

AN ABSTRACT OF THE THESIS OF

Richard Truman Reynolds for the degree of Doctor of Philosophy  
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Accipiter.

Abstract approved: \_\_\_\_\_

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E. Charles Meslow

Sharp-shinned Hawks (Accipiter striatus), and Cooper's Hawks (A. cooperii) in the conifer forests in northwestern Oregon and A. striatus, A. cooperii, and Goshawks (A. gentilis) in the conifer forests of eastern Oregon were syntopic during the nesting season.

In this study density of nests, nest success, and utilization of food and habitat resources by each Accipiter in both northwestern and eastern Oregon were determined for 1969 through 1974. Abundance of birds and small, diurnal mammals in the forests of eastern Oregon and the abundance of birds in the forests of northwestern Oregon were estimated in faunal surveys of a variety of conifer forest types. In addition, the occurrence of small mammals in eastern Oregon and their relative abundances were qualitatively estimated.

The physiography and vegetative structure of Accipiter nest sites were quantified in both study areas, and differences in habitat variables among the sites of each species were examined by multivariate analysis of variance and discriminant analysis. These analyses showed that, while nest sites of each Accipiter in both areas had similar physiographic features, they differed in the structure of the vegetation. These differences were associated with the successional stage of the forest stands selected by each species: A. striatus nested in dense, 40-60-year-old, even-aged stands of conifers, A. cooperii in 50-80-year-old, dense conifer stands with slightly larger, more widely spaced trees, and A. gentilis in dense,

conifer stands with large overstory trees and a dense understory of regenerating conifers.

The following differences in the prey resources of the two study areas were noted; eastern Oregon had (1) nearly one half the species and density of birds, (2) a size-frequency distribution shifted somewhat toward larger birds, and (3) more species and a greater density of mammals than northwestern Oregon. Mean size of prey (12.8 g) captured by A. striatus in northwestern Oregon was significantly smaller than prey (28.4 g) captured by the same species in eastern Oregon. The diet of A. striatus in both areas was composed almost entirely of birds (<5% mammals). Mean size of prey of A. cooperii in both areas was nearly the same (134.7 g and 136.3 g) and each was significantly larger than mean sizes of prey of A. striatus. However, prey size and taxonomic composition of diets of A. cooperii varied; 74% birds ( $\bar{x}$  = 79.2 g) and 25% mammals ( $\bar{x}$  = 296.4 g) in northwestern Oregon and 47% birds ( $\bar{x}$  = 123.7 g) and 53% mammals ( $\bar{x}$  = 147.5 g) in eastern Oregon. Mean size of prey (306.6 g) of A. gentilis in eastern Oregon was significantly larger than mean size of prey of A. cooperii and consisted of 53% birds ( $\bar{x}$  = 195.5 g) and 45% mammals ( $\bar{x}$  = 445.2 g).

An analysis of the utilization of prey sizes, prey taxa, and foraging height zones demonstrated that partitioning of food in both areas occurred primarily in the prey size dimension. However, A. cooperii and A. gentilis, which broadly overlapped in the size dimension, showed increased partitioning of prey taxa. In eastern Oregon, use of foraging zones by A. cooperii and A. gentilis was nearly identical; both species captured prey primarily from the lower zones (ground-shrub and shrub-canopy). There was, however, little overlap on this dimension between A. striatus and its congeners in either study area as A. striatus almost entirely limited its foraging to the upper canopy.

Although it was not determined if food resources were limiting, a review of the feeding ecology of Accipiter in Oregon, in view of some

predictions of competition theory, supported the hypothesis that the different body sizes of coexisting members of this genus evolved in response to competition for food resources during the breeding season.

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# FOOD AND HABITAT PARTITIONING IN TWO GROUPS OF COEXISTING ACCIPITER

## INTRODUCTION

Since Lotka (1925), Volterra (1926, 1931), and Gause (1934), demonstrated that differences in resource utilization are necessary conditions for competitive coexistence, ecologists have investigated how and to what extent similar species differ in their resource use. As a result, a large body of mathematical, laboratory, and field investigations support the statement that two similar species can not coexist. However, due to the difficulty of demonstrating the ecological conditions required for competitive coexistence (Wiens 1977; Connell 1975), the occurrence and prevalence of competitive coexistence in nature is poorly understood.

Partitioning of food has been investigated in the genus Accipiter, a group of hawks associated with forests and which feed principally on birds and mammals. For a review of the distribution, ecology, and taxonomy of this genus see Brown and Amadon (1968) and Wattell (1973). Probably the main impetus behind the food studies of Accipiter was the body size relationships that occur among coexisting species; small forms tend to co-occur with large forms and, because males are much smaller than females in this genus, there are two body sizes for each species foraging for similar prey. Studies of the food of nesting Sparrowhawks (A. nisus) and Goshawks (A. gentilis gentilis) in Europe, indicated these species partitioned food on the basis of size; the smaller A. nisus captured small prey and A. gentilis captured larger prey (van Beusekom 1972; Opdam 1975). A similar partitioning occurred among Sharp-shinned Hawks (A. striatus), Cooper's Hawks (A. cooperii), and Goshawks (A. g. atricapillus) in North America (Storer 1966). In addition, the amount of dietary overlap and the degree of limiting similarity of the North American species has received considerable attention (Storer 1966; Hespenheide 1975; MacArthur 1972). However, food data used in these treatments were from Storer's (1966) listing of stomach contents of hawks collected from various locations in each

season (mostly fall and winter) over a number of years. Since prey availability changes geographically, seasonally, and annually, it is difficult to determine whether the differences in prey among Accipiter indicated by Storer (1966) were due to differences in prey availability or to competitive interactions. Consequently, there is doubt concerning the validity of the conclusions of these authors.

In the conifer forests of eastern and southwestern Oregon, A. striatus, A. cooperii, and A. gentilis nest and forage in the same habitat, whereas in similar forests in northwestern Oregon only A. striatus and A. cooperii coexist (Reynolds and Wight 1978). In this paper I present data on the habitat and food resources in these areas and their utilization by Accipiter during nesting. I address the relative importance of prey size, prey taxon, and foraging zone and tactic on the variability of the diet of each hawk and on the degree of overlap of their diets. Also discussed are the foraging strategies associated with the shape and location of the utilization functions of each Accipiter on the prey resource axes, and the adaptive apportionment of the nesting duties between the sexes associated with these foraging strategies.

## STUDY AREAS

This study included spring and summer surveys for Accipiter nests in all major forest types in Oregon except the western juniper (Juniperus occidentalis) forests in central Oregon and the narrow band of Sitka spruce (Picea sitchensis) forests along the immediate northwest coast. Each forest type surveyed contained a variety of tree species but all types were dominated by conifers. Oregon forests are primarily montane and cover extensive areas. For example, the western half of Oregon is almost entirely forested and is dominated by cordilleras continuous from the Sierra Nevada in California to southeastern Alaska. Scattered among these mountains, however, are wide flat-bottomed valleys with little woodland. Eastern Oregon is essentially a high plateau (600-1500 m) forming the western portion of the Great Basin. Eastern Oregon contains numerous small to large mountain ranges (and associated forests), ranging from 1800 to above 2700 m, separated by various distances of arid brushlands. Franklin and Dyrness (1973) described the vegetational zones and associated tree species as well as the edaphic and climatic characteristics of each major forest type in Oregon.

I divided Oregon into 2 subregions on the basis of occurrence of breeding pairs of A. g. attricapillus (Reynolds and Wight 1978). However, since the distribution of this species was restricted to drier forests, the subregions approximated the major environmental conditions associated with xeric vs. mesic forest types. The first, "northwestern Oregon," consisted of the Coast Range. This subregion is densely forested and has cool, wet winters and mild summers. Here, forests are dominated by continuous stands of Douglas-fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla). The other subregion, "eastern Oregon," included the remainder of the state. Eastern Oregon contained the Cascade Range, the Siskiyou Mountains in southwestern Oregon, and the smaller mountain ranges east of the Cascades. Except for the Siskiyou and the lower west slopes of the Cascades, this region is generally above 1000 m and is characterized

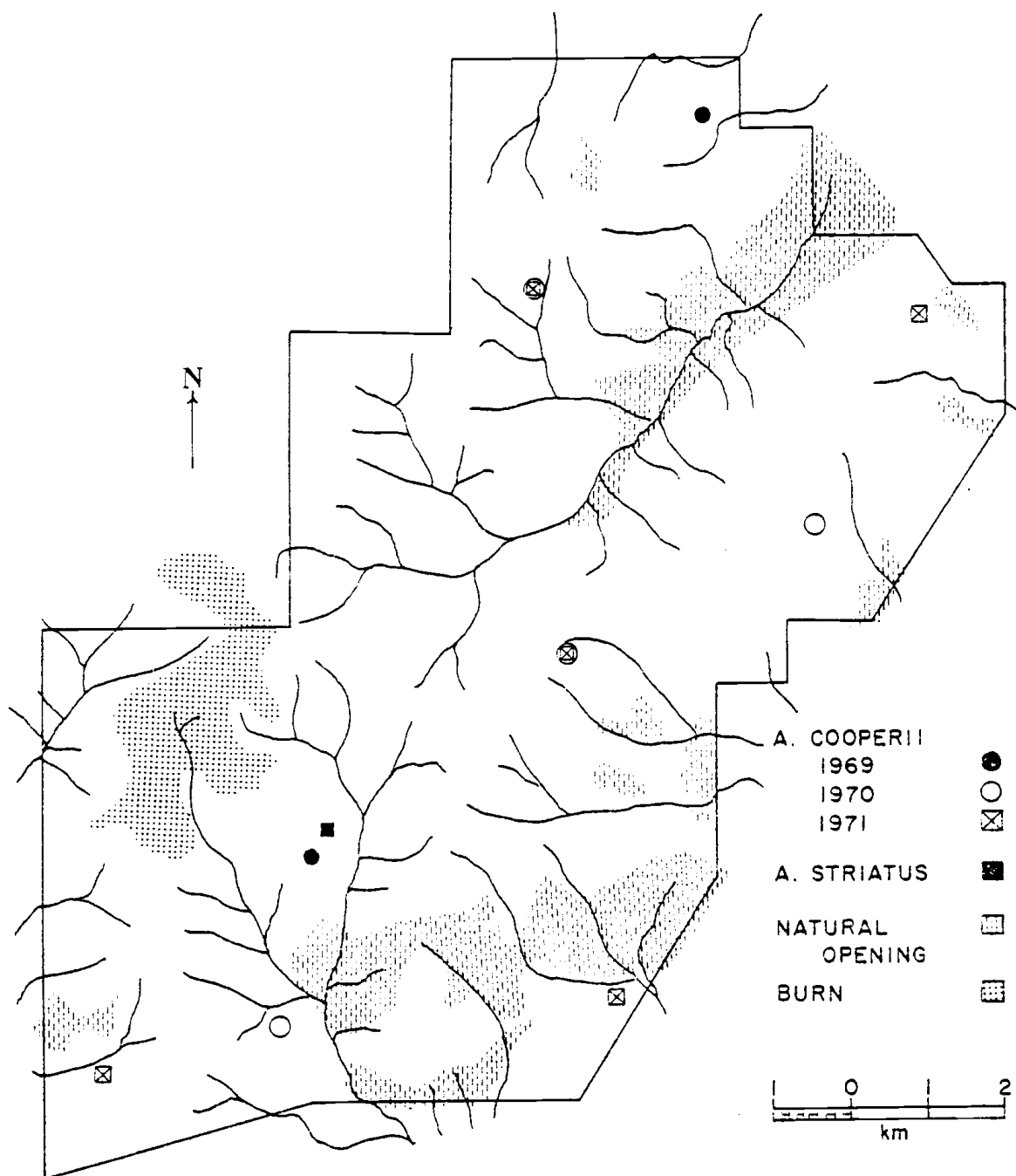
by cold winters and hot, dry summers. Forests in this subregion are dominated by mixed conifer stands, e.g., ponderosa pine (Pinus ponderosa), white fir (Abies concolor), Douglas-fir, and western larch (Larix occidentalis). The Siskiyou are characterized by warm, wet winters and hot, dry summers. Forests here are dominated by mixed conifer and sclerophyll types, e.g., ponderosa pine, incense-cedar (Libocedrus decurrens), Douglas-fir, tan oak (Lithocarpus densiflorus), and Pacific madrone (Arbutus menziesii) (Franklin and Dyrness 1973).

Throughout both subregions a mosaic of forest stands of various successional stages, species composition, slope, and aspect existed. Historically the mosaic was maintained by fire, wind, and/or disease. Currently these same phenomena are operating but their effect has been surpassed by extensive tree harvesting. Clear-cut logging, initiated in the Douglas-fir forests in western Oregon in the late 1800s and continued to the present produced a patchwork of blocks 16 to 80 ha in size and in ages ranging from 0 to 80 or 100 years old. However, stands in excess of 200 years old remain at higher elevations in the Cascades. In the more xeric forests east of the crest of the Cascades both selective and overstory removal logging produced a mosaic that is less well defined. Although stands here were cut in somewhat larger blocks, the principle effect of logging has been a reduction in the number of mature trees. Residual stands of mature forest were relatively scattered and usually small (less than 1 km<sup>2</sup>). Stands of young, regenerating conifers were numerous and in places extensive.

Distribution of Accipiter in both subregions was determined during nest searches in 1969 through 1974 (Reynolds and Wight 1978). Density of nests in both subregions was established by intensively searching two areas. The Corvallis area, 9284 ha, was 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). Elevation of this area ranged from 80 to 500 m and was of moderate topographical relief. Except for some narrow valley bottoms (fenced pastures) and one burned area in various stages of regeneration, the forests of this study area were continuous.



