 47% birds ($\bar{x}$ = 123.7 g) and 53% mammals ($\bar{x}$ = 147.5 g) in eastern Oregon. Mean prey size of *A. gentilis* in eastern Oregon (306.6 g) was significantly larger than that of *A. cooperii* and consisted of 55% birds ($\bar{x}$ = 195.5 g) and 45% mammals ($\bar{x}$ = 445.2 g). An analysis of prey sizes, prey taxa, and foraging heights indicated that, in general, food was partitioned in both areas primarily according to prey size. In eastern Oregon, however, where *A. cooperii* and *A. gentilis* overlapped broadly in prey size, these species tended to take different prey taxa. Both *A. cooperii* and *A. gentilis* foraged primarily in the lower zones (ground-shrub and shrub-canopy), whereas *A. striatus* foraged in the upper canopy. *Received 8 January 1982, resubmitted 16 February 1983, accepted 9 March 1984.*

DIETS of members of the genus *Accipiter*, a group of forest hawks that feed principally on birds and mammals, have been examined in North America (Storer 1966, MacArthur 1972, Snyder and Wiley 1976, Reynolds 1979) and Europe (Van Beusekom 1972, Opdam 1975). The impetus behind most of these studies has been the body-size relationships that occur among the coexisting species (small forms tending to co-occur with large) and the fact that, males being smaller than females, there are two body sizes within each species. These studies indicate that the primary differences among diets in *Accipiter* are in prey size and prey type; small species generally capture small birds, whereas the larger species capture large birds and mammals. Dietary overlap and the degree of limiting similarity among the North American species have also been examined (MacArthur 1972, Hespenheide 1975). Diets used in these studies, however, were from Storer's (1966) listing of stomach contents collected from various locations in all seasons and over a number of years. Because prey composition and abundances vary geographically and seasonally, it cannot be determined whether the diet differences reported by Storer were due to seasonal and regional differences in prey availability or to different patterns of selectivity from similar distributions of available prey. Given the importance that the genus *Accipiter* has assumed in evaluations of existing theories of community structure, it is essential to reexamine the feeding ecology of these species with data from a relatively small area and from a season when all members of an assembly are known to co-occur.

In the conifer forests of the eastern and southwestern portions of Oregon, *A. striatus*, *A.*

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cooperii, and *A. gentilis* nest and forage in the same habitat, whereas in the conifer forests of northwestern Oregon, only *A. striatus* and *A. cooperii* coexist during breeding (Reynolds and Wight 1978). Here, we compare the food resources in these two areas and their use by *Accipiter* during nesting. We examine the importance of prey size, prey taxon, and foraging zone to the variability of the diet of the hawks and the degree to which their diets overlap. We also discuss foraging strategies that are the consequence of the relative position and shape of the respective utilization functions on a food resource whose size-frequency distribution is approximately lognormal. Finally, we consider several patterns in the feeding ecology of Oregon *Accipiter* in light of the supposition that competition for food is an important organizing force in *Accipiter* assemblages.

STUDY AREAS

This study included spring and summer surveys of *Accipiter* nests in all major forest types in Oregon except the open western juniper (*Juniperus occidentalis*) forests of central Oregon and the narrow band of Sitka spruce (*Picea sitchensis*) forests along the Pacific Coast. Reynolds and Wight (1978), Reynolds et al. (1982), and Franklin and Dyrness (1973) describe the forests included in this study. Forests in western Oregon occurred from sea level to 1,800 m. Eastern Oregon is a high plateau (600–1,500 m) forming the western portion of the Great Basin; it contains numerous small to large mountain ranges with associated forests that range from 800 to 2,700 m above sea level. These ranges are separated by varying expanses of arid brushlands.

We divided Oregon into two regions based on the presence or absence of nesting *A. gentilis* (Reynolds and Wight 1978) (Fig. 1). The northwestern region consisted of the northern half of the Coast Range. This region is densely forested and, because of its proximity to the Pacific Coast and the prevailing westerly winds, has cool, wet winters and mild, dry summers. These forests are dominated by continuous stands of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). The remainder of the state, hereafter referred to as eastern Oregon, included the Cascade Range (east and west slopes), the Siskiyou Mountains in southwestern Oregon, and all the mountain ranges east of the Cascades: The Wallowa, Blue, Ochoco, Steen's, Bly, and Warner mountains. Except for the Siskiyous and the lower west slopes of the Cascades, this region is characterized by cold winters and hot, dry summers. Forests on the west slope of the Cascades are dominated by Douglas-fir and western hemlock, whereas those on the east slope and on the mountains east of the Cascades are dominated by mixed stands of ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and Douglas-fir. The Siskiyous are characterized by warm, wet winters and hot, dry summers. Forests in these mountains are dominated by mixed conifer and sclerophyll types: ponderosa pine, incense-cedar (*Libocedrus decurrens*), Douglas-fir, tan oak (*Lithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*) (Franklin and Dyrness 1973).

The distribution of nesting *Accipiter* in both regions was determined during nest searches in 1969–1974 (Reynolds and Wight 1978). We determined nesting densities in both regions by intensively searching two areas. The Corvallis area (9,284 ha) is in northwestern Oregon on the east slope of the Coast Range approximately 8 km northwest of Corvallis, Benton County (T. 10S and 11S; R. 5W and 6W) (Fig. 1). The Bly area (11,741 ha) is in the Bly Mountains of eastern Oregon approximately 24 km northeast of Bly, Lake County (T. 15E and 16E; R. 36S). For a description of these areas see Reynolds and Wight (1978). The Corvallis area was searched during the nesting seasons of 1970–1971 and the Bly area during the nesting season of 1974.

METHODS

Diet determination.—*Accipiter* regularly remove pelage and plumage from their prey in the nesting area or on the nest itself. These hawks regurgitate pellets, and, although most of the bone is digested, keratinous parts are not. On each visit to a nest site, all remains and pellets found in plucking areas or on nests were completely picked up. Nests in or near the intensive study areas received 3–4 visits per week, whereas the more distant nests received 4–6 visits per month. During identification, all remains in a day's collection were lumped and reconstructed by matching the remiges, rectrices, and bills of birds and the fur, skull parts, and feet of mammals. This procedure minimized the possibility of over-counting the number of individuals of each species. The age (young or adult) of prey was determined by the presence or absence of sheathed feathers in birds and the body size, pelage, or degree of bone ossification in mammals. Weights of adult birds and mammals were obtained from the literature and from museum specimens at Oregon State University (Reynolds 1979) (Appendix 1). Where it was not possible to distinguish males from females in collections, mean weights for the sexes were used. We assumed the weights of "young" prey to be one-half of their adult weight. For mammals and precocial birds, we felt this choice approximated their mean weights through the season. Assigning one-half the adult weight, however, undoubtedly overestimated the weight of most nestlings and underestimated that of fledged young of altricial birds. Again, we assumed that this approximated the average weight of young birds. Weights

of prey identified to genus were estimated by averaging weights of all members of that genus in each study area. Several regurgitated pellets contained reptilian scales and bird bills. These were quantified in the same manner: their presence was compared to other collections made on that or previous days to prevent double counting.

Limitations of the diet data.—Diets of raptors have been determined from prey remains (Uttendörfer 1939, Opdam 1975, Opdam et al. 1977, Boshoff and Palmer 1980, Wikman and Tarsa 1980, Newton and Marquiss 1982), but, the method is not entirely free of bias (Snyder and Wiley 1976). Höglund (1964) found differences between prey from nest sites and those from stomachs. Some of these differences, however, were attributed to the geographical and temporal separation of collections (Höglund 1964). Snyder and Wiley (1976) found that collections of remains and pellets from nests gave biased estimates of the diets of Red-shouldered Hawks (*Buteo lineatus*), especially of reptiles, amphibians, and arthropods, and Schipper (1973) showed that birds and mammals are underestimated in prey remains of harriers (*Circus*). Our nest observations and pellet examinations indicated that Oregon *Accipiter* fed to a limited extent on reptiles and arthropods. Additionally, adults may have consumed items away from nests or delivered completely plucked prey. We recognize that our diets represent only a portion of what was consumed. Although our intent was to gain a random diet sample, the extent and direction of bias in our collections is unknown, because we did not make extensive observations at nests.