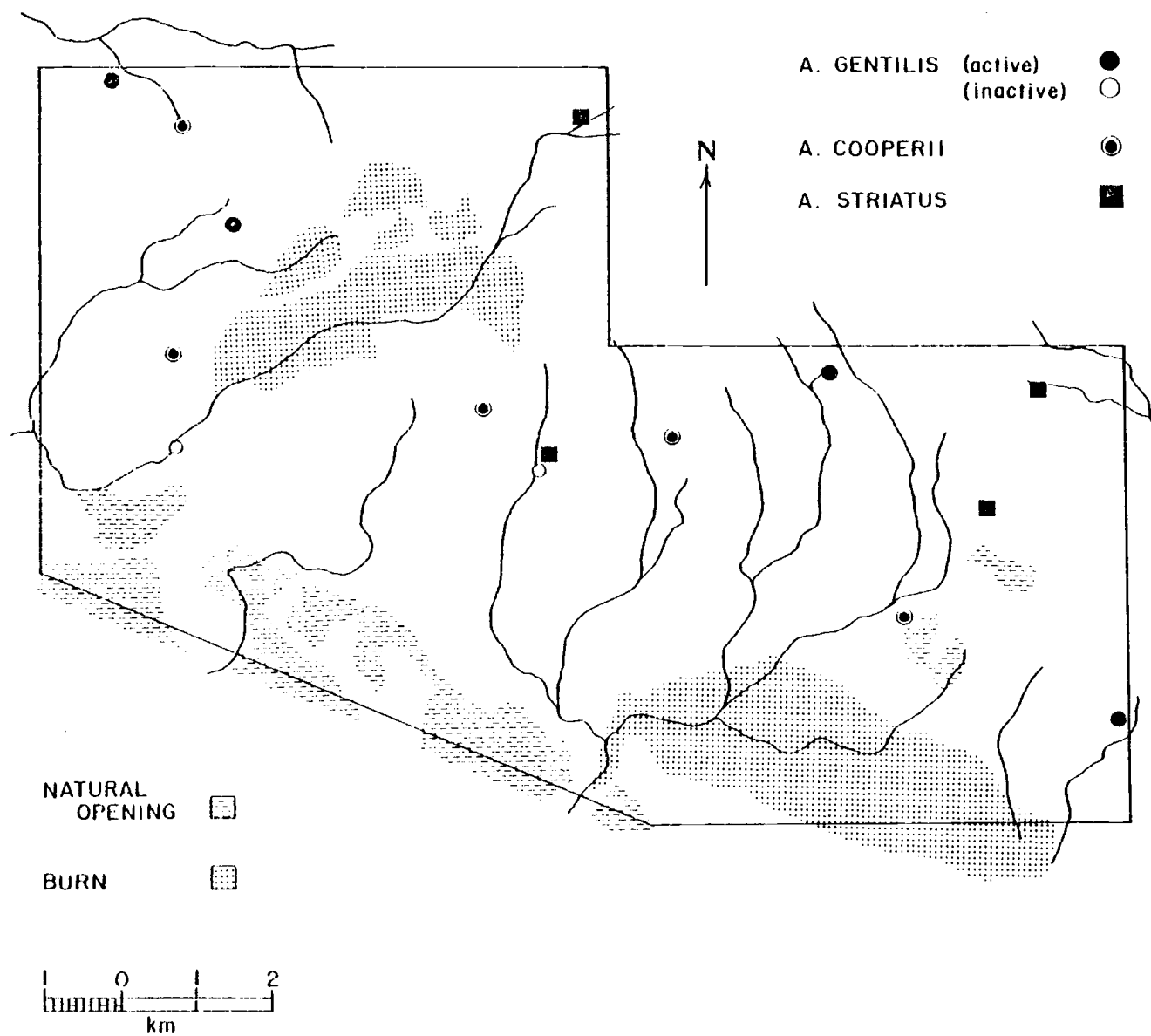
Figure 1. Corvallis study area. Indicating main drainages and Accipiter nest locations.



Douglas-fir, the dominant tree, existed in pure stands or in stands mixed with western hemlock, red alder (Alnus rubra), grand fir (Abies grandis), or bigleaf maple (Acer macrophyllum). On some dry, south-facing slopes small stands of Oregon white oak (Quercus garryana) persisted. A major portion of the Corvallis study area was composed of young (<100 years) stands of Douglas-fir, although stands of all age classes were represented. This area was searched during the nesting seasons of 1970 and 1971 (Reynolds and Wight 1978).

The Bly area, 11741 ha, was in the Gearhart Mountains of eastern Oregon approximately 24 km northeast of Bly, Lake County (T. 15E and 16E; R. 36S) (Fig. 2). Elevation ranged from 1430 to 2130 m and was of moderate relief. Except for 2 burned areas in early regeneration and small natural openings, forests of this study area were continuous. Tree species composition ranged from pure stands of ponderosa pine at lower elevations (southwest portion), through mixed stands of ponderosa pine and white fir at mid-elevations, to mixed and pure stands of white fir and lodgepole pine (Pinus contorta) at upper elevations (north and east portions). Although stands of all age classes in each timber type were represented the most common type was mature ponderosa pine overstory with mixed understory of ponderosa pine and white fir. The Bly area was searched during the nesting season of 1974 (Reynolds and Wight 1978).

Figure 2. Bly study area. Indicating main drainages and Accipiter nest locations.



## METHODS

### Nesting Habitat

Nest sites of Accipiter were defined as the portion of a forest stand containing the nest and the structural features of vegetation (tree density, height, canopy closure, etc.) and physiographic conditions (slope, aspect, surface water, etc.) used by a nesting pair during the breeding season (Reynolds and Meslow in prep.). Physiographic conditions (% slope, slope-aspect, presence or absence and distance to water and clearings) were noted for each active nest found, and 26 nest sites were chosen for quantification of their vegetative structure. The 26 sites were distributed as follows: eastern Oregon, 5 A. striatus sites, 5 A. cooperii sites, and 7 A. gentilis sites; northwestern Oregon, 5 A. striatus, and 4 A. cooperii sites. The point-centered quarter technique (Cottam et al. 1953) was used for sampling the vegetation. Six sampling points were established; 4 randomly and 2 non-randomly (1 at the nest tree, and 1 at the primary prey plucking area). Each point was divided into 4 quadrats and, for the nearest tree greater than 6 cm diameter breast high (dbh) in each, the species, distance from the point, dbh, crown depth, tree height, and percent of trunk with dead limbs were recorded. Canopy closure above each of the 6 points were determined by estimating the percent of sky obstructed by canopy vegetation. Percent cover by ground vegetation (grasses, forbs, shrub species) was also estimated.

Preliminary examination of a number of nest sites of Accipiter indicated a high degree of homogeneity of vegetative structure, both within individual sites and among sites of conspecifics. Due to the within-site homogeneity I felt 6 sampling points per site was sufficient for obtaining a quantitative description of the vegetation. Alternatively, the sites to be characterized were distributed between subregions according to my preliminary estimate of the structural variance among nest sites of conspecifics within each. Thus, because

A. cooperii sites in northwestern Oregon appeared to be the least variable and A. gentilis sites in eastern Oregon the most variable, 4 sites and 7 sites, respectively, were characterized. A complete description of the vegetation and physiography of forest stands selected for nesting by each Accipiter in both subregions is presented by Reynolds and Meslow (in prep.).

### Food

Remains of prey (features, fur, bones) were collected from prey handling or plucking areas in 5 A. striatus and 20 A. cooperii nest sites in northwestern Oregon from 1970 to 1973. Most of the 480 total prey remains from this subregion were from nest sites either within the Corvallis study area or within 45 km of it. Additionally, 463 prey were collected from 14 nest sites of A. striatus, 17 of A. cooperii, and 57 of A. gentilis in eastern Oregon. This collection included prey from the nests of all 3 species in the Bly area during 1974.

Prey items were identified with the aid of a reference collection. Remains of avian prey consisted of remiges and retrices with some body feathers and occasionally a foot or bill. Remains of mammalian prey consisted of fur, heads and occasional legs, hind quarters, or whole carcasses. On each visit to a nest all remains were collected and placed in marked envelopes. During identification, each item was reconstructed by matching remiges and retrices of birds and the fur, skull, and feet (if available) of mammals. This procedure provided a conservative estimate of the number of each prey consumed between collection visits. The age (young or adult) of prey items was determined by the presence or absence of epitrachium-enclosed feathers in birds and size, pelage, and the degree of bone calcification in mammals. However, since most birds progressed rapidly through the feather growth stage and whole carcasses or long bones of mammals were rarely found, the frequency of young prey reported here is a conservative estimate of their actual frequency in the diets. Body

weights of adult birds and mammals were obtained from the literature or from a series of museum specimens at Oregon State University (Appendix 1). For species in which males differed in size from females, mean weights were used. If prey were identified as young, body weights were assumed to be one-half adult weight. Weights of prey items that could be identified only to genus were estimated by averaging weights of all members of the genus occurring in the study area. Regurgitated pellets were collected from nest sites of each species. However, since most of the bone was digested, and feathers and fur were discolored and frequently reduced to a powder, most pellets served little purpose. However, all pellets were examined and some contained reptilian scales and bird bills.

This method for determining food habits of Accipiter has been used previously (Uttendorfer 1939), but is not without limitations. For example, Hoglund (1964) demonstrated differences in prey collected from nest sites and those obtained from stomach analysis. Some of these differences, however, can be attributed to geographical and temporal separation of collections (Hoglund 1964). Other problems included the degree of difficulty of finding plucked pelage versus plucked feathers; remains of birds were rendered more obvious by white down, whereas pelage frequently blended with the forest floor. Further, there were differences in the extent of prey handling within nest sites among Accipiter; A. striatus delivered nearly all items to the nest area prior to plucking, whereas A. cooperii and A. gentilis usually delivered partially plucked prey. The differences resulted in smaller, more easily overlooked prey remains of the 2 larger Accipiter. Thus, my lists of prey of A. cooperii and A. gentilis have a greater probability of being incomplete.

Within Accipiter, males are considerably smaller than females and may capture smaller prey (Storer 1966). In addition, males do much of the foraging from prior to egg laying to about mid-way through the nestling period. Thereafter both sexes forage. Since I collected prey remains from the beginning of pair formation (April) to the age of independence of the young (August) and did not attempt to



distinguish between prey of males and females, our data represent a combination of prey captured by both sexes.

To determine the abundance of the prey resources in both subregions I followed two procedures: in eastern Oregon I censused birds and diurnally active, small mammals in five principal forest types in the Bly study area during late June and early July of 1974 with a variable circular plot technique (Reynolds et al. in prep.). Censuses were conducted over a period of several days (minimum = 2 days) in each of the five types between 0600 and 1130 hours (Pacific Daylight Time). In addition to each individual's occurrence, its foraging behavior and vertical position in the forest was noted. I did not census birds or mammals in northwestern Oregon. However, Anderson (1970) censused the avifauna in five forest types within or adjacent to my Corvallis study area in 1968-69, and Mannan (1977) censused birds in the breeding season of 1976 in Douglas-fir stands 24-55 km southwest of my Corvallis study area. To describe the size-frequency distribution and total abundance of birds in the various forest types in northwestern Oregon, I combined Anderson's and Mannan's census data by calculating a mean density per species in 4 stands (from 70-200-years-old) censused by Mannan (1977) and averaged these means to means derived in the same manner from Anderson's (1970) "late spring" and "early summer" censuses in 9 stands dominated by conifers (stands 2-10) (Appendix 1). For species not common to both studies, I used densities reported in either one or the other.

A possible source of error associated with combining densities derived in the above manner was the probable expansion of the cumulative species total above the number of birds breeding in any given year due to the year-to-year changes in avifaunal composition. However, since it is easier to demonstrate a species' presence than absence, estimates of occurrences are conservative depending upon the adequacy of sampling. A combination of the densities of the above studies may, therefore, approximate actual abundances. It remains to be pointed out, however, that my estimate of the avifaunal composition in eastern Oregon (1 breeding season) was conservative relative to the

combined estimate for northwestern Oregon. Finally, since populations of small, diurnal mammals in northwestern Oregon had not been censused, I subjectively determined their relative densities by noting their abundances during nest searches and revisits to Accipiter nest sites.

To determine if species of Accipiter partitioned the food resource by foraging in different vertical layers of the forest, all birds and mammals were assigned to 1 of 5 height zones on the basis of where each was most likely to be encountered by a foraging Accipiter (i.e., the zone within which each was most commonly observed). Zone boundaries were chosen so that they occurred at interfaces of two structurally different layers on the forest. To determine if accipiters specialized on members of different foraging guilds (Root 1967, Willson 1974) within these zones and thereby employed different foraging tactics, I assigned all species in each zone to foraging guilds based on major food source (Fig. 3).

I did not determine body weights of Accipiter nesting in Oregon. However, I collected 13 specimens during the non-breeding season, and, since their weights (with the possible exception of A. gentilis) (Table 1) approximated weights of Accipiter previously reported (Storer 1955, Craighead and Craighead 1956, McGowan 1975, and Henny pers. com.), I chose to use those in Storer (1955). Weights of A. gentilis collected in Oregon (this study; Henny pers. com.) indicated this species may be 50 to 100 g smaller in Oregon than on the remainder of the North American continent. This trend has not previously been documented.

To estimate the number of prey required for an Accipiter family from 1 May to 20 August, I adapted an energetics model from Wiens and Innis (1974). The energy required for maintenance of metabolic functions is closely related to body weight and ambient temperature (Brody 1945, Kendeigh 1969). I used Kendeigh's (1969) formulation to approximate the existence energy requirements for an adult Accipiter at ambient temperature of 30°C,

$$M_{30} = 0.5404 W^{0.7545}$$

where M = existence energy, and W = body weight of the hawk (Table 2).

Figure 3. Schematic showing physiognomic layers, vertical foraging zones, and prey foraging guilds within each zone in Oregon conifer forests.

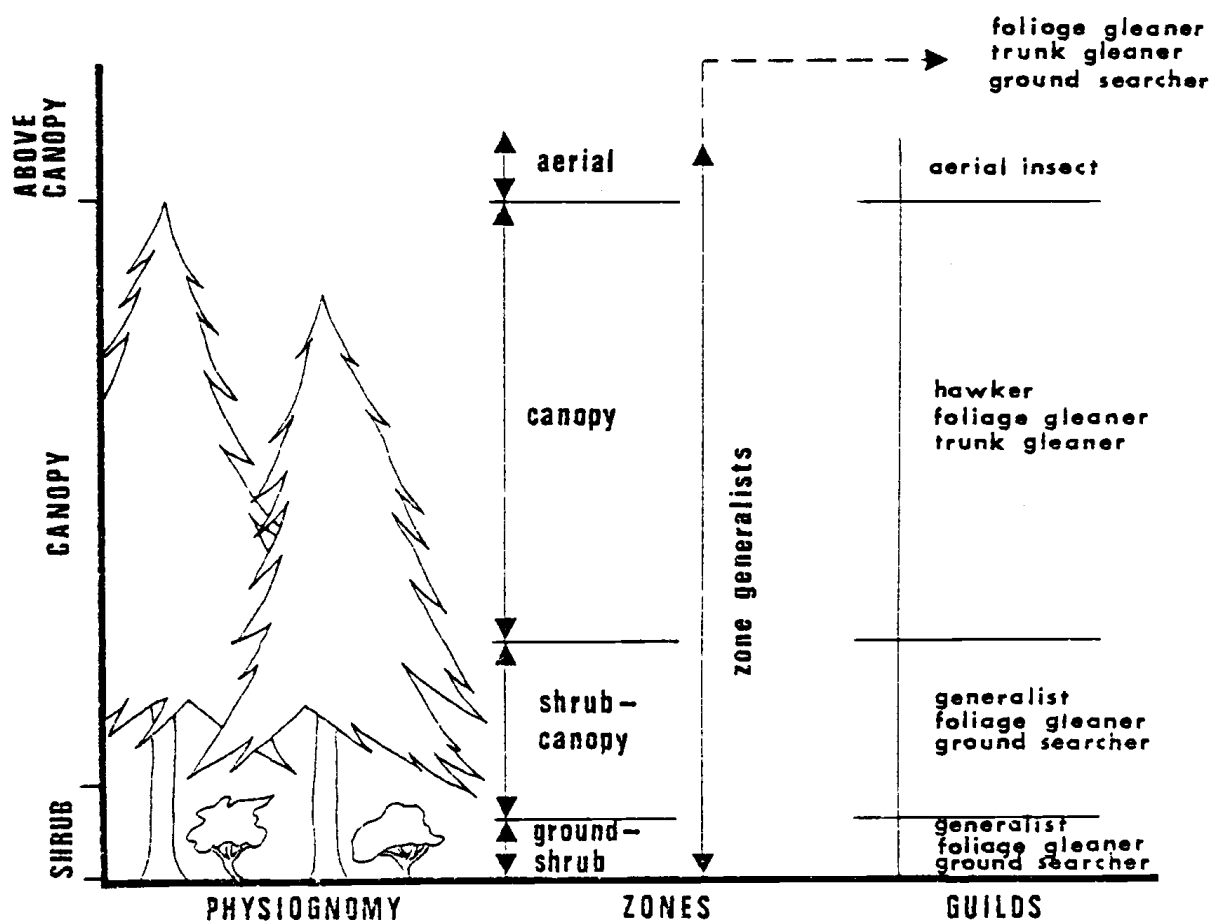


Table 1. Body weights of Accipiter from various regions in North America.

Species	Location	Sex	Weight (g)	Source
<u>A. striatus</u>	Oregon	male	86(1) <sup>1</sup>	This study
	Oregon	female	162(4)	This study
	Oregon	male	96(4)	Henny (pers. com.)
	Oregon	female	177(5)	Henny (pers. com.)
	Northeastern U.S.	male	99	Storer (1955)
	Northeastern U.S.	female	171	Storer (1955)
	Northcentral U.S.	male	102(98)	Craighead and
	Northcentral U.S.	female	179(92)	Craighead (1956)
<u>A. cooperii</u>	Oregon	male	302(2)	This study
	Oregon	female	444(4)	This study
	Oregon	male	284(24)	Henny (pers. com.)
	Oregon	female	493(8)	Henny (pers. com.)
	Northeastern U.S.	male	295	Storer (1955)
	Northeastern U.S.	female	441	Storer (1955)
	Northcentral U.S.	male	380(34)	Craighead and
	Northcentral U.S.	female	561(143)	Craighead (1956)
<u>A. gentilis</u>	Oregon	male	737(2)	This study
	Oregon	male	740(7)	Henny (pers. com.)
	Oregon	female	970(13)	Henny (pers. com.)
	Northeastern U.S.	male	818	Storer (1955)
	Northeastern U.S.	female	1137	Storer (1955)
	Northcentral U.S.	male	860(62)	Craighead and
	Northcentral U.S.	female	1095(114)	Craighead (1956)
	Alaska	male	858(15)	McGowan (1975)
	Alaska	female	1015(16)	McGowan (1975)

<sup>1</sup> Number of specimens.

Table 2. Adult weight, clutch size, number of young, and the length of the nestling and fledgling periods for Accipiter in Oregon.

Species	Mean <sup>1</sup> Weight (g) Adult		Mean <sup>2</sup> Clutch Size	Egg <sup>3</sup> Weight (g)	Mean <sup>2</sup> Nestling Number	Nestling Period (days)	Mean <sup>2</sup> Fledgling Number	Fledgling Period (days)
	♂	♀						
<u>A. striatus</u>	99.0	171.0	4.6	19.2	2.7	23	2.7	30
<u>A. cooperii</u>	295.0	441.0	3.8	35.0	2.1	29	2.1	35
<u>A. gentilis</u>	818.0	1137.0	3.2	63.7	1.7	36	1.7	37

<sup>1</sup> From MacArthur (1972).

<sup>2</sup> Mean clutch size and number of young from combined western and eastern Oregon data.

<sup>3</sup> Egg weight = EW = .741 (female weight)<sup>0.633</sup> (see Rahn, et al. 1975).

To include the energetic cost of activity of adult birds I increased their metabolic demands 40 percent over the existence level. In addition, because the ability of birds to extract energy from food is limited, the energetic demand was increased to account for digestive efficiency. I assumed (Kale 1965, Wiens and Innis 1974) that 70 percent of the energy intake was metabolically available, and the calculated metabolic demands were multiplied by 1.43. Thus, the total energy demand for adults was

$$M_{\text{adult}} = M_{30}(1.43)(1.4) \text{ kcal.}$$

To determine the energetic cost of egg production (EC), I calculated egg weight (EW) of Accipiter from regression equations relating avian body weight to egg weight (Rahn et al. 1975) (Table 2). Multiplying egg weight times the estimated caloric value per gram (1.05 kcal/g wet weight) (King 1973), and assuming egg production efficiency of 73 percent (King 1973, Wiens and Innis 1974), the total energetic demand for producing an average-sized clutch (CS) was

$$EC = EW (CS)(1.05)(1.37) \text{ kcal.}$$

Although nestlings have negligible energy demands due to activity, their demands due to growth (MN) may be considerable. My estimate of the cost of 20 percent of the daily existence energy for growth was taken from nestling Redback Shrikes (Lanius collurio) (Diehl 1971 [in Wiens and Innis 1974]). Thus, for an average number of young per nest (NS) (Table 2) over the entire nestling period (NP) (Table 2) the energy demand was

$$MN = (M_{30} + .20 M_{A_{30}}) 1.43 (NS)(NP) = M_{A_{30}}(1.20)(1.43)(NS)(NP).$$

Finally, for fledglings we assumed, as did Wiens and Innis (1974), that existence metabolism was increased 10 percent by activity.

During the fledgling period growth is less rapid than during the nestling period, and I assumed that daily existence energy demands during this period (MF) were elevated 5 percent due to growth.

Therefore energy demands for an average number of fledglings per nest (FS) (Table 2) for the 112 days (FP) was

$$MF = (M_{30} + 0.10 M_{30} + 0.05 M_{30}) 1.43 (FS)(FP) = M_{30}(1.15)(1.43)(FS)(FP).$$

### Statistical Procedures

The student's t-test (one-tailed) was used to determine if differences between mean sizes of prey of Accipiter were significant at the 0.05 level. In the analytic treatment of nesting habitat I employed a step-wise discriminant analysis (BMD 07M, Health Sciences Computing Facility, UCLA) to find the best reduced-rank model for effectively describing the measured differences in nest sites selected by coexisting Accipiter. The resulting discriminant function was the linear combination of habitat variables that maximizes the ratio (F) of the between-group mean squares to the within-group mean squares in a single classification of analysis of variance (Morrison 1967; Cooley and Lohnes 1971). Since the step-wise procedure adds the "next best" variable to the model and tests for differences among group means one can, by choosing an appropriate level of probability, determine the best combination of variables (non-significant variables deleted) that describes differences among groups.

Although the discriminant functions gave some indication of the nature of group differences, they did not demonstrate the accuracy with which cases (sampling points) were classified into their correct groups. To examine the accuracy of the discriminant functions a classification procedure, based on posterior probabilities, was used. The procedure was not used for predicting group membership but simply to display the classification validity of the habitat variables.

In the statistical treatment an average for each of the 7 habitat variables from the 4 trees sampled around each point was determined. Canopy closure estimates, however, was represented by a single observation at each point. Prior to discriminant analysis, tests for skewness and kurtosis revealed that the distributions of the habitat variables were approximately normal.

To calculate indices of niche breadth I used Levins' (1968) formula

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

where  $p_i$  is the proportion of prey among the categories in each



dimension. The value of  $B$  varies from 1 to  $\underline{n}$ , where  $\underline{n}$  is the number of categories. If prey are equally common in each category, then  $B = \underline{n}$ ; if all prey belong to only one category, then  $B \approx 1$ . Since the number of categories of prey were not equal in each dimension, niche width values were standardized for comparison to fractions (0-1) of maximum possible niche width by the formula

$$B_{\text{standard}} = (B-1)/\underline{n}-1.$$

Niche overlap indices were measured by the MacArthur and Levins (1967) formula

$$\alpha_{uji} = \Sigma U_i U_j / \Sigma U_i^2 \text{ and } \alpha_{uij} = \Sigma U_i U_j / \Sigma U_j^2$$

where  $U_i$  is the frequency of utilization of a resource category by species  $i$ , and  $U_j$  is the utilization by species  $j$ . With this formulation,  $\alpha$  is an asymmetrical measure of dietary overlap; that is, species  $i$  may have greater overlap on  $j$  than species  $j$  on  $i$ . The value of  $\alpha$  ranges from 0 with no overlapping use of resources to 1 for complete overlap and may exceed 1 if niche widths are unequal. The usual procedure in calculating  $\alpha$  is to determine the use of a particular resource category by each species relative to its use of other categories (i.e.,  $\Sigma U_i = \Sigma U_j = 1$ ) (MacArthur and Levins 1967; Colwell and Futuyma 1971). However, I found it necessary to calculate a measure of niche overlap from the actual numbers of prey captured from each category. Thus, I adapted the MacArthur-Levins formula (after Ricklefs 1973, p. 518) by substituting  $N_i$ , the number of prey in each category, for  $U_i$ :

$$\alpha_{nji} = \Sigma N_i N_j / \Sigma N_i^2 \text{ and } \alpha_{nij} = \Sigma N_i N_j / \Sigma N_j^2.$$

## RESULTS AND DISCUSSION

### Distribution and Density

The distribution of nesting pairs of Accipiter in Oregon was described by Reynolds and Wight (1978). They reported that each of the 3 species nested in all forested areas in the state except in northwestern Oregon where A. gentilis was absent. In addition, there were no elevational limits to nesting in any species; A. striatus nested from 120 to 2010 m, A. cooperii from 15 to 1760 m, and A. gentilis from 580 to 1860 m.

Nest searches were begun in the Corvallis area in 1969; 2 A. cooperii and 1 A. striatus nests were located. Intensive searching began in 1970 and was continued through 1971. During 1970 and 1971, 4 and 5 A. cooperii nests were found, giving densities of 1 nest per 2321 ha in 1970, and 1 nest per 1857 ha in 1971 (Fig. 1). Mean distance between nests of A. cooperii in the Corvallis area for both years combined was 5.3 km (range 3.7-6.9 km, S.D. = 1.05). Although nests of A. striatus were found in adjacent areas, none was found within the Corvallis study area during 1970 or 1971.

In 1974, 4 A. striatus nests, 5 A. cooperii nests and 4 A. gentilis nests were found in the Bly area giving an overall density of 1 nest/903 ha (1 A. striatus nest/2750 ha, 1 A. cooperii nest/2200 ha, and 1 A. gentilis nest/2750 ha) (Fig. 2). Mean distance between nests of conspecifics in the Bly area were: A. striatus, 4.1 km (range 1.8-6.0 km, S.D. = 2.12); A. cooperii, 3.5 km (range 2.6-4.4 km, S.D. = 0.79); A. gentilis, 5.6 km (range 2.4-8.4 km, S.D. = 3.00). Distances between nests of conspecifics outside the areas approximated mean distances found within them.

### Occurrence of Nesting and Productivity

A. gentilis in Oregon 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). Most A. cooperii occupied their nest sites

by mid-April and had completed clutches by mid-May ( $\bar{x}$  for northwestern Oregon = 11 May, for eastern Oregon = 19 May). A. striatus occupied their nest sites by the first of May and had completed clutches by the end of May ( $\bar{x}$  = 25-26 May) (Reynolds and Wight 1978). Elevation of a nest site had little relation to date of clutch completion for any species. Incubation required approximately 32 days for each species, whereas nestling periods lasted 34-37 days for A. gentilis, 28-30 days for A. cooperii, and 21-24 days for A. striatus. Due to faster growth of the smaller hawks, fledging in each species differed by no more than 10-12 days despite the fact that A. striatus began nesting later than A. cooperii, which, in turn, began later than A. gentilis (Fig. 4). After fledging the young of each species depended upon the adults for food for 30 to 40 days before becoming self-dependent and leaving the nest areas.

Productivity, estimated from clutch size and fledging success, of A. striatus showed no clear trends from northwestern to eastern Oregon; number of eggs per clutch was slightly larger but number of young fledged per nest was less in northwestern Oregon (Table 3). The lower fledgling rate in northwestern Oregon reflected a mortality of nestlings probably associated with pesticides (Snyder et al. 1973). A. cooperii in northwestern Oregon had slightly larger clutches and a higher fledging success than their A. cooperii in eastern Oregon. Mean clutch size and fledging success of A. gentilis in Oregon were similar to productivity estimates from other populations in North America and Europe (Reynolds and Wight 1978).

To determine the year-to-year constancy of Accipiter populations we investigated the number of years nest sites were occupied and the relative constancy of number of pairs of Accipiter in an area. Within Oregon A. gentilis had the highest fidelity towards a specific nest site; of 63 nest sites of A. gentilis, 15, 7, 2, 1 were reoccupied during the 2nd, 3rd, 4th and 5th year, respectively. Site tenacity of A. cooperii was somewhat less; none of 34 nest sites being occupied for more than 3 years. Six of the 34 were reoccupied during the second year and 1 during the third year. A. striatus had the lowest

Figure 4. Duration and temporal overlap of nesting in A. striatus, A. cooperii, and A. gentilis in northwestern and eastern Oregon.

	Pairing	□	incubation
■	nestling		fledgling

||||| □ ■ ||||| A. GENTILIS

||||| □ ■ ||||| A. COOPERII

||||| □ ■ ||||| A. STRIATUS

1 APRIL                      1 JUNE                      1 AUGUST

Table 3. Clutch size and fledging success of Accipiter in northwestern and eastern Oregon.<sup>1</sup>

Species	Eastern Oregon		Northwestern Oregon	
	No. eggs	No. fledged	No. eggs	No. fledged
<u>A. striatus</u>	4.0(4) <sup>2</sup> (0.82) <sup>3</sup>	2.67(9) <sup>2</sup> (1.22) <sup>3</sup>	4.7(6) <sup>2</sup> (.82) <sup>3</sup>	2.50(6) <sup>2</sup> (2.07) <sup>3</sup>
<u>A. cooperii</u>	3.8(6)(.82)	2.21(14)(1.42)	3.9(11)(1.22)	2.50(20)(1.67)
<u>A. gentilis</u>	3.2(5)(0.45)	1.7(48)(0.89)	-	-

<sup>1</sup> Some totals differ from Reynolds and Wight (1978) as estimates of minimum clutch size and fledging success for additional nests are included here.

<sup>2</sup> Number of nests.

<sup>3</sup> Standard deviation(s).

reoccupancy rate as only 2 of 11 sites revisited were reoccupied during the second year (Reynolds and Wight 1978). The number of pairs of A. cooperii in the Corvallis area during 1970 (4) and 1971 (5) gave some indication of the annual constancy of the number of pairs. The low density of A. striatus in the Corvallis area may have been related to local pesticide contamination (Snyder et al. 1973) or to overlooking nests during searches. Further data are required to better establish the annual stability of Accipiter populations in Oregon.