Because we collected remains from before egg laying (April) to independence of the young (August), the data represent a combination of the prey of both sexes. Because males do nearly all the foraging from before egg laying through the mid-nestling period (Snyder and Wiley 1976, pers. obs.), however, the diets are mainly those of males.

Food resources.—Using the variable circular-plot method (Reynolds et al. 1980), we censused birds in stands representative of five forest types on the Bly study area in late June and early July 1974. Four of the stands were dominated by ponderosa pine (1 old-growth, 2 mature, 1 second-growth) but had differing compositions and densities of understory conifers. The fifth was mature lodgepole pine (*P. contorta*). The census period was 8 min at each of 8–10 stations established at 100-m intervals in each type. Censuses were conducted over several days (minimum 2 days) in each of the five types between 0600 and 1130 (Pacific Daylight Time). The abundance of birds in northwestern Oregon was taken from Anderson (1970) and Mannan (1977). Anderson (1970) used the sample count method (Bond 1957, Anderson 1972) to census breeding birds in five forest types within or adjacent to our Corvallis study area in 1968–1969, and Mannan (1977), using the same technique,

counted birds in the breeding season of 1976 in Douglas-fir stands 24–55 km southwest of our Corvallis area. We combined Anderson's and Mannan's data by calculating an unweighted mean density per species in four conifer stands (from 70–200 yr old) censused by Mannan (1977) and averaged these means with means derived from Anderson's (1970) "late spring" and "early summer" counts in nine stands dominated by conifers. For species not recorded in both studies, we used the densities reported in either one or the other.

A possible bias associated with combining bird densities in this manner is an expansion of the total density estimate above the true number in any given year due to the year-to-year changes in species composition. Because it is easier to demonstate a species' presence than absence, however, estimates of abundances are probably conservative, and the combined list may more closely approximate the true composition and abundances. Due to differences in the duration of sampling periods and in census techniques, our eastern Oregon estimates are not directly comparable to the Anderson-Mannan estimates. Our intent, however, was to gain only a general picture of the size-frequency distibution of the avifaunas. Thus, the need for direct comparability was not great. Due to problems associated with determining true densities of birds in tall forests (Verner in press) and the structural and floristic similarities of stands censused within each area, we felt that using unweighted means across all stands censused was sufficient for our purposes. Moreover, the intermixing of ages and types of stands in these large study areas precluded an accurate estimate of the total area in each type, and, because of possible area-effects on actual densities in this mix of small and large stands, abundances weighted by area would, in themselves, be very rough estimates. A ranking of the relative abundance of diurnally active small mammals in both study areas was developed on the basis of frequency of observation of species during each field season.

By assigning all bird and mammal species to one of four height zones (ground-shrub, shrub-canopy, canopy, aerial) where each was most commonly observed, we examined the possibility that *Accipiter* partitioned food by foraging in different layers of the forest. Species not clearly assignable to a single zone (those likely to be found in two or more zones) were considered zone generalists. Because prey were assigned to the zone where they spent most of their time, we assumed that *Accipiter* were most likely to capture an individual of a prey species in the zone assigned to it. It is possible that prey are more vulnerable and captured more frequently when they were outside their zone. Observations of capture attempts, however, indicated that prey are at least frequently pursued within their zone.

Niche breadths were calculated according to Levins' (1968) equation

$$B = 1/\sum p_i^2,$$

where p_i is the proportion of prey among the categories in each dimension. The value of B varies from 1 to n, where n is the number of categories. If prey are equally common in each category, then $B = n$; if all the prey occur in one category, then $B = 1$. Because the numbers of categories were not equal in each niche dimension (prey size, 14; zone, 5; taxa, 24), niche-width values were standardized for comparison with fractions (0–1) of maximum possible niche width by

$$B_{standard} = (B - 1)/(n - 1),$$

where n is the maximum number of categories.

Niche overlaps were calculated according to MacArthur and Levins' (1967) equations

$$\alpha_{ji} = \sum U_i U_j / \sum U_j^2 \text{ and } \alpha_{ij} = \sum U_i U_j / \sum U_i^2,$$

where U_i is the frequency of utilization of a resource category by species i, and U_j is the utilization by species j. Values of α range from 0, for no overlap, to 1, for complete overlap, and may exceed 1 when niche widths are unequal. For calculating w, the common standard deviation of two utilization functions required for an evaluation of the theory of limiting similarity among the *Accipiter* assemblages, we use weighted averages of the variances (Sokal and Rohlf 1981) of the functions being compared.

RESULTS

DISTRIBUTION, DENSITY, AND NESTING CHRONOLOGY

Each *Accipiter* species nested in all major forest types surveyed except in northwestern Oregon, where *A. gentilis* was absent. No major differences in the elevation of nests among species were found (Reynolds and Wight 1978). In 1970 and 1971, four and five *A. cooperii* nests were found in the Corvallis study area (one nest per 2,321 ha and one nest per 1,857 ha, respectively) (Fig. 1). Although nests of *A. striatus* were found in and adjacent to the Corvallis area in 1969, none was found within the boundary during 1970 or 1971. In 1974, four *A. striatus* nests, five *A. cooperii* nests, and four *A. gentilis* nests were found in the Bly study area (one *A. striatus* nest per 2,750 ha, one *A. cooperii* nest per 2,200 ha, and one *A. gentilis* nest per 2,750 ha). In our state-wide surveys (1969–1975), we found a complete complement of species in each *Accipiter* assemblage during breeding in all large areas containing a variety of stand densities and ages. Perhaps due to the lack of

suitably dense nesting sites (Reynolds et al. 1982), however, *A. striatus* did not nest in large expanses of open conifer forests.

Accipiter gentilis appeared at their nests in late March and early April, but dates of clutch completion extended from early April to late May ($\bar{x} = 6$ May). *Accipiter cooperii* appeared at their nests by mid-April and had completed clutches by mid-May ($\bar{x}$ for northwestern Oregon = 11 May, for eastern Oregon = 19 May). *Accipiter striatus* were first seen at nests in early May and had completed clutches by the end of May (northwestern, $\bar{x} = 25$ May; eastern, $\bar{x} = 26$ May) (Reynolds and Wight 1978). Incubation required approximately 32 days for each species, and the nestling period lasted 34–37 days for *A. gentilis*, 27–30 days for *A. cooperii*, and 21–24 days for *A. striatus*. Due to the faster growth rate of the young of the smaller hawks, the date of fleding of all species differed by no more than 10–12 days. After fledging, the young of each species were dependent upon the adults for food for 30–40 days before leaving the nest areas.

PREY RESOURCES

Size and taxa.—The estimate of the total density of birds in northwestern Oregon was 1,640 birds (58 species) per 100 ha, nearly twice the number of species (30) and more than double the density (688/100 ha) of birds in the Bly area. To assess the density estimate for eastern Oregon, we compared our densities to densities determined by spot-mapping in five conifer stands in the Blue and Wallowa mountains in northeastern Oregon (R. W. Mannan pers. comm.). This comparison indicated that, although there was an average of 200 birds per 100 ha more in Mannan's stands than in the Bly area, the total number in eastern Oregon forests was approximately one-half of that in northwestern Oregon.