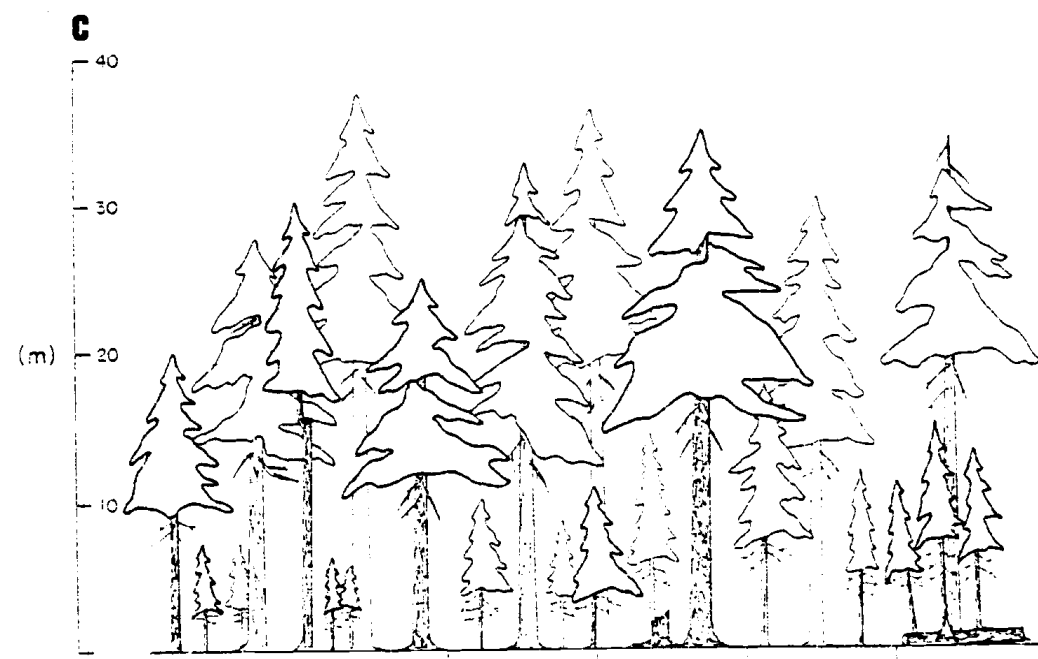
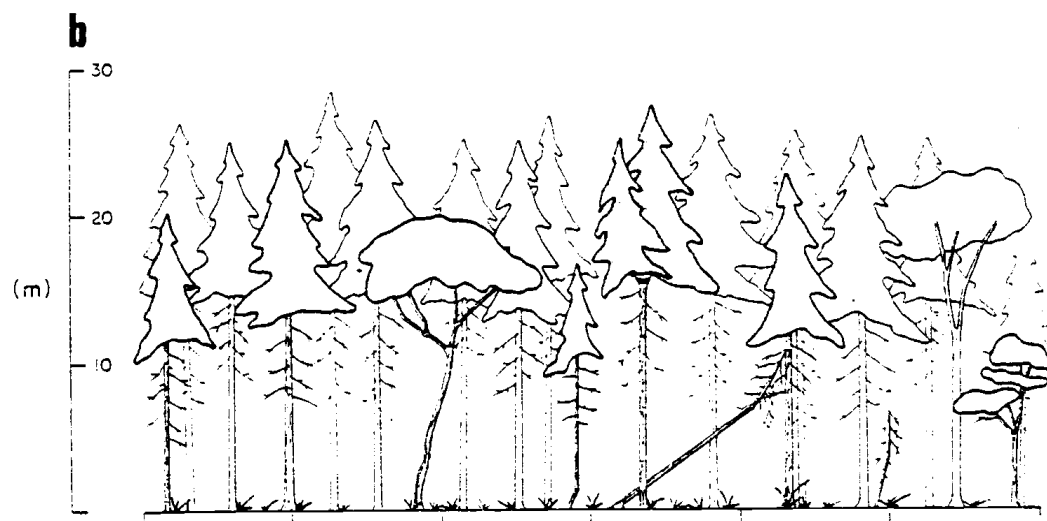
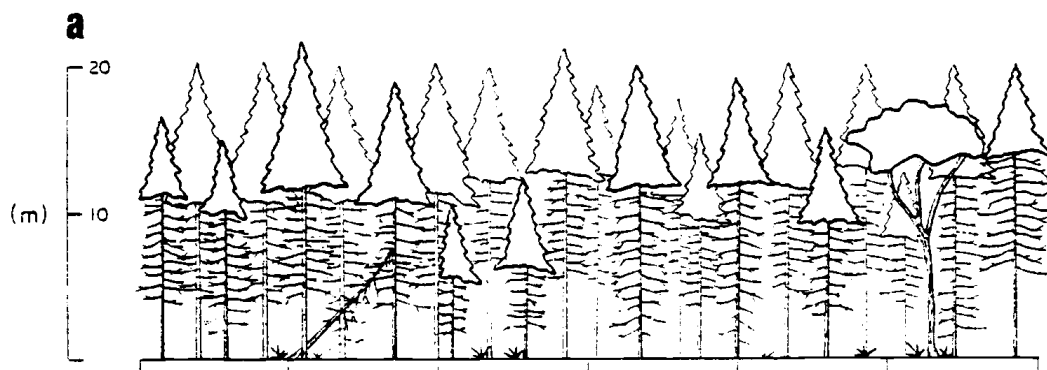
### Nesting Habitat

In general, nesting habitat of Accipiter in both subregions differed in structure that was associated with successional stage; A. striatus nested in young (40-60 year-old), even-aged, dense stands of conifers, A. cooperii in 50-80 year-old, dense, even-aged conifer stands with slightly larger, more widely spaced trees, whereas A. gentilis nested in dense, 100-500 year-old conifer stands with mature overstory trees and numerous, shade-tolerant, understory trees of varying heights and ages (Fig. 5). However, several physiographic features were common to all nest sites in Oregon. Most notable was a tendency for sites to be on moderate slopes (0-30%) with north-to-east aspects. In addition, nest sites of each species frequently contained either springs or small streams passing either through them or immediately adjacent to them. Associated with the north-to-east slope aspects in Oregon are reduced amounts of solar radiation, reduced evaporation, greater soil moisture, cooler temperature and higher humidity beneath the canopy (Sukachev and Dylis 1964). The more mesic conditions on these slopes usually allow greater tree density and increased canopy closure and shading, a critical habitat requirement of Accipiter in Oregon (Reynolds and Meslow in prep.).

In eastern Oregon the discriminant function discriminated among sites of each species after the entry of the first variable (tree height) but could not discriminate ( $P < 0.05$ ) between sites of

Figure 5. Schematic of the vegetative structure showing typical nest sites of Accipiter in conifer forests in Oregon. a) A. striatus, b) A. cooperii, c) A. gentilis.





A. striatus and A. cooperii with additional variables (Table 4). Although F-ratios between the A. cooperii-A. gentilis and A. striatus-A. gentilis comparisons decreased with the addition of each variable, the function continued to discriminate between them after the addition of all variables. Thus, although A. gentilis sites differed in all variables from those of A. striatus and A. cooperii, habitat variables in nest sites of A. striatus and A. cooperii, with the exception of tree height, were similar.

Discriminant analysis indicated that nest sites of A. cooperii and A. striatus were also similar in northwestern Oregon. F-ratios decreased with the addition of each variable, but became non-significant ( $P < 0.05$ ) after inclusion of percent canopy closure and tree density.

The coefficients of the 1st canonical variable (Table 5), which accounted for 92.65 percent of the total cumulative dispersion of the among group variance, indicated that nest sites in eastern Oregon differed primarily in tree size (dbh), crown depth, and to a lesser degree, tree density: A. striatus nested in dense stands of small diameter trees with little crown depth and A. gentilis nested in stands of large, more widely spaced trees with deep crowns. A. cooperii selected stands intermediate in these characteristics. In northwestern Oregon the coefficients of the 1st canonical variable, which accounted for all the among variance, indicated that A. striatus and A. cooperii nested in forest stands that differed by a ratio of tree diameter to tree density; A. striatus in dense stands of small diameter trees and A. cooperii in stands of larger more widely spaced trees.

In northwestern Oregon 15 of 54 (27.8%) sampling points were misclassified by the discriminant function, while 36 of 102 (35.3%) sampling points from nest sites in eastern Oregon were misclassified (Table 6).

Table 4. Results of discriminant analysis of the vegetation of nest sites of Accipiter.

Location	Variable	df	Groups		
			<u>striatus-cooperii</u>	<u>cooperii-gentilis</u>	<u>striatus-gentilis</u>
Eastern	Tree height	99	4.62*	13.19*	35.45*
( <u>A. striatus</u> vs.	Tree density	98	2.45	11.77*	24.97*
<u>A. cooperii</u> vs.	d.b.h.	97	1.78	10.74*	21.16*
<u>A. gentilis</u> )	Crown depth	96	2.22	8.22*	15.98*
	Bole height	95	2.18	6.62*	13.70*
	% bole with limbs	94	1.98	5.50*	11.36*
	% canopy closure	93	1.68	4.77*	9.72*
Northwestern	% canopy closure	52	6.67*	-	-
( <u>A. striatus</u> vs.	Tree density	51	4.29*	-	-
<u>A. cooperii</u> )	d.b.h.	50	3.09	-	-
	Bole height	49	2.30	-	-
	% bole with limbs	48	1.84	-	-
	Tree height	47	1.51	-	-
	Crown depth	46	-	-	-

\*F-ratio,  $p < 0.05$

Table 5. Coefficients of 1st canonical variable in comparisons of vegetation among nest sites of Accipiter.<sup>1</sup>

Variable	Comparison	
	Eastern Oregon	Northwestern Oregon
d.b.h.	-3.25	1.09
Tree density	0.15	-0.14
Bole height	0.11	0.02
Tree height	0.06	-0.01
% bole with limbs	-0.01	-0.01
% canopy closure	0.01	0.04
Crown depth	4.09	-

<sup>1</sup> Values are coefficients of a linear combination of the 7 habitat variables and, therefore, provide a relative measure of the importance of each variable in distinguishing nest sites of each Accipiter.

Table 6. Classification of sampling points in nest sites of Accipiter.

Northwestern Oregon				Eastern Oregon				
	<u>striatus</u>	<u>cooperii</u>	Total		<u>gentilis</u>	<u>cooperii</u>	<u>striatus</u>	Total
<u>cooperii</u>	15	9	24	<u>gentilis</u>	28	10	4	42
<u>striatus</u>	6	24	30	<u>cooperii</u>	6	15	9	30
				<u>striatus</u>	0	7	23	30
Misclassified 15 (27.8%)				Misclassified 36 (35.3%)				

### Food Resources

The combined census results of Anderson (1970) and Mannan (1977) gave a total of 656 birds per 40 ha (58 species) in the forests of northwestern Oregon; nearly twice the species (30) and density (275/40 ha) of birds I found in the Bly area (Appendix 1). Since my density figure seemed low I compared it to a mean density of birds determined with the spot-mapping technique in five stands dominated by conifers in the Blue and Wallowa mountains in northeastern Oregon (Richmond pers. com.). Although density in these stands averaged 81 birds per ha greater than the Bly area, this comparison substantiated the fact that bird numbers in eastern Oregon forests were about one-half those in northwestern Oregon.

In the Bly area, golden-mantled ground squirrels (Spermophilis lateralis), yellow-pine chipmunks (Eutamias amoenus), and chickarees (Tamiasciurus douglasii) were recorded during the censuses (Appendix 1). These species totaled to 26 mammals per 40 ha. In addition, mountain cottontails (Sylvilagus nuttalli), snowshoe hares (Lepus americanus), least chipmunks (E. minimus), northern flying squirrels (Glaucomys sabrinus), gray squirrels (Sciurus griseus), and Townsend's (S. townsendii) and Belding's ground squirrels (S. beldingi), and bushy-tailed woodrats (Neotoma cinerea) occurred locally or were uncommon throughout eastern Oregon forests. In addition to the species recorded during the census, only snowshoe hares and northern flying squirrels were ubiquitous and consistently common in the forests of this subregion. In northwestern Oregon the number of species of small, diurnal and crepuscular mammals was less than in eastern Oregon. Brush rabbits (S. backmani), snowshoe hares, Townsend's chipmunks, northern flying squirrels, chickarees, gray squirrels, and bushy-tailed and dusky-footed woodrats (Neotoma fuscipes) occurred in northwestern Oregon. However, only snowshoe hares, Townsend's chipmunks, flying squirrels, and chickarees were ubiquitous and consistently common.

A plot of the percent of birds per 40 ha in 50 g classes in both subregions shows that numbers of birds declined as body size increased (75-80% of the total weighed less than 50 g) (Fig. 6). Plots of the number of birds and bird biomass in log weight categories normalized these distributions and indicated a separation of the number and biomass curves (Fig. 7a and 7b); indicating that although the majority of coniferous forest birds were about the size of Parus, biomass in each size class increased to about the size class that includes robins then gradually declined or was highly variable over the uncommon larger birds. Inclusion of the full compliment of diurnal mammals in these plots would, since mammals were from intermediate to large relative to birds, raise the middle and right portions of these curves.

Prey Zone and Foraging Guild. Forests in northwestern Oregon supported nearly twice the density of birds than did eastern Oregon. These differences probably stemmed from the more mesic conditions and the subsequent greater development of vegetation in all layers of the forests in northwestern Oregon. The most obvious density difference occurred in the shrub layer; 15 percent of the birds in northwestern Oregon occurred in this layer while less than 3 percent occurred here in eastern Oregon (Fig. 8a). Additionally, nearly 60 percent of the birds in northwestern Oregon occurred in upper canopy zone while only 40 percent occurred here in eastern Oregon. The ratio of biomass to numbers in the upper canopy layer was greater in eastern Oregon than in northwestern Oregon. This difference was likely related to the high productivity of the mesic northwestern forests and their greater tree density, and foliage volume (Franklin and Dyrness 1973) which, although little is known of standing stocks of invertebrates or seeds in these forests, probably supported larger stocks of these foods and ultimately larger populations of small insectivorous and granivorous birds. Finally, when compared to northwestern Oregon, eastern Oregon had a greater percent of birds classified as zone generalists. This difference stemmed from a direct increase in the number of zone generalists (e.g., 29 robins/40 ha in eastern vs. 4/40 ha in

Figure 6. Size-frequency distribution of birds/40 ha in northwestern Oregon, and birds and small mammals/40 ha in eastern Oregon conifer forests. Fifty gram weight categories.



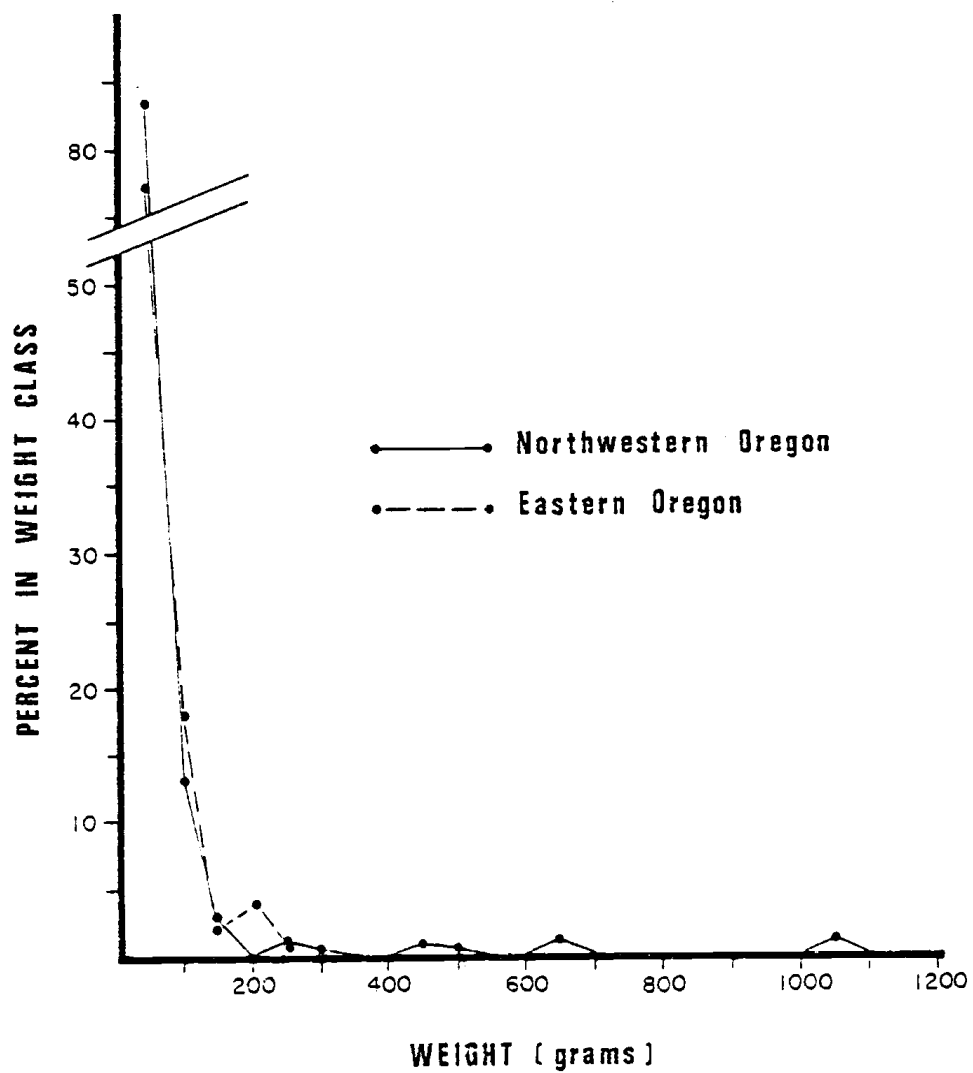


Figure 7. Percent number and biomass of birds/40 ha in  
a) northwestern Oregon and birds and mammals/40 ha in  
b) eastern Oregon conifer forests.  $\text{Log}_{10}$  weight  
categories.

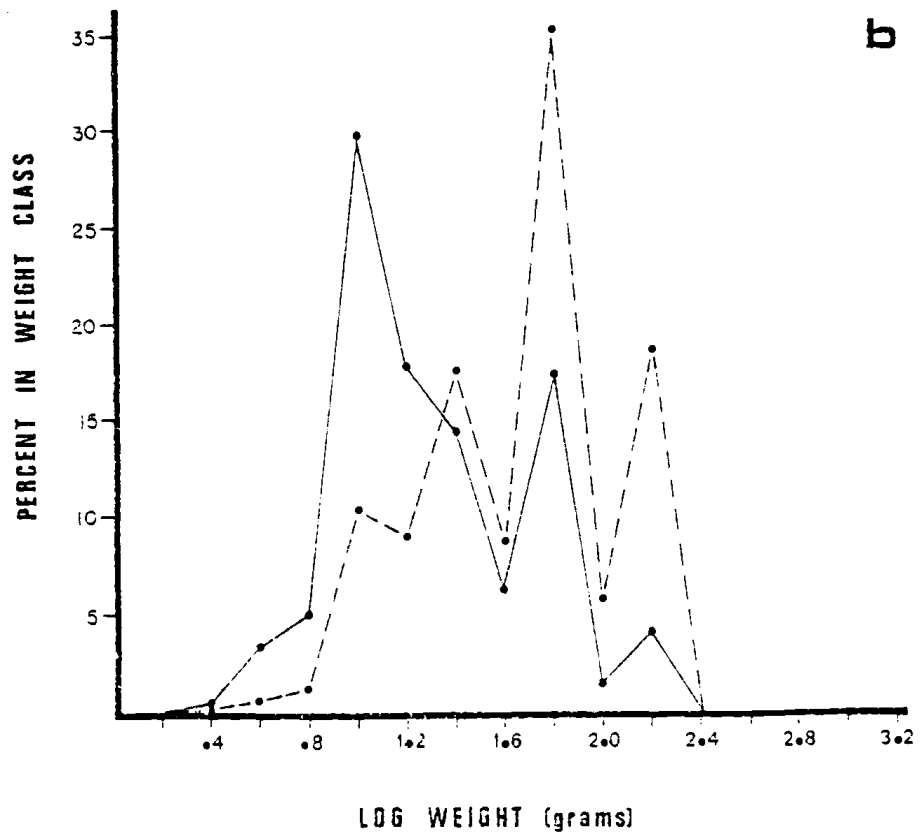
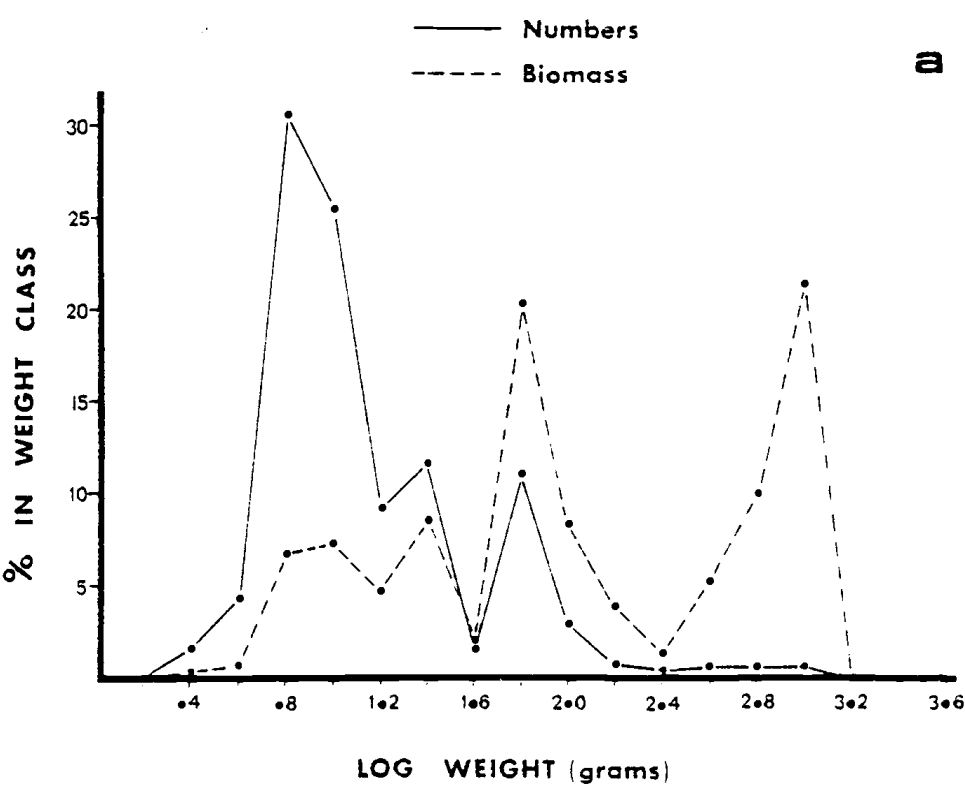
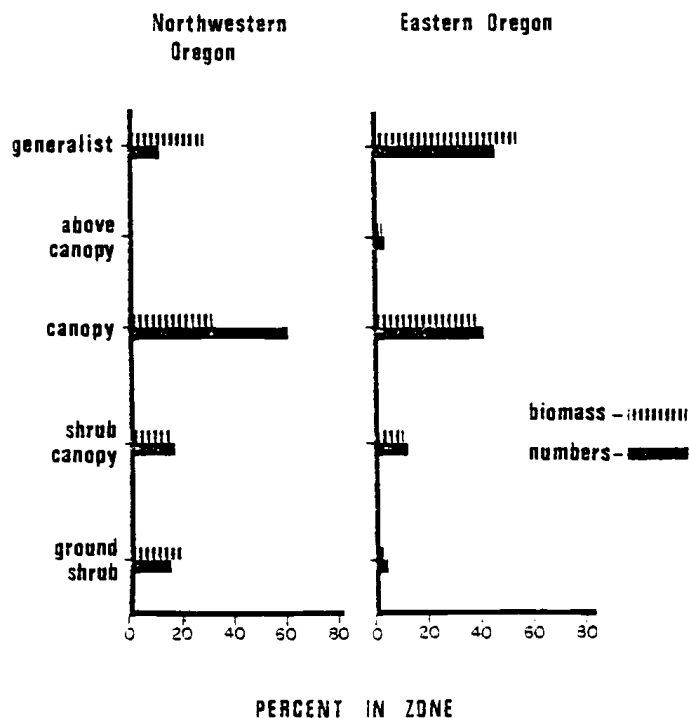
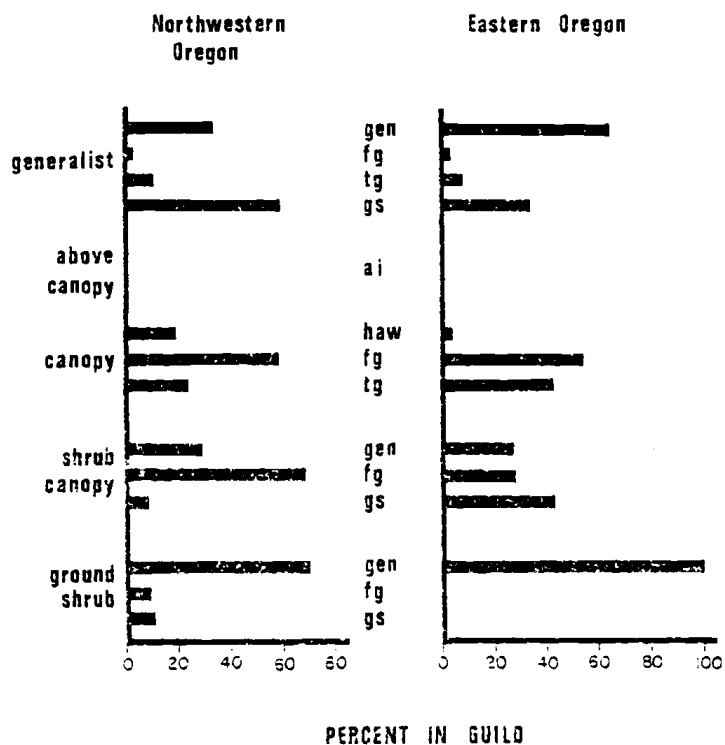


Figure 8. Percent number and biomass (a) of birds/40 ha occurring in each foraging zone and (b) the percent occurring in each foraging guild within each zone in northwestern and eastern Oregon.

a



b



northwestern Oregon) and a concomitant decrease in upper-canopy specialists in eastern Oregon.

With the exception of the above-canopy zone, bird numbers and biomass increased in consecutively higher zones in both subregions (Fig. 8a). This increase does not reflect the entire situation, however, since the density of small mammals was not included. Although most mammals available to Accipiter were zone generalists (tree climbing sciurids), one occurs only in the upper canopy (Glaucomys), and a number (Leporidae and Spermophilus) occurred only in the ground-shrub layer (Appendix 1). Inclusion of these mammals would increase the numbers of prey in the zone generalist category and prey biomass in the ground-shrub layers in both subregions.

Some major differences in guild composition between subregions were, (1) a greater percent of trunk gleaners in the canopy zone, (2) a reduced percent of foliage gleaners in both the shrub-canopy and ground-shrub zones in eastern Oregon, and (3) a greater percent of ground-searchers in both the ground-shrub and the generalists zones in western Oregon. Finally, the percent of foraging generalists in the generalist zone in northwestern Oregon was about one half the percent in eastern Oregon (Fig. 8b). Most of the above differences were probably related to the greater development of vegetation in all canopy layers, but especially in the ground-shrub and shrub-canopy zones in northwestern Oregon.

#### Diets of Accipiter

A total of 199 prey (97.5% birds; 2.5% mammals) was identified from 4 A. striatus nests and 281 prey (72.2% birds, 26.0% mammals, and 1.8% reptiles) were collected from 20 A. cooperii nests in northwestern Oregon (Appendix 2). In eastern Oregon 116 prey (98.3% birds, 1.7% mammals) were collected from 9 A. striatus nests and from 18 nests of A. cooperii 120 prey (47.5% birds, 52.5% mammals) were collected. From 59 nests of A. gentilis 227 prey (54.6% birds, 42.7% mammals) were identified (Appendix 2). Of the combined northwestern

and eastern Oregon prey of each hawk, 53 (16.8%) of A. striatus, 93 (23.2%) of A. cooperii, and 26 (11.5%) of A. gentilis were young (nestlings or fledglings).

Prey Size. Mean prey size of A. cooperii in northwestern Oregon (134.7 g) was highly significantly larger (both geometric and arithmetic means) than mean size of prey of A. striatus (12.8 g) in the same subregion ( $P < 0.005$ ) (Table 7). In eastern Oregon the mean size of prey of A. striatus (28.4 g), of A. cooperii (136.2 g), and of A. gentilis (306.6 g) were each highly significantly different ( $P < 0.005$ ).

Overall mean sizes of prey of A. cooperii in both study areas were nearly identical despite the fact that the mean size of mammalian prey in northwestern Oregon was twice as large as mammals captured in eastern Oregon and mean size of birds taken in northwestern Oregon was about one half that taken in eastern Oregon. Further, although the ratio of mammal to bird mean sizes was larger in northwestern Oregon (3.8) than in eastern Oregon (1.2), the overall mean prey sizes were nearly identical because A. cooperii captured more mammals in eastern (53.1% of the diet) than in northwestern Oregon (25.5%) (Fig. 9). Mean size of prey of A. striatus in eastern Oregon was nearly twice as large as prey captured by A. striatus in northwestern Oregon (also significantly larger [ $P < 0.005$ ]). Although mean prey size was enlarged by 2 flying squirrels taken in eastern Oregon (Appendix 2), mean size of birds was also twice that of birds taken in northwestern Oregon. The 2 flying squirrels were the only mammals captured by A. striatus in eastern Oregon, and, although I assigned them adult weights (201.4 g), each may have been young animals.