The rank order, in decreasing frequency of observation, of four of the most common diurnally active small mammals in eastern Oregon was: yellow-pine chipmunk (*Eutamius amoenus*), golden-mantled ground squirrel (*Spermophilus lateralis*), chickaree (*Tamiasciurus douglasii*), and snowshoe hare (*Lepus americanus*). In all, 12 species were recorded. The ranking of the most commonly observed mammals in northwestern Oregon was: Townsend chipmunk (*E. townsendii*), chickaree, brush rabbit, (*Sylvilagus bach-*
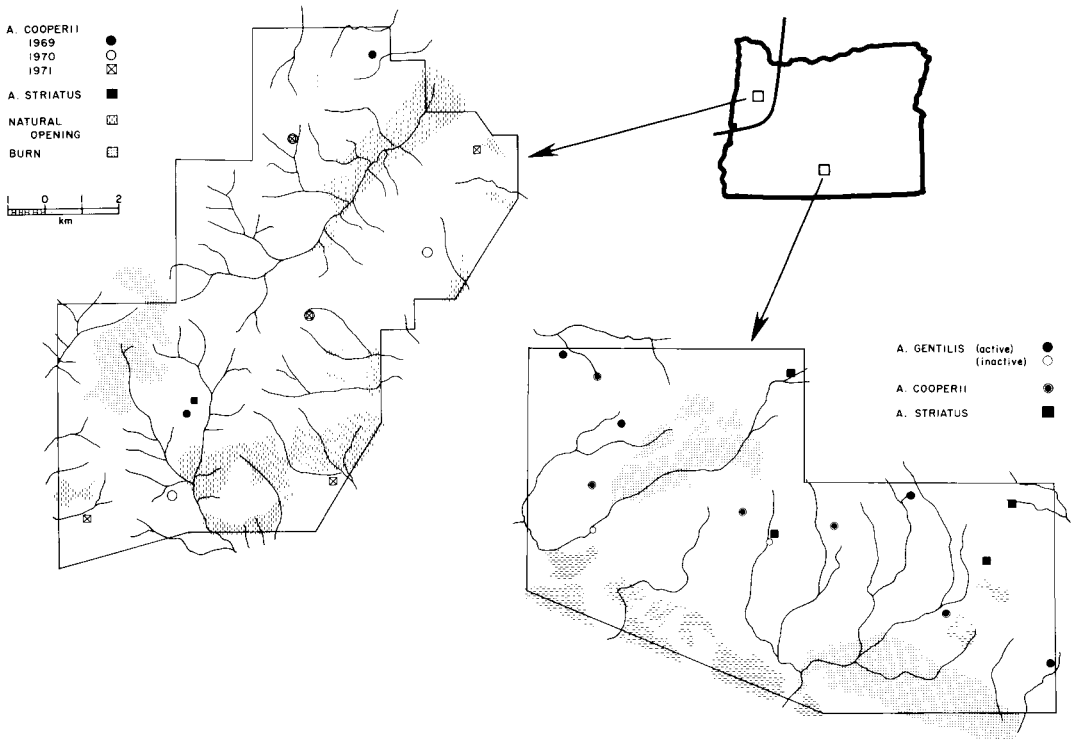
Fig. 1. Locations of the Corvallis study area in northwestern Oregon and the Bly study area in eastern Oregon. The boundary between the two regions is indicated.

manii), and western gray squirrel (*Sciurus grise-us*). A total of 11 species was recorded.

Frequency distributions of birds in 50-g weight classes indicated that bird numbers declined precipitously as body size increased in both areas (75–80% of the birds weighed less than 50 g). To achieve an approximate normalization of these distributions, we used a log transformation of bird weights (Fig. 2). Superimposing total biomass on these figures indicated that, although the majority of forest birds was of the size of *Parus* sp. ($\bar{x} = 10.6$ g), biomass increased to the size class that includes American Robins (*Turdus migratorius*) ($\bar{x} = 81.2$ g) and then became highly variable over the more uncommon larger birds. Lacking quantitative data, we do not include mammals in these figures. Because mammals are intermediate to large, relative to birds, however, their inclusion would raise the middle and right portions of these curves. The essential point of these findings is that the avifaunas in both areas (and this is probably true of mammals as well) have an approximately lognormal size-frequency distribution.

Zone.—There were notable differences between the two avifaunas in the occurrence of birds in height zones in the ground-shrub, canopy, and generalist categories. Of the birds in northwestern Oregon, 15% occurred in the ground-shrub, compared with less than 3% in eastern Oregon. This difference is undoubtedly related to the greater development of the shrub layer in the moist forests of western Oregon. Although nearly 60% of the birds in northwestern Oregon and 40% in eastern Oregon occurred in the upper canopy, the ratio of biomass to numbers in this layer was greater in eastern than in northwestern Oregon. The greater abundance of smaller birds in the canopy zone in northwestern Oregon is probably related to the high primary productivity of the forest in this region. Although little is known about standing stocks of invertebrates or seeds in these forests, the greater tree density and foliage volume of these forests probably sup-
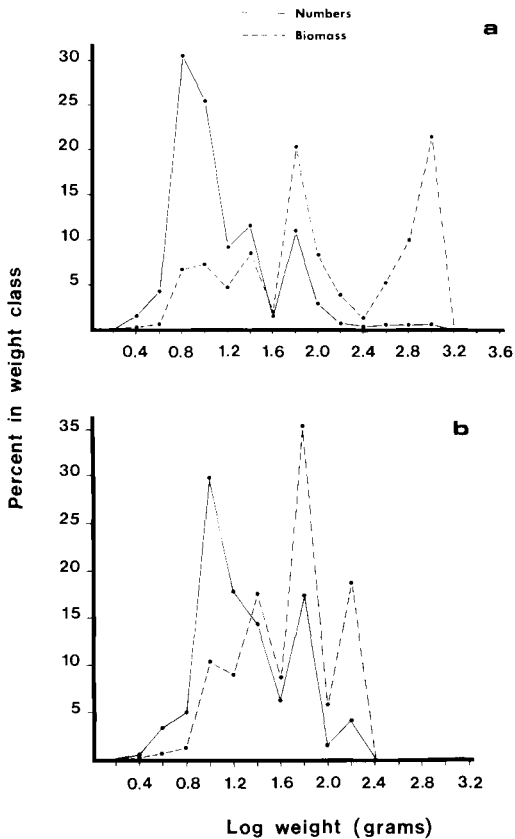
Fig. 2. Percentage by number and biomass of birds/100 ha in (a) northwestern Oregon and (b) eastern Oregon conifer forests. Log_{10} weight categories.

port more of these foods and, ultimately, larger populations of small insectivores. Eastern Oregon forests had a greater percentage of birds in the zone-generalist category. This difference stemmed not only from an increase in the number of zone generalists (e.g. 73 robins/100 ha in eastern vs. 10/100 ha in northwestern Oregon) but a concomitant decrease in canopy specialists in eastern Oregon. In both regions, bird numbers and biomass generally increased in consecutively higher zones up to, but not including, the aerial zone.

Most mammals available to *Accipiter* are zone generalists (tree squirrels), although one (*Glaucomys*) occurs primarily in the canopy zone and others (*Lepus* and *Spermophilus*) occur only in the ground-shrub layer. Including mammals in these figures would increase the numbers of

prey in the zone generalist and ground-shrub zones in both regions.

DIETS

Prey size.—A total of 199 prey was identified from 5 *A. striatus* nests, and 281 prey were collected from 20 *A. cooperii* nests in northwestern Oregon. In eastern Oregon, 116 prey were collected from 9 *A. striatus* nests, and 120 prey were collected from 18 nests of *A. cooperii*. From 59 nests of *A. gentilis*, 227 prey were identified (Appendix 1). Combining both regions, we could identify 16.8% of the prey of *A. striatus*, 23.2% of the prey of *A. cooperii*, and 11.5% of the prey of *A. gentilis* as either young mammals or nestling and fledgling birds.

One-tailed Student's *t*-tests (Sokal and Rohlf 1981) were used on the log-transformed prey weights to test the null hypotheses that there were no differences among mean size of *Accipiter* prey. Bartlett's test (Sokal and Rohlf 1981) indicated that the variances of the three diets in eastern Oregon were homogeneous (x^2 = 2.438, df = 2, $P < 0.01$), whereas those in northwestern Oregon were significantly heterogeneous (x^2 = 10.209, df = 1, $P > 0.01$). The mean size of *A. cooperii* prey in northwestern Oregon (134.7 g, mean from untransformed data) was significantly larger than the mean size of *A. striatus* prey (12.8 g) in the same region ($P < 0.005$) (Table 1). In eastern Oregon, the mean sizes of *A. striatus* prey (28.4 g), of *A. cooperii* prey (136.3 g), and of *A. gentilis* prey (306.6 g) were also highly significantly different from one another ($P < 0.005$).

The mean size of *A. cooperii* prey in both study areas was nearly identical in spite of the fact that mammalian prey size ($\bar{x}$ = 296.4 g, untransformed) in the northwest was twice that in eastern Oregon ($\bar{x}$ = 147.5 g) and the size of birds taken in northwestern Oregon ($\bar{x}$ = 79.2 g) was about half of that in eastern Oregon ($\bar{x}$ = 123.7 g). Overall prey sizes were similar because *A. cooperii* captured more mammals in eastern (53.1%) than in northwestern Oregon (25.5%). The mean size of *A. striatus* prey in eastern Oregon was nearly twice that of prey in northwestern Oregon ($P < 0.005$). Although the mean was enlarged by two chickarees taken by this hawk in eastern Oregon, the mean size of birds alone (25.4 g) was twice that of birds taken in northwestern Oregon ($\bar{x}$ = 11.8 g). The chickarees were the only mammals captured by

TABLE 1.   Number and weight (g) of prey in diets of *Accipiter* in eastern and northwestern Oregon (untransformed data).