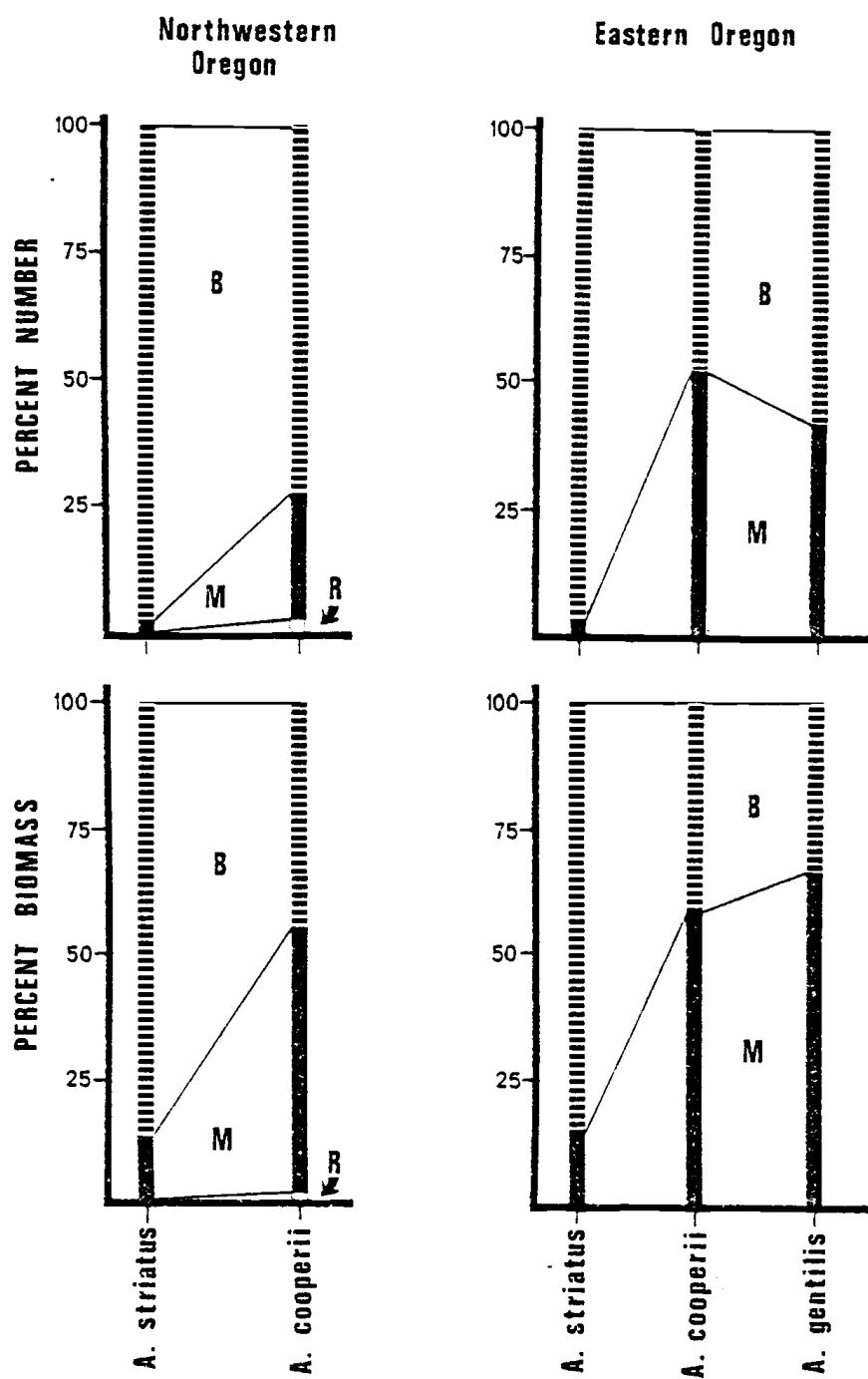
In eastern Oregon the coefficient of variation (cv) of prey size was greatest for A. cooperii, followed by A. gentilis and was the least for A. striatus. In northwestern Oregon the cv of prey size of A. cooperii was greater than that of A. striatus (Table 6). Most interesting, however, was the nearly identical cv of prey size of

Table 7. Number (#), mean ( $\bar{X}$ ), standard deviation (SD), maximum, minimum, and coefficient of variation (CV) of prey weight (grams) in diets of Accipiter in northwestern and eastern Oregon.

		A. striatus			A. cooperii				A. gentilis		
		Bird	Mammal	Total	Bird	Mammal	Reptile	Total	Bird	Mammal	Total
NORTHWESTERN	#	194	5	199	202	73	5	280			
	$\bar{X}$	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	1246.0	678.5	50.0	678.5			
	MIN	3.8	23.7	3.8	7.0	10.0	10.0	7.0			
	CV	-	-	111.9	-	-	-	137.6			
EASTERN	#	114	2	116	53	60	-	113	121	97	218
	$\bar{X}$	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	1150.0	713.0	-	1150.0	1505.0	1118.6	1505.0
	MIN	5.6	201.4	5.6	8.8	25.0	-	8.8	17.6	36.8	17.6
	CV	-	-	112.2	-	-	-	130.3	-	-	118.7



Figure 9. Percent composition by number and biomass of birds (B), mammals (M), and reptiles (R) in the diets of Accipiter in northwestern and eastern Oregon.



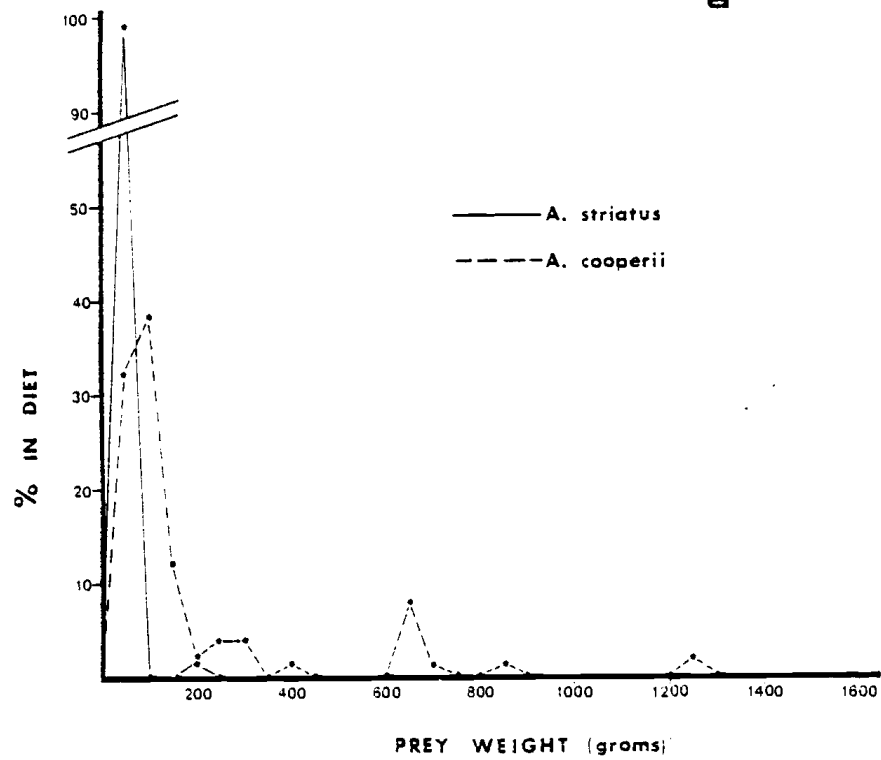
A. cooperii in both areas and A. striatus in both areas. Finally, the minimum and maximum prey size of A. cooperii and A. striatus in eastern and in northwestern Oregon were similar: 5.6 to 201.4 g and 3.8 to 167.0 g for A. striatus and 8.8 to 1150.0 g and 7.0 to 1246.0 g for A. cooperii (Table 6).

Except for A. striatus, mean prey weights of Accipiter in Oregon were considerably different from combined male and female mean prey weights of non-breeding Accipiter reported by Storer (1966) (A. striatus, 23.0 g; A. cooperii, 44.2 g; A. gentilis, 459.5 g). The larger mean prey of A. gentilis reported by Storer (1966) probably reflected a reduced winter abundance of smaller migrant birds, but may in part reflect the apparent tendency (discussed above) for A. gentilis in eastern and northern North America to be somewhat larger than A. gentilis in Oregon (Table 1). Mean prey size for this species in Oregon was, however, very near the 312 g reported for nesting A. g. gentilis in Europe (Uttendorfer 1939). The much smaller mean weight of prey of non-breeding A. cooperii is, however, difficult to explain.

A plot of the percent of total prey in 50 g classes in the diet of A. striatus and A. cooperii in both subregions (Fig. 10) indicated the location and extent of overlap of the utilization functions on an arithmetic scale. However, a plot of the log of prey size (Fig. 11), which makes the utilization functions more symmetrical and more uniformly spaced on the resource axes, demonstrated more clearly the relative locations and overlaps of the functions. These plots included only the percent of each diet that occurred in each size class. That is, the areas under each curve were equal. Since smaller accipiters have relatively greater energetic requirements per unit of weight and the ratio of prey size to predator size decreased with decreasing size of Accipiter (except for A. gentilis) (Table 8), pairs of A. striatus required more prey per unit time than A. cooperii. If the prey resources have a limited capacity of renewal (i.e., not an instantaneous rate) then the harvesting of a prey has a lasting effect on future availability of that prey. Thus, the assessment of the true dietary overlap of one Accipiter on the other requires their

Figure 10. Size-frequency distribution of prey in the diet of Accipiter. a) northwestern Oregon, b) eastern Oregon. Fifty gram weight categories.

a



b

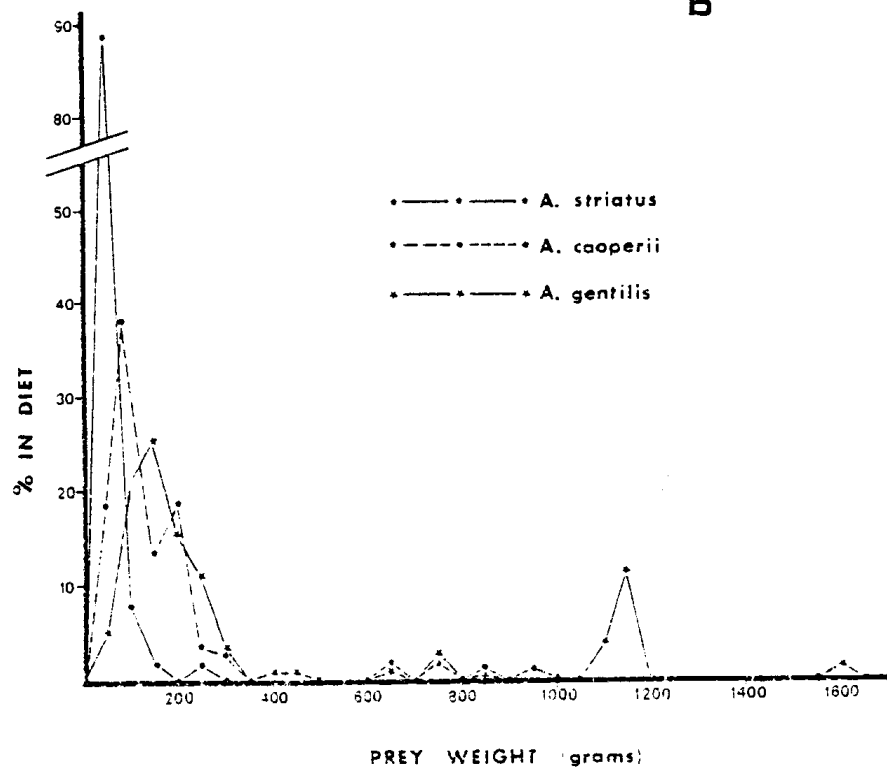
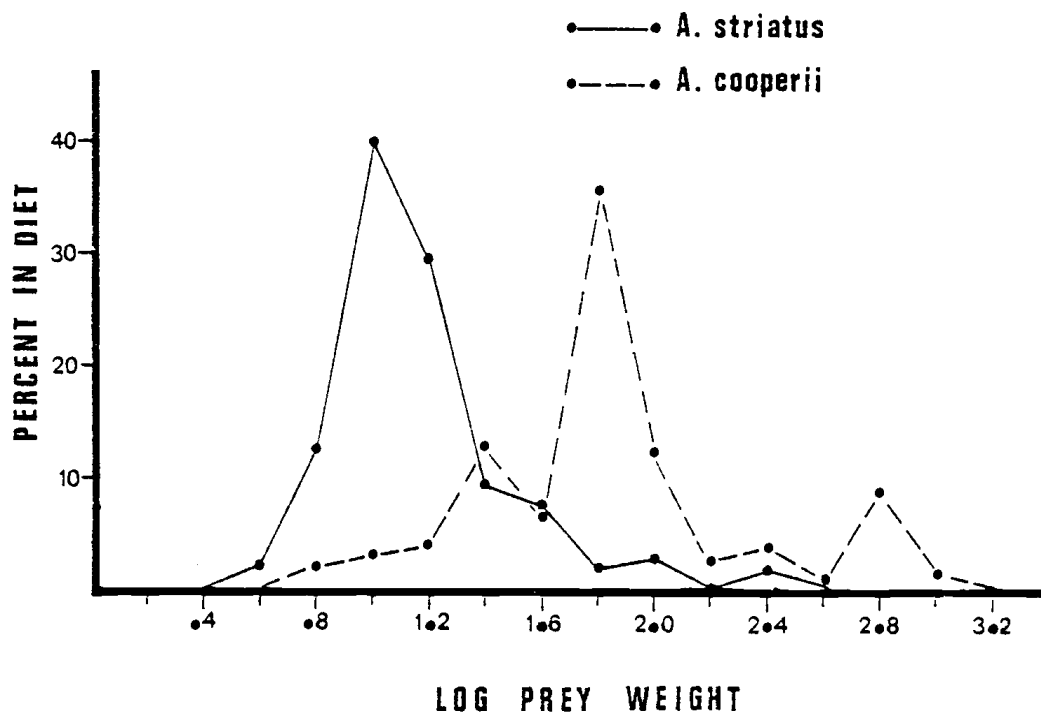


Figure 11. Size-frequency distribution of prey in the diet of Accipiter. a) northwestern Oregon, b) eastern Oregon.  $\text{Log}_{10}$  weight categories.

a



b

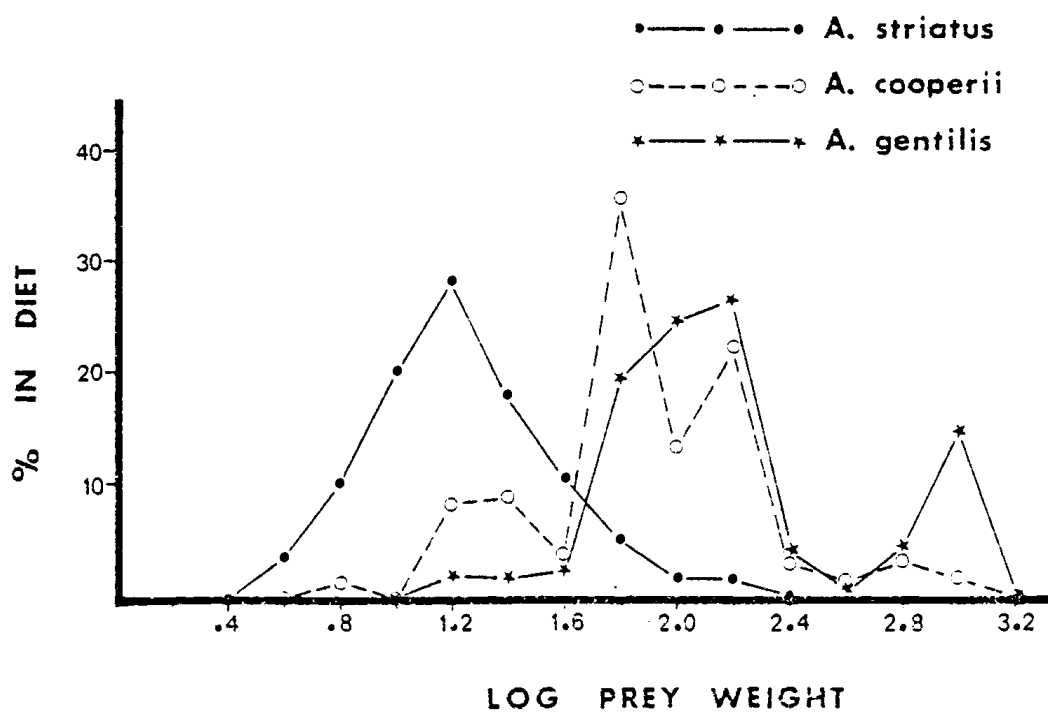


Table 8. Ratio of mean prey size (grams) to Accipiter body size (males and females combined) in northwestern and eastern Oregon.