	A. striatus			A. cooperii				A. gentilis		
	Bird	Mammal	Combined	Bird	Mammal	Reptile	Combined	Bird	Mammal	Combined
Eastern Oregon										
Number	114	2	116	53	60	—	113	121	97	218
Mean	25.4	201.4	28.4	123.7	147.5	—	136.3	195.5	445.2	306.6
SD	22.3	0	31.8	212.7	138.5	—	177.6	207.0	414.9	363.9
Max.	148.8	201.4	201.4	1,150.0	713.0	—	1,150.0	1,505.0	1,118.6	1,505.0
Min.	5.6	201.4	5.6	8.8	25.0	—	8.8	17.6	36.8	17.6
Northwestern Oregon										
Number	194	5	199	202	73	5	280			
Mean	11.8	53.1	12.8	79.2	296.4	18.6	134.7			
SD	9.2	56.9	14.3	113.9	245.4	15.7	185.3			
Max.	81.2	167.0	167.0	1,246.0	678.5	50.0	678.5			
Min.	3.8	23.7	3.8	7.0	10.0	10.0	7.0			

A. striatus in eastern Oregon, and, although we assigned them adult weights (201.4 g), each may have been a young animal.

Except for *A. striatus*, mean prey weights of *Accipiter* in Oregon were considerably different from the combined mean prey weights of male and female *Accipiter* reported by Storer (1966) (*A. striatus*, 23.0 g; *A. cooperii*, 44.2 g; *A. gentilis*, 459.5 g). The larger mean size of *A. gentilis* prey reported by Storer may reflect a reduced winter abundance of small migrants and the fact that males probably accounted for half of the prey in his data, whereas males in our study accounted for a considerably larger proportion. The mean size of *A. gentilis* prey in Oregon, however, was very near the 312 g reported for nesting *A. g. gentilis* in Europe (Uttendörfer 1939). The much smaller weight of *A. cooperii* prey reported by Storer (1966) is perplexing.

The avifauna was less diverse and less abundant in eastern Oregon than in northwestern Oregon. The size-frequency distribution of the eastern avifauna, however, favored larger individuals, and there was an apparently greater abundance of mammals. That birds in the diets of *A. striatus* and *A. cooperii* in eastern Oregon were of a larger mean size may be a reflection, to a degree, of the different size-frequency distibution of birds there. Also, the extent to which *A. cooperii* captured mammals (53.1%) in eastern Oregon may have been a response to the lower abundance of birds in that region. Other diet studies of *A. cooperii* indicate that this hawk takes an equivalent percentage of mammals in

other areas as in northwestern Oregon (Hamerstrom and Hamerstrom 1951, 15%; Meng 1959, 18%; Duncan 1966, 33%; Storer 1966, 17%; Snyder and Wiley 1976, 30%). The percentage of prey by weight class in the diets (Fig. 3) indicates the location, width, and extent of overlap of the utilization functions in both study areas.

Prey taxa.—The taxonomic composition of the diet of *Accipiter* was examined by grouping birds into families and subfamilies, mammals into genera, and reptiles into class (Fig. 4). Each of the taxa taken by *A. striatus* and *A. cooperii* in northwestern Oregon was taken in different proportions except Fringillidae, *Glaucomys*, *Zapus*, and *Microtus*. The three mammals, however, formed a minor proportion of the diets (less than 2% by number), whereas the fringillids contributed nearly 14% to the diet of each.

With the exception of Picidae and Turdinae, *A. striatus* (11.2% and 11.2%, respectively) and *A. cooperii* (7.1% and 10.6%) in eastern Oregon took prey taxa in different proportions. Picidae and Turdinae also occurred at a similar frequency in the diet of *A. gentilis* (9.6% and 11.1%). Principal differences among the bird taxa captured by *A. cooperii* and *A. gentilis* were in the proportions of Fringillidae and Corvidae. There were some minor differences among the proportions of Accipitridae, Phasianinae, and Columbidae taken. No mammalian prey except *Spermophilus* (17.7% for *A. cooperii* and 10.6% for *A. gentilis*) was captured by these species in near equal frequencies. Major differences in mammalian taxa taken by *A. cooperii* and *A. gentilis*
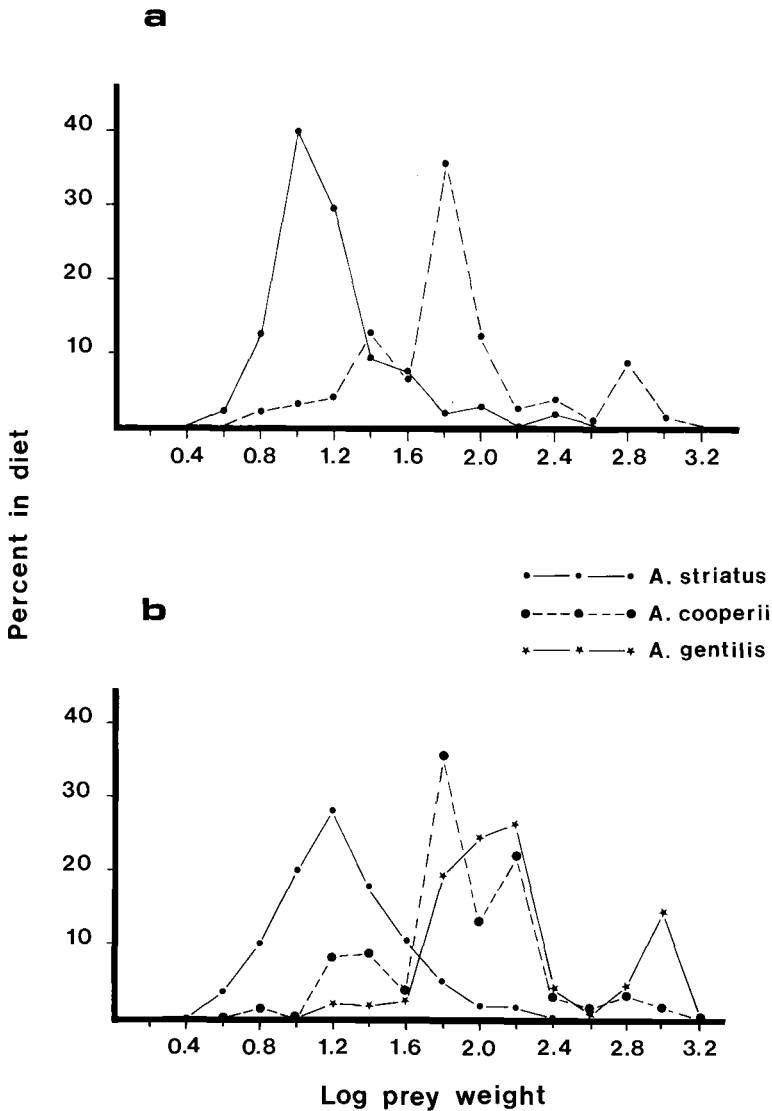
Fig. 3. Size-frequency distribution of prey in the diet of *Accipiter* in (a) northwestern Oregon and (b) eastern Oregon. Log_{10} weight categories.

occurred among *Lepus, Eutamius, Glaucomys,* and *Tamiasciurus.*

Foraging zone.—Percentages of prey taken from foraging zones by *Accipiter* in both study areas (Fig. 5) suggested that *A. striatus* foraged primarily in the upper canopy, whereas *A. cooperii* foraged in the ground-shrub and canopy-shrub zones. Other than the fact that *A. gentilis* took a slightly higher percentage of prey from the ground-shrub layer, there appeared to be no major differences in zone use between

A. cooperii and *A. gentilis.* There was a slight tendency for *A. cooperii* to forage closer to the ground in eastern than in northwestern Oregon.

DISCUSSION

NICHE CHARACTERISTICS

As *Accipiter* body size increased, niche width in the prey-size dimension (arithmetic scale,
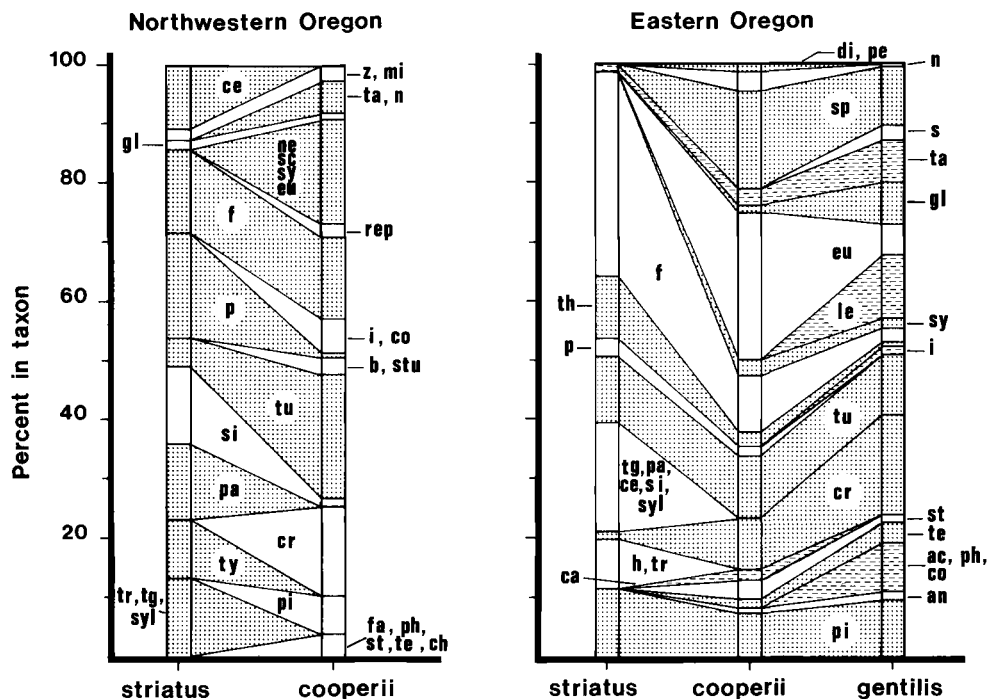
Northwestern Oregon

Eastern Oregon

Fig. 4. Taxonomic composition of diets of *Accipiter* in northwestern and eastern Oregon. an, Anatidae; fa, Falconidae; ac, Accipitridae; te, Tetraoninae; ph, Phasianinae; ch, Charadriidae; co, Columbidae; st, Strigidae; ca, Caprimulgidae; tr, Trochilidae; pi, Picidae; ty, Tyrannidae; h, Hirundinidae; cr, Corvidae; pa, Paridae (= Paridae, Aegithalidae); si, Sittidae; ce, Certhiidae; tg, Troglodytidae; tu, Turdinae; syl, Sylviinae; b, Bombi-cillidae; stu, Sturnidae; p, Parulinae; th, Thraupinae; f, Fringillidae (= Cardinalinae, Emberizinae, Fringilli-nae); i, Icterinae; ne, *Neurotrichus*; sc, *Scapanus*; sy, *Sylvilagus*; le, *Lepus*; eu, *Eutamius*; gl, *Glaucomys*; ta, *Tamias-ciurus*; s, *Sciurus*; sp, *Spermophilus*; di, *Dipodomys*; n, *Neotoma*; pe, *Perognathus*; z, *Zapus*; mi, *Microtus*; rep, Reptilia.

50-g weight classes) also increased (0.0004 and 0.12 for *A. striatus* and *A. cooperii* in northwestern Oregon; 0.01, 0.15, and 0.39 for *A. striatus*, *A. cooperii*, and *A. gentilis* in eastern Oregon). The same pattern, with the exception of *A. striatus* in eastern Oregon, occured for log-transformed prey weights (Table 2). Although *A. striatus* in eastern Oregon captured prey from fewer size classes (9), it had a niche width greater (log scale) than that of its cogeners, the result of a more nearly equal use of the size classes. For consumers whose prey are lognormally distributed, the smaller consumer, because of far more numerous prey and shorter search time beween captures, should take only the most profitable prey and, therefore, would have a relatively restricted diet breadth. Larger consumers, feeding on rarer items, would have longer search times between captures and should therefore use a wider range of food sizes

(Schoener 1969). The different search times and foraging strategies explain why the utilization functions of *Accipiter* become more symmetrical and of nearly equal width when plotted logarithmically.

Maximum prey size increased with increasing *Accipiter* size and was probably limited by the ability of individuals to subdue larger prey. Minimum prey size, however, did not vary in proportion to *Accipiter* weight. *Accipiter striatus* was limited by availability on the left end of the food-size axis (smaller birds and mammals did not occur), and, thus, its utilization function was truncated here (Fig. 3). Because the two larger species are capable of taking small birds and mammals it is not surprising that their utilization curves trailed to the left. Because of their greater absolute energetic demands, however, larger *Accipiter* should avoid pursuit of small prey unless the cost of pursuit and cap-
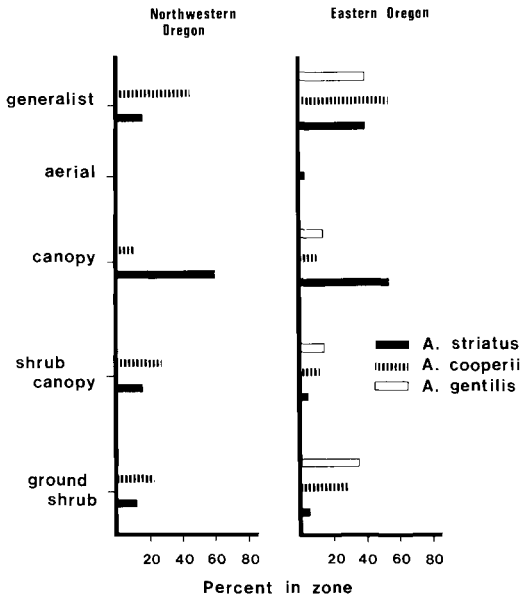
Fig. 5. Percentage of prey captured from each foraging zone by *Accipiter* in northwestern and eastern Oregon.

TABLE 3. Ratio of mean prey size to *Accipiter* body size (males and females combined) in northwestern and eastern Oregon.

Location	Species	Mean prey size (g)	Mean predator size (g)[a]	Prey/predator
Northwestern	*A. striatus*	12.8	135.0	0.09
	A. cooperii	134.7	368.0	0.37
Eastern	*A. striatus*	28.4	135.0	0.21
	A. cooperii	136.3	368.0	0.37
	A. gentilis	306.6	977.0	0.31

[a] *Accipiter* weights from Storer (1966).

hawks have greater striking power (Storer 1966, Goslow 1971), one would intuit that the prey weight to predator weight ratios should increase with *Accipiter* body size. Any power gained through size by *A. gentilis*, however, was perhaps counteracted by its being a prey-size generalist in an area on the resource axis where prey numbers are low and truncated on the right. Thus, the effect of large prey is minimized by their relative rarity and low frequency of capture.

Niche width in the taxa dimension also increased as body size of *Accipiter* increased (Table 2). In both regions, each species captured prey that were significantly different in mean weight (Table 1), and each used the two major taxa (birds and mammals) in different proportions (northwestern, $\chi^2 = 48.3$, df = 1, $P < 0.0001$; eastern, $\chi^2 = 72.9$, df = 2, $P < 0.0001$). As body size increased, a greater percentage of mammals was taken. Differences in mean mammal versus mean bird weights in the diets of

ture is sufficiently small (e.g. young, inexperienced prey or when a sufficient element of surprise is involved). The observed utilization patterns are in accordance with Wilson's (1975) view that there exists an asymmetry in competitive relations in a size series of predators. Large predators eat things unavailable to smaller consumers, but the reverse is not true (but see below). It is interesting that the ratio of mean prey size to predator size increased from *A. striatus* to *A. cooperii* but then decreased for *A. gentilis* (Table 3). Because heavier-bodied

TABLE 2. Numbers of prey categories and standardized niche width[a] with respect to weight (g) of prey, prey taxon, and foraging zone in northwestern and eastern Oregon.