Location	Species	Mean Prey Size (g)	Mean Predator Size (g)	Prey/ Predator
Northwestern	<u>A. striatus</u>	12.8	135.0	.09
	<u>A. cooperii</u>	134.7	368.0	.37
Eastern	<u>A. striatus</u>	28.4	135.0	.21
	<u>A. cooperii</u>	136.3	368.0	.37
	<u>A. gentilis</u>	306.6	977.0	.31



utilization functions to reflect the actual number of prey taken from each size category. In addition, since, from the uniform spacing of nests (Fig. 1 and 2), home ranges of Accipiter appeared to be non-overlapping and size of home range decreased with a decreasing body size (Fig. 12), the number of nesting pairs on an area may differ for each species. Thus the impact of each Accipiter on the prey populations must be estimated by the actual number of pairs nesting on an area. I estimated the total impact on the food resource by all pairs of Accipiter in the intensive study areas when each species co-occurred on the nesting area (1 May to 20 August) by expanding the prey required per pair to the numbers of pairs found in each area. For eastern Oregon I used the ratio of 4 pairs of A. striatus to 5 pairs of A. cooperii to 4 pairs of A. gentilis. Several pairs of A. striatus may have been missed during our nest searches. Consequently, our estimate of total predation by this species was conservative. Pairs of A. striatus were not located in the Corvallis area during 1971 and 1972. Reynolds and Wight (1978) attributed this to a greater probability of missing A. striatus relative to the larger species during a nest search and to a possible reduction of the number of pairs due to pesticides (Snyder et al. 1973). Since pairs of A. striatus were located in and around the Corvallis area in 1969 and 1970, I used a ratio of 1 pair of A. striatus to 1 pair of A. cooperii for northwestern Oregon. I did not determine whether or not non-breeding Accipiter occurred on our study areas, but feel it is reasonable to assume that their numbers were few.

The total calculated energy requirements for one family of each Accipiter for 112 days are presented in Table 9. With the total kcals required per pair, the percent composition by number and weight in the diet from all nests of each species in each subregion, and the caloric equivalent per gram (wet weight) of bird (1.757 kcal/g) (Cummings and Wuycheck 1971), mammal (1.501 kcal/g) (Gorecki 1965), and reptilian tissue (1.757 kcal/g) (my estimate), I proportionally expanded the number of prey in the diet samples to yield the total number required to supply the calculated energy demands. A plot of the total number

Figure 12. Relationship of home range size to Accipiter body size.  
See Appendix 3.

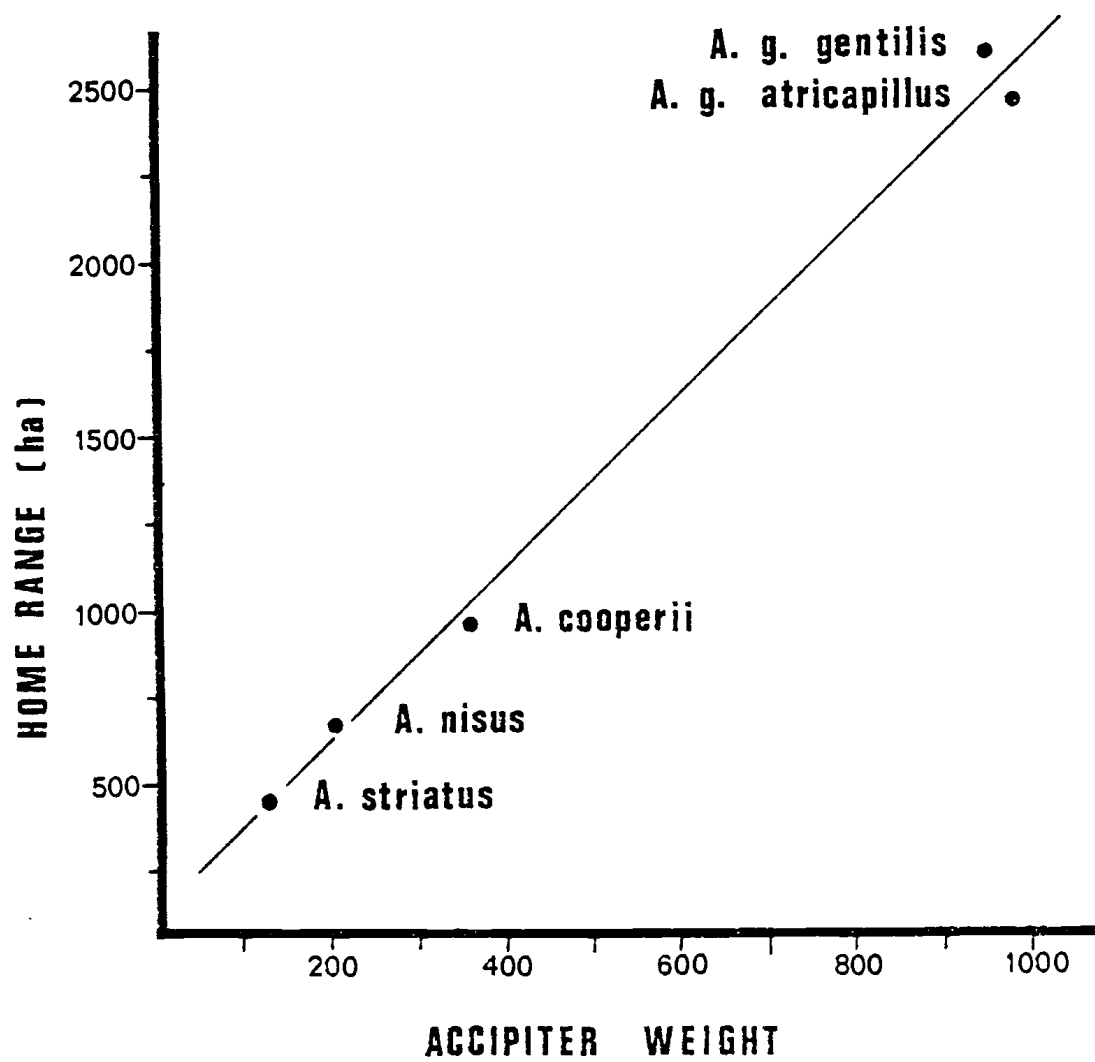


Table 9. Kcal required for adult existence and activity (MA), clutch production (EC), growth of nestlings (MN), and fledgling growth and activity (MF) for Accipiter during 112 days of the nesting season. (see text for specifics)

Species	MA		EC	MN	MF	Total
	Male	Female				
<u>A. striatus</u>	3881.3	5863.5	127.1	14386.1	17982.6	42240.5
<u>A. cooperii</u>	8847.9	11984.8	191.3	38459.6	44480.4	103962.0
<u>A. gentilis</u>	19101.6	24489.8	293.2	102656.3	101111.7	247652.5

or prey required in log weight categories showed a significant change in the area under the curves (Fig. 13a). For example, to meet their energetic needs from 1 May to 12 August A. striatus in northwestern Oregon must capture 1875 items and A. cooperii must capture 455 items.

A similar log plot of the number of prey required by the three species in eastern Oregon (Fig. 13b) indicated that, whereas the area under the curves was greatest for A. striatus, the differences among the three species were not as great as in northwestern Oregon. The difference between study areas was due to the fact that A. striatus in eastern Oregon captured prey twice as large as its counterpart in northwestern Oregon (fewer prey were required), and, since gram equivalents were less for mammals than for birds and mammals make up a great proportion of the diet of A. gentilis by weight (Fig. 9b), A. gentilis must capture more prey than A. cooperii to meet their energetic requirements.

Foraging Zone and Prey Guild. Percent prey taken from forest zones by Accipiter (Fig. 14) demonstrated that A. striatus spent much of its time foraging within the upper canopy while A. cooperii tended to forage within the ground-shrub and canopy-shrub zones. Major differences in zone utilization between A. cooperii and A. gentilis in eastern Oregon did not occur, although there was a tendency for A. gentilis to take a slightly greater percent prey from the ground-shrub layer (Fig. 14). Noteable differences in utilization of zones between northwestern and eastern Oregon were, 1) a tendency of A. cooperii to forage closer to the ground in eastern Oregon, and 2) the preponderance of zone generalists in the diet of each Accipiter in eastern Oregon (Fig. 14).

Distinct preferences for one or more guilds within any of the height zones were not detected in either subregion. However, grouping prey taken from each zone into 6 guilds (Fig. 15) demonstrated that A. striatus in northwestern Oregon specialized on trunk and foliage gleaners while A. cooperii captured mostly ground searchers and guild generalists, though some foliage gleaners (20%) were taken. Similar

Figure 13. Size-frequency distribution of total prey required by Accipiter from 1 May - 12 August in a) northwestern (representing 1 pair of A. striatus to 1 pair of A. cooperii) and b) eastern Oregon (representing 4 pairs of A. striatus to 5 A. cooperii to 4 A. gentilis). See text for details.

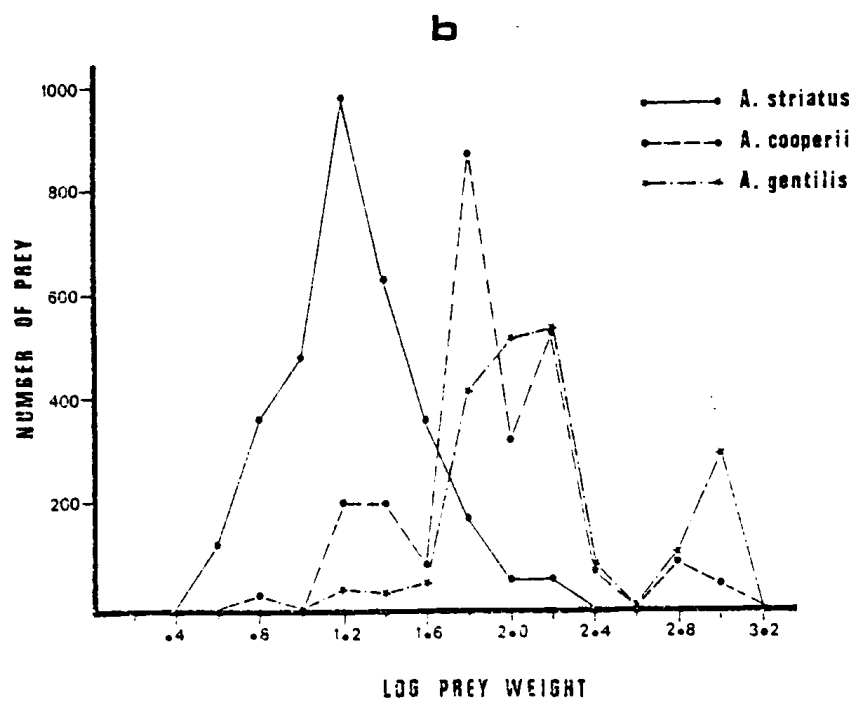
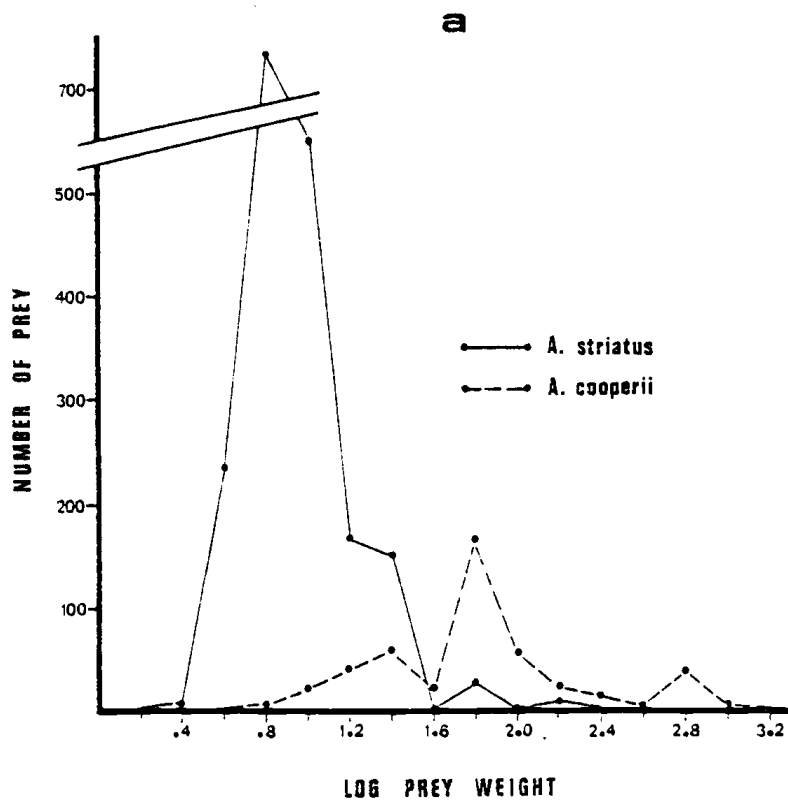


Figure 14. Percent of prey captured from each foraging zone by Accipiter in northwestern and eastern Oregon.