Location	Species	Number[b]	Size[c]	Number[b]	Taxon	Number[b]	Zone
Northwestern	*A. striatus*	9	0.21	10	0.33	4	0.37
	A. cooperii	12	0.34	18	0.36	4	0.57
Eastern	*A. striatus*	9	0.35	11	0.21	5	0.33
	A. cooperii	11	0.29	13	0.29	4	0.42
	A. gentilis	10	0.32	16	0.45	4	0.58

(Niche width spans the Size, Taxon, and Zone column groups.)

[a] Standardized niche width = $B_s = (B - 1)/(n - 1)$.
[b] Numbers of prey categories utilized.
[c] Log prey weights.

TABLE 4. Overlap (α) with respect to log prey size, taxon, zone, and total α's (α summation) in northwestern and eastern Oregon.

Location	Interaction	Niche dimension			Total overlap α_u
		Size α_u	Taxon α_u	Zone α_u	
Northwestern	α_{sc}[a]	0.14	0.31	0.46	0.30
	α_{cs}	0.20	0.33	0.61	0.38
Eastern	α_{sc}	0.37	0.33	0.62	0.44
	α_{cs}	0.32	0.43	0.71	0.49
	α_{cg}	0.81	0.54	0.86	0.74
	α_{gc}	0.87	0.79	1.06	0.91
	α_{sg}	0.16	0.19	0.55	0.30
	α_{gs}	0.15	0.36	0.77	0.43

[a] s = *A. striatus*; c = *A. cooperii*; g = *A. gentilis*.

Accipiter may reside in a difference in the degree of difficulty of capture of the two taxa; mammals, being limited to fewer planes of escape, may be easier to capture than birds. Larger mammals in the diets, however, may simply reflect the fact that available mammals tended to be larger than birds. For example, Steller's Jay (*Cyanocitta stelleri*), 106.6 g, and American Robin, 81.2 g, were the largest of the most common birds in Oregon forests, whereas the smallest mammals commonly captured were *Eutamius*, 67.5 g. Additionally, each of all the species of mammals, except *Eutamius*, that contributed more than 5% to the diets in both assemblages was larger than 160 g (Appendix 1).

Niche width with respect to zone also increased with increased *Accipiter* size. This pattern appeared to be largely associated with an interdependence of the prey size and foraging zone. Small birds in western conifer forests tend to be gleaners (warblers, nuthatches) or hawkers (flycatchers), and they occur mostly in the mid- to upper-canopy portions of the forests. As a result, *A. striatus*, a small-bird specialist, appeared to be a zone specialist. In contrast, larger birds and mammals tended to be associated with the lower strata or were zone generalists. Thus, *A. gentilis* and *A. cooperii*, both of which captured birds and mammals of intermediate to large size in all zones, were zone generalists. In general, the standardized niche widths in the size dimension were the narrowest, whereas those in zone dimension were the broadest.

Niche-overlap values (Table 4) were consistently lowest in the prey-size dimension (5 of 8 possible cases), whereas the remaining lowest values occurred in the taxon dimension. In general, *A. striatus* and *A. cooperii* had the least amount of overlap of prey size, and *A. cooperii* and *A. gentilis* had the largest amount. *Accipiter striatus* and *A. cooperii* in eastern Oregon overlapped to a lesser extent than the same species pair in the northwest. The above patterns also held in the taxon and zone dimensions. The range of overlap values (prey size) of *Accipiter* (0.14–0.87) is comparable to ranges reported for other suites of vertebrates. Oregon niche overlap values, however, averaged 0.38 ($n = 8$, SD = 0.30), a value lower than the average for heteromyid rodents ($\bar{x} = 0.55$) (Brown and Lieberman 1973), seed-eating birds ($\bar{x} = 0.997$) (Pulliam and Enders 1971), and owls ($\bar{x} = 0.58$) (Herrera and Hiraldo 1976) but somewhat higher than the average for lizards ($\bar{x} = 0.32$) (Pianka 1973) and the two species of *Accipiter* in Europe ($\bar{x} = 0.22$) (Van Beusekom 1972).

Overlap values for prey size, taxon, and zone were combined to estimate the total overlap among *Accipiter*. If the proportions of different food sizes taken were the same in all zones and taxa, then the resource dimensions would be independent, and the total overlap would be a product of the α's in each dimension (May 1975, Cody 1974). The overlap of *Accipiter* in each dimension, however, was strongly correlated with that in every other (size-taxa, $r = 0.89$; size-zone, $r = 0.73$; taxa-zone, $r = 0.97$), indicating that the niche dimensions were interdependent. We therefore present the arithmetic mean ("summation α," Cody 1974) of the α's as an estimation of the upper bound of the true multidimensional overlap (May 1975) (Table 4).

COMPETITIVE COEXISTENCE?

For competition to effect a divergence of morphological characters such that competing species segregate on or use different portions of one or more resources, a number of conditions is required. One condition is that the resources must be in limited supply (Lack 1944) and the supply must be limiting through a significant portion of the life histories of the competitors (Wiens 1977). Further, the structure and abundance of the limiting resource must have at least some constancy through time (Wiens 1977). If, for example, bill or body size responds to competition in the breeding season by becoming smaller, then to accommodate re-

duced size, suitable conditions during other seasons must exist. The requirement of resource constancy through time also applies to between-generation times (Wiens 1977) to the extent that the utilization function of a population must have some constancy in order for an adjacent species to respond. Thus, because of the relatively short duration of this study, it is not possible to demonstrate that morphological differences or foraging-habitat differences in *Accipiter* have resulted from competitive interactions. Several patterns in the feeding ecology of Oregon *Accipiter*, however, support the supposition that competition may be important in organizing *Accipiter* assemblages.

Although breeding begins earlier for the larger species, each *Accipiter*, for the most part, is in an equivalent stage of nesting, especially from the mid-portions of the breeding season. Each *Accipiter* assemblage occurred in the same habitat from April through August, and our observations of foraging birds indicated that horizontal partitioning of habitat for foraging did not occur. Thus, the conditions for competition—spatial and temporal overlap—were extant, and, if competition is occurring (or has in the past), it is probably exploitative in nature.

May and MacArthur (1972) and May (1973, 1974) examined the question of how similar the ecological niches of two or more species can be and still allow coexistence. These authors found that small-scale environmental stochasticity can impose significant limits on the tolerable degree of niche overlap. Their conclusions regarding the effects of stochasticity, however, have been challenged by Feldman and Roughgarden (1975), Abrams (1975), and Turelli (1981). Turelli (1981), using an invasion criterion for determining limits to similarity rather than the near-equilibrium linearization criterion of May (1973), found that practical limits to similarity can be obtained by ignoring stochasticity and performing a deterministic analysis. Nevertheless, Turelli (1981) used an analytic technique that provided conditions for the coexistence of competitors in a random environment. Because his analysis dealt with situations in which the environmental variation was relatively small, he found that the difference between the stochastic and deterministic limits to similarity were typically small. Turelli also found that exact limits to similarity are extremely model dependent. May and MacArthur's (1972) stochastic approach, which as-

sumed one-dimensional Gaussian niches, predicted niche-separation levels of about $d/w = 1$–2, where d is the distance between the means of the utilization functions and w is their common standard deviation, for communities structured by competition. May (1973) reviewed the available evidence regarding species packing and cited four examples for which resource-utilization data were available and in which d/w was equal to about 1, regardless of the level of environmental fluctuations. Abrams (1975) claimed, however, that none of the four examples cited by May (1973) had been studied enough to rule out segregation along niche dimensions other than that noted by May. Abrams (1975) stressed that most detailed studies have found that resource partitioning frequently occurs in several dimensions and that, in these cases, $d/w = 1$ is not applicable.

Although one must take into account the simplifications of these niche-overlap models, the ratios of the Oregon assemblages approximated the predicted values: northwestern, *A. striatus*-*A. cooperii*, $d/w = 2.2$; eastern, *A. striatus*-*A. cooperii*, 1.8, *A. cooperi*-*A. . gentilis*, 0.8. The low value of the *A. cooperi*-*A. gentilis* ratio (closer packing) may be related to Roughgarden's (1974) contention that, for species whose utilization functions are leptokurtic (thick tails and sharp peaks), tighter packing is possible because much of the resource utilization is concentrated in the narrow peaks. Because each of the polymodal functions of these species has a secondary hump on opposite ends (Fig. 3), overlap is further reduced. The tighter packing of the two larger species in the prey size dimension, however, may also reflect the tendency for these species to partition prey taxa.

Also of interest are the large separations of the niches of *A. striatus* and *A. cooperii* in both assemblages. Given that larger competitors gain a competitive advantage over smaller animals because they harvest things unavailable to smaller animals., one may ask what factors are maintaining the large distances between *A. striatus* and its cogeners. The answer may lie with Wilson's (1975) "K' advantage," a concept that takes into account the number of animals as well as the searching capacity of individuals. In competitive situations, Wilson's model permits comparisons between consumer populations that differ in body size and metabolism. In his treatment of a highly skewed prey-size distribution, Wilson found that the outcome of
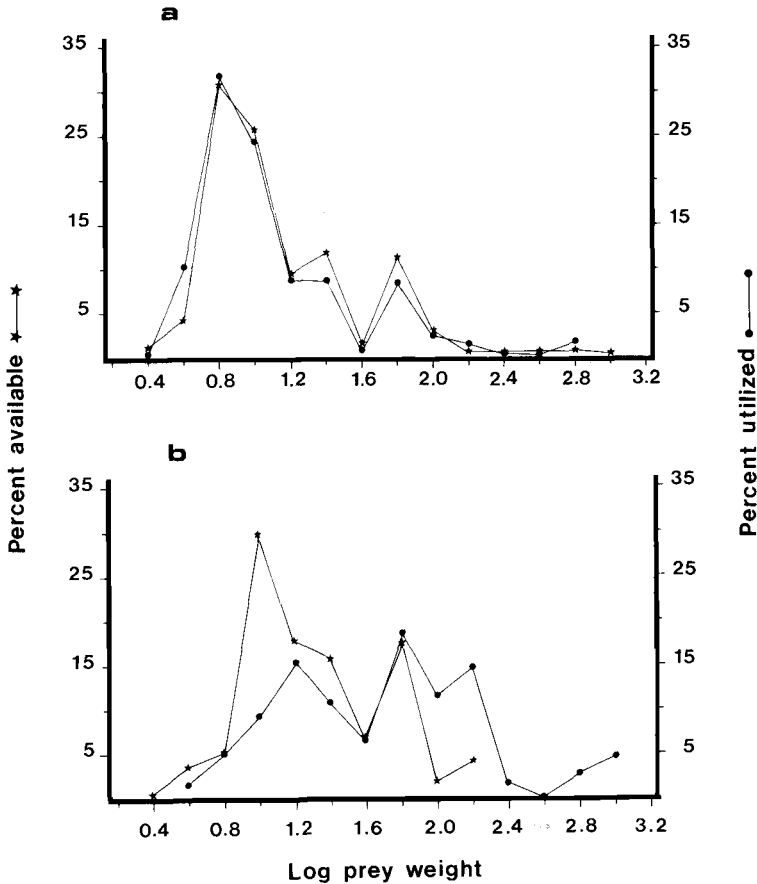
Fig. 6.   Total utilization curve (diets of all species combined) of *Accipiter* and prey availability curve (birds only) for (a) northwestern and (b) eastern Oregon. See text for explanation.

competition between large and small competitors depends on where the competitors lie on the resource spectrum. When prey availability (Wilson's kw/r expression) is greater in the region of the resource axis where the smaller consumer is more successful, the advantage of the larger consumer will be mitigated; the smaller competitor takes the advantage and may displace and cause adjacent species to become larger.

The large displacement between the utilization means of *A. striatus* and *A. cooperii* may be further enhanced by the fact that *A. striatus* had capture rates [determined from observed frequencies of prey deliveries to nests and predicted from an energetics model (Reynolds MS)] 2–4 times those of its cogeners (see also Opdam 1975). Greater harvesting rates, stemming from relatively greater metabolic demands and a

smaller prey-predator size ratio (Table 3), resulted in expanded utilization functions for *A. striatus* relative to its cogeners, which, in turn, resulted in greater (asymmetrical) overlap (see Schoener 1974). The predicted outcome of this asymmetry is that the functions be displaced somewhat beyond a d/w of 1. The larger prey-predator size ratio of *A. cooperii*, relative to that of *A. gentilis*, tended to equalize the capture rates and, therefore, the areas under the utilization curves of both species.

Additional evidence for competition is the extent to which the combined utilization functions of all species (summation of the curves of each species) included the entire size range of the avian prey at or near the proportions in which the prey occurred (Fig. 6). The congruence of these two curves in northwestern Oregon is striking. In eastern Oregon, the rela-

tionship between resources and utilization was less exact. Here, *A. striatus* captured most of its prey from one size class larger than peak availability. This may have been a response to the reduced diversity and abundance of avian prey in eastern Oregon, the effects of the combined harvesting by each *Accipiter*, or both. Further, the right-hand portion of the combined utilization curve continued above and beyond the availability curve. The extension of the combined curve reflects the extent to which both *A. cooperii* and *A. gentilis* used mammals—taxa not included in the resource curves. Had mammals been included, the similarity of the resource and utilization curves for eastern Oregon would increase, and that for northwestern Oregon would decrease. Nevertheless, both assemblages clearly used the entire range of prey size available—an expected characteristic of an assemblage the members of which have diverged morphologically in response to competition for a resource.

Finally, because of the structure and abundance of the food resource and the nature of the *Accipiter* size-prey size relationship, birds and small mammals are perhaps an ideal resource for partitioning. The sizes of small mammals and birds and the agility with which they escape predators (Howland 1975) put physical and energetic constraints on predator body size; large *Accipiter* cannot forage efficiently for small prey and small *Accipiter* cannot, without risk of injury, subdue prey much larger than themselves. As a result, no single species could exploit the entire prey-size range in Oregon forests. Furthermore, it is unlikely that predation on these top-level consumers is holding *Accipiter* populations at levels sufficiently low so that food resources do not become limiting. *Accipiter* are relatively large mobile birds, and, perhaps because of this, we found no instances of predation on adults. However, large owls (*Bubo, Strix*) and the larger *Accipiter* occasionally take nestlings or fledged young, although we found this to be rare during our studies.

CONCLUSIONS

Because we were unable to determine whether or not the food resources were limiting, we examined our results for insights into the character or style of what may be competitive coexistence in two *Accipiter* assemblages. If competition is occurring, our data (based on the relative amounts of overlap among the dimensions) indicate that prey size, and to a limited extent prey taxa, are the primary resource characters structuring western North American *Accipiter* communities. In our study areas two types of niche shifts were identified: a doubling of the prey size of *A. striatus* and shifts of *A. cooperii* toward a greater exploitation of the smaller mammals and larger birds. Whether competition was involved or not, the niche shifts of *A. cooperii* resulted in reduced overlap with the smaller, bird-specializing *A. striatus* and with the larger, mammal and bird generalist *A. gentilis*.

Why *A. cooperii* did not shift its diet upward in size in northwestern Oregon where it was "released" is unclear. Perhaps a shift was unnecessary, because the resources were not limiting. Alternatively, the answer may lie in the *Accipiter* size-prey size relationship. The prey-size shift of *A. striatus* and the prey-taxa shift of *A. cooperii* represented changes in the shape of the utilization functions but not in location of the functions. Whether these shifts were responses to the lower productivity of eastern Oregon forests or the competitive environment (both of which result in less abundant resources) was not determined. These shifts, however, were certainly related to a flexibility in choice of prey and to the different resource abundances within the prey-size range of the predator in each region. A shift in the location of a niche on a resource axis of consumers like *Accipiter* may depend to a large extent upon the biogeography of the species. Given the energetic and physical constraints that determine the location and bounds of the *Accipiter* size-prey size relationship, one would not expect large shifts in the location of a utilization function without also noting a concomitant change in the size of the predator. That a morphological divergence would occur depends on the temporal and geographic predictability of the species makeup of the assemblages. That is, if the areas of sympatry are large relative to the areas where fewer than all the species components coexist, any selection for a change in body size in that area may be swamped by gene flow from the more ubiquitous sympatric populations. Although the area in Oregon that contained three *Accipiter* species is much larger than the area where only *A. striatus* and *A. cooperii* coexisted, the area containing the full complement of species compared with areas contain-

ing some fraction of these in western North America is unknown. Also unknown is the extent of gene flow between populations of any of these species.

Finally, there were no obvious differences in the structure or the abundance of the food resources between the two study areas that would account for the lack of nesting *A. gentilis* in northwestern Oregon. We guess that the absence of this species is related to two structural characteristics of the forests. The well-developed shrub layer that occurs over most of the region undoubtedly impairs the detection and pursuit of prey that occur on the ground or in the shrub layer—a zone heavily used by *A. gentilis* in eastern Oregon. Thus, *A. gentilis* may have been excluded from this area by reduced prey availability. Possible also is the scarcity of suitable nesting habitat. Nest sites used by *A. gentilis* in Oregon consist of mature or old-growth conifers (Reynolds et al. 1982), a stand type that has been reduced to relatively few small and scattered patches by tree harvests and wildfires. The affect of a general reduction of the age of a forest due to tree harvests on the foraging habitat of *A. gentilis* is unknown.

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APPENDIX. Weights and foraging zones of birds, mammals, and reptiles in the diets of *Accipiter* in northwestern and eastern Oregon.

				Diets				
				Northwestern Oregon		Eastern Oregon		
Species	Weight (g)	Source[a]	Zone[b]	*striatus*	*cooperii*	*striatus*	*cooperii*	*gentilis*
Anas platyrhynchos	1,150.0	29	1				1	2
Accipiter cooperii	368.0	61	3					1
Falco sparverius	114.0	15	3	1				
Phasianus colchicus	1,246.0	53	1	2				
Dendragapus obscurus	1,050.0	5	5				1	5
Bonasa umbellus	619.0	12	1		(1)c		1	2
Unidentified grouse	834.5		5	1				1
Callipepla californica	139.0	11	1	1				
Oreortyx pictus	243.9	28	1					9 (1)c
Charadrius vociferus	82.4	23	1	1				
Columba livia	376.7	*d	5	1				
Zenaida macroura	120.0	23	1	1				7
Otus kennicottii	172.0	15	3	1 (1)				1
Bubo virginianus	1,505.0	15	3					1
Asio otus	245.0	15	3				1	
Aegolius acadicus	83.0	17	3	1			2	1
Chordeiles minor	57.8	44	5				2	
Selasphorus rufus	3.8	32	2	(1)c				
Melanerpes lewis	106.0	6	3	1				1
Sphyrapicus varius	45.9	28	3	3		2		1
S. thyroideus	50.0	6	3	2		2		1 (1)
Picoides pubescens	28.2	4	3	2 (1)			1	
P. villosus	68.0	23	3	1		1	(1)c	1
P. albolarvatus	58.0	7	3			1		
Picoides spp.	48.3		3			6		1
Colaptes auratus	148.8	28	5		4 (1)	1	5 (1)	14 (1)
Dryocopus pileatus	282.0	*d	3					1
Contopus borealis	34.5	28	3	1 (1)	1			
C. sordidulus	12.8	14	3	1		1		
Empidonax difficilis	10.0	14	3			1		
Empidonax spp.	9.8		3	14 (2)		6		
Tyrannus verticalis	42.0	21	3			1		
Tachycineta thalassina	15.7	*e	4			1		
Perisoreus canadensis	74.6	55	5				1	3 (2)
Cyanocitta stelleri	106.6	28	2		10 (15)	1	8 (1)	17 (12)
Aphelocoma coerulescens	72.3	23	2		3			
Unidentified jay	89.4		2	(1)	8 (4)			1
Pica nuttalli	173.5	34	5					1
Parus atricapillus	11.2	4	2	1	(1)			
Parus spp.	10.6		3	12 (4)		8		
Psaltriparus minimus	5.9	14	2	9				
Sitta canadensis	10.3	28	3	17 (8)	3 (1)	4 (1)c		
Certhia americana	8.4	23	3	17 (7)	1	3		
Thryomanes bewickii	9.3	14	2	(1)		1		

APPENDIX. Continued.

| | | | | Diets | | | | |
| | | | | Northwestern Oregon | | Eastern Oregon | | |
Species	Weight (g)	Source[a]	Zone[b]	striatus	cooperii	striatus	cooperii	gentilis
Troglodytes troglodytes	8.9	28	1	6 (1)				
Regulus satrapa	5.6	28	3	6 (10)		1		
Regulus spp.	5.7		3			3		
Sialia mexicana	27.9	*e	5			2	1	
Myadestes townsendi	31.7	28	5	1				
Catharus ustulatus	25.0	28	1	5	1			
C. guttatus	26.3	28	1	2				
Catharus spp.	25.6		1	1	1 (1)	6	1	
Turdus migratorius	81.2	28	5	1	32 (23)	3	5 (2)	15 (5)
Ixoreus naevius	79.3	*e	5	1	1	2	3	3 (1)
Bombycilla cedrorum	33.5	23	5		1 (3)			
Sturnus vulgaris	74.5	4	5		4			
Vermivora celata	8.2	14	2	1		1		
Dendroica petechia	8.9	14	2	1				
D. coronata	10.4	14	3	1		1 (1)		
D. nigrescens	7.9	14	3	9 (5)	1			
D. occidentalis	8.3	14	3			1		
Oporornis tolmiei	10.3	14	1	3				
Wilsonia pusilla	7.0	14	2	10 (2)	1			
Unidentified warbler	8.8		2	1 (1)	1 (1)		(1)	
Piranga ludoviciana	26.9	14	3	1	1 (3)	9 (3)	(3)	(2)
Pheucticus melanocephalus	42.4	14	2		2			1
Pipilo erythrophthalmus	39.0	28	2		7 (5)	1	1	
Spizella passerina	15.0	23	5			3		
Passerella iliaca	32.3	*e	2				1	
Melospiza melodia	21.0	23	2	1	1 (1)			
Zonotrichia leucophrys	24.1	14	1		1			
Junco hyemalis	17.6	28	5	14 (2)	10 (10)	26 (1)	7 (1)	2
Agelaius phoeniceus	61.4	4	1		2			
Sturnella neglecta	89.0	31	1		1			2
Euphagus cyanocephalus	64.7	*e	5		(1)			
Molothrus ater	38.7	23	2		5 (3)			
Carpodacus purpureus	23.8	28	3				1	
Carpodacus spp.	22.4		3			5		2
Carduelis pinus	13.0	14	5	10 (1)	1	4		
C. tristis	11.3	4	2		(1)			
Unidentified sparrow	20.0		2		1		4	3
Unidentified bird					9			
Neurotrichus gibbsi	10.0	*d	1		1			
Scapanus orarius	53.9	*d	1		2			
Scapanus spp.	66.7		1		2			
Sylvilagus bachmani	644.0	*d	1		18 (4)		1	
S. nuttalli	713.0	*d					1 (1)	2
Sylvilagus spp.	678.5		1		1			1
Lepus americanus	1,118.0	*d	1					19
Lepus spp.	1,118.0	*d	1					5
Eutamias townsendi	89.3	*d	5		22			3
E. minimus	36.8	*d	5					1
E. amoenus	49.3	*d	5				1	
Eutamias spp.	67.5		5	1 (1)	1 (1)	1 (1)	26 (1)	7
Glaucomys sabrinus	167.0	*d	3	1	2		1	15
Tamiasciurus douglasi	201.4	*d	5		7	2	3	13
Sciurus griseus	759.0	*d	5					4 (1)
Spermophilus lateralis	166.1	*d	1				20	17
S.townsendi	132.0	*d	1					2
S. beldingi	268.0	*d	1					4

APPENDIX.   Continued.

Species	Weight (g)	Source[a]	Zone[b]	Northwestern Oregon		Eastern Oregon		
				striatus	cooperii	striatus	cooperii	gentilis
Dipodomys ordii	55.3	*d	1				1	
Perognathus spp.	25.0	*d	1				1	
Neotoma cinerea	289.2	*d	1					1
N. fuscipes	224.1	*d	1		2			1
Neotoma sp.	256.6		1		9		3	1
Microtus spp.	25.0	*d	1	3	2			
Zapus trinotatus	23.7	*d	1	1	1			
Unidentified mammal							3	6
Sceloporus occidentalis	10.0	*f	1		3			
Gerrhonotus spp.	13.0	*f	1		1			
Thamnophis spp.	50.0	*f	1		1			

[a] See numbered literature citation.

[b] (1) ground-shrub; (2) shrub-canopy; (3) canopy; (4) aerial; (5) generalist.

[c] Numbers in parentheses are juvenal (see text).

[d] Oregon State University Museum.

[e] R. Stewart (pers. comm.).

[f] R. Nussbaum (pers. comm.).

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