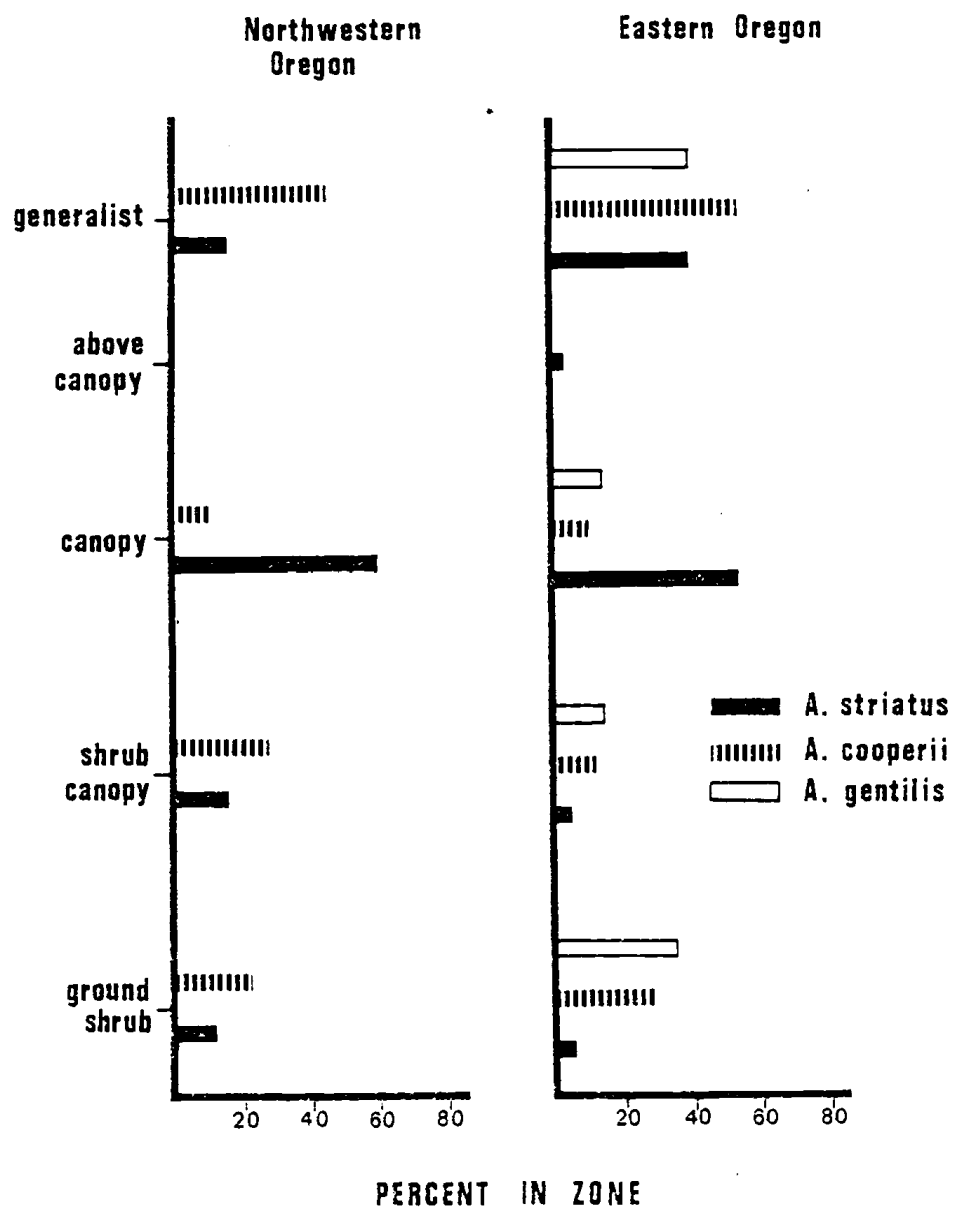
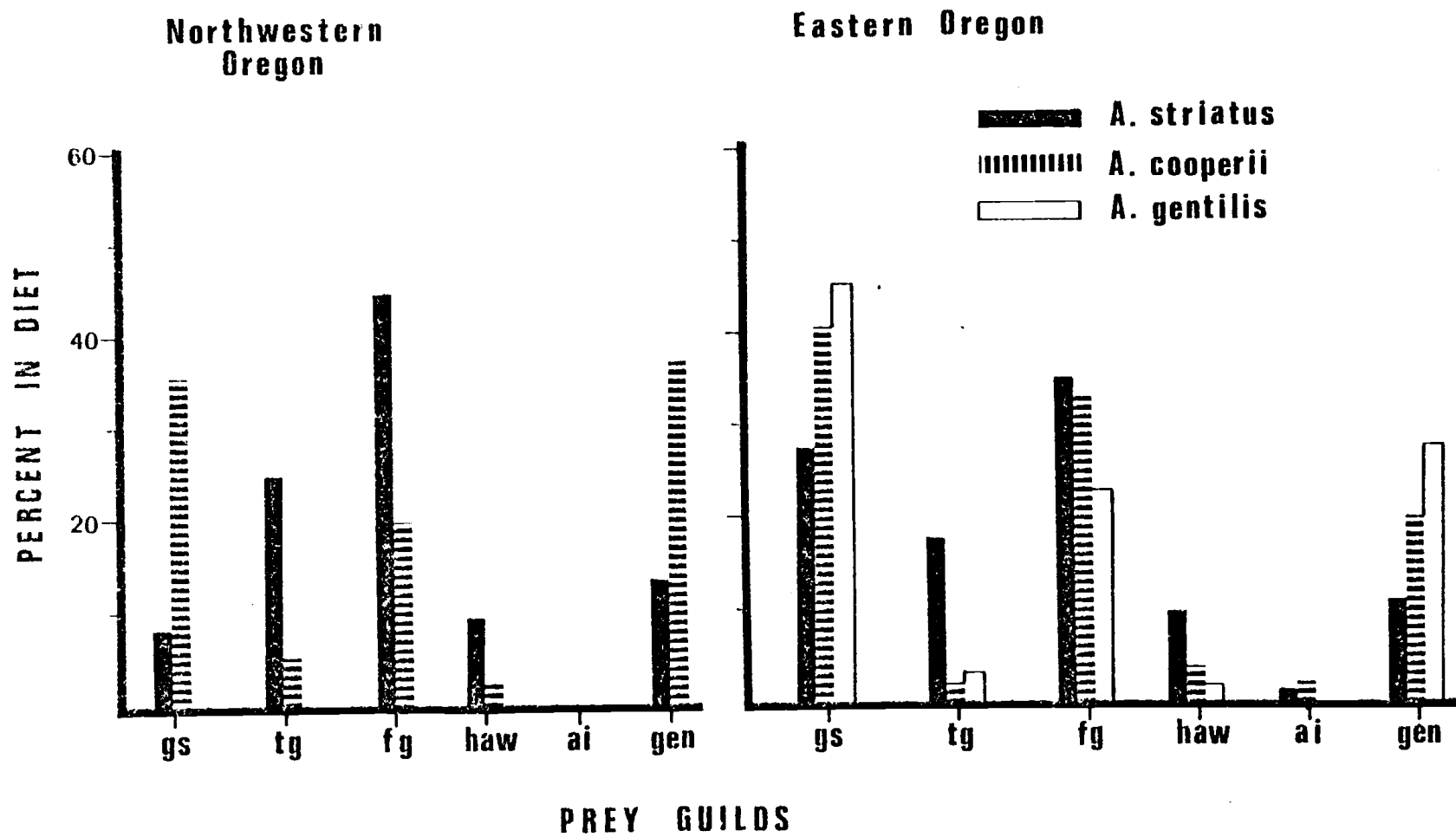


Figure 15. Percent of prey captured from each prey foraging guild by Accipiter in northwestern and eastern Oregon. Data presented here represents a summation over all foraging zones. gs - ground searcher, tg - trunk gleaner, fg - foliage gleaner, haw - hawk, ai - aerial insectivore, gen - generalists.



trends were not discerned in eastern Oregon where all species captured a large percentage of ground-searchers and foliage gleaners; however, members taken from these guilds by A. striatus were birds whereas the majority taken by A. cooperii and A. gentilis were mammals. Further, the diet of A. striatus was composed of 20 percent trunk gleaners while less than 5 percent of the diets of A. cooperii and A. gentilis consisted of this guild. Of note was the similar prey guild preferences of A. cooperii and A. gentilis in eastern Oregon.

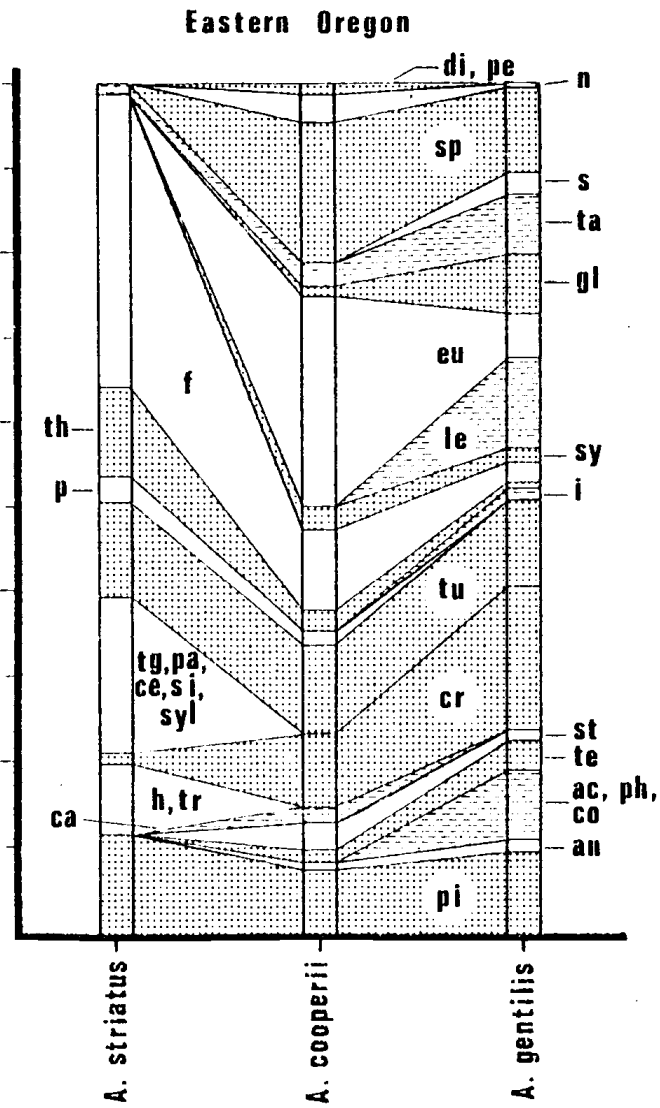
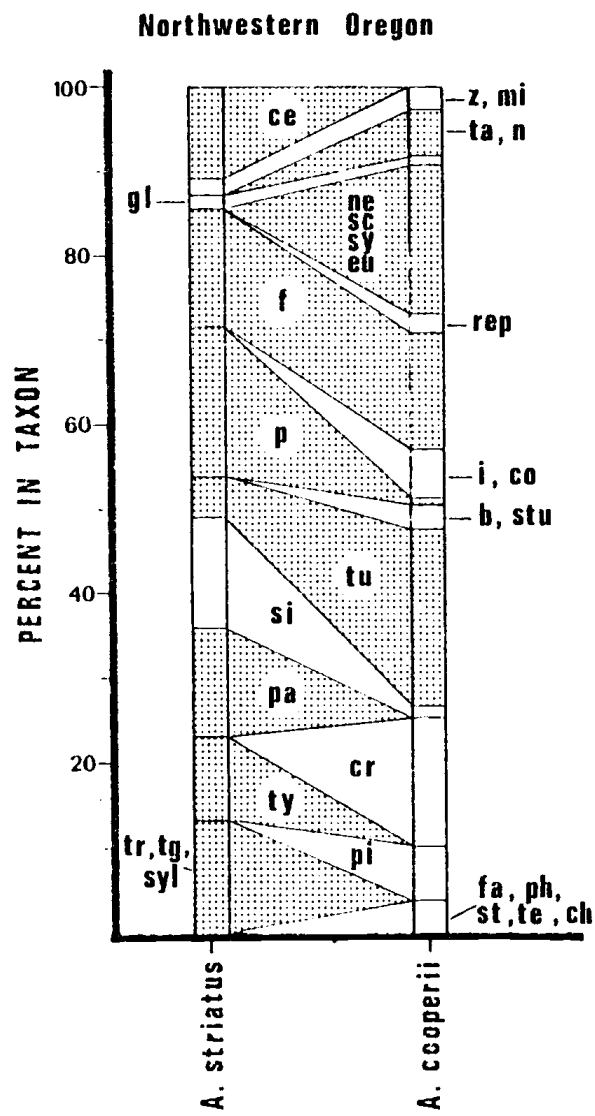
Prey Taxa. Taxonomic composition of the diet of Accipiter was examined by grouping birds into families, mammals into genera, and reptiles into class (Fig. 16). A. striatus and A. cooperii in northwestern Oregon differentially used all taxons except Fringillidae and Glaucomys, Zapus, and Microtus. These mammalian genera, however, formed an insignificant proportion of the diet of both predators (each less than 2%) whereas fringillids made up nearly 14 percent of the diet of each.

In eastern Oregon A. striatus and A. cooperii followed the same pattern. Picidae and Turdidae, each of which contributed 7 percent and 11 percent, respectively, and Tamiasciurus, a minor taxa in the diet of both, were taxa taken by both hawks. Turdidae and Picidae also occurred at about the same percentage in the diet of A. gentilis. Principal differences among the bird taxa captured by A. cooperii and A. gentilis occurred in the Fringillidae, Corvidae, and some minor differences among the Accipiteridae, Phasianidae, and Columbidae. No mammalian prey other than Spermophilus (17.7% for A. cooperii and 10.6% for A. gentilis), were captured in equal frequency by either species. Major differences in mammalian taxa taken by A. cooperii and A. gentilis occurred among Lepus, Eutamias, Glaucomys, and Tamiasciurus (Fig. 16).

#### Competitive Coexistence

To demonstrate the potential of competition to effect a divergence of morphological characters such that competing species

Figure 16. Taxonomic composition of diets of Accipiter in northwestern and eastern Oregon. AN, Anatidae; FA, Falconidae; AC, Accipiteridae; TE, Tetronidae; PH, Phasianidae; CH, Charadriidae; CO, Columbidae; ST, Strigidae; CA, Caprimulgidae; TR, Trochilidae; PI, Picidae; TY, Tyrannidae; H, Hirundinidae; CR, Corvidae; PA, Paridae; SI, Sittidae; CE, Certhiidae; TG, Troglodytidae; TU, Turdidae; SYL, Sylviidae; B, Bombicillidae; STU, Sturnidae; V, Vireonidae; P, Parulidae; I, Icteridae; TH, Thrupidae; F, Fringillidae; RE, Reptilia; NE, Neurotrichus; SC, Scapanus; SY, Sylvilagus; LE, Lepus; EU, Eutamias; GL, Glaucomys; TA, Tamiascus; S, Sciurus; SP, Spermophilus; DI, Dipodomys; N, Neotoma; Pe, Perognathus; Z, Zapus; PE, Peromyscus; M, Mustela; MI, Microtus.



segregate on or use different portions of one or more resources, a number of ecological conditions are required. One condition is that one or more of the resources 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). Additionally, populations of the competing species must be at an equilibrium with respect to their sizes (Vandermeer 1972; May and MacArthur 1972) and their utilization functions (Wiens 1977), and the population equilibrium must be determined by resource limitations. Stated differently, habitats of each competitor must be filled or saturated at a level determined by the resource levels and not, say, by predation or other factors (Connell 1975). Further, the structure and abundance of resources in question must have some constancy through time (Wiens 1977); what an animal does in one season must somehow relate to what it did in previous seasons and in future seasons. If, for example, body size responds to competition in one season (e.g., breeding) by becoming smaller, then conditions during other seasons (e.g., non-breeding) must be such to accommodate reduced size. The requirement of resource constancy through time also applies to between-generation times (Wiens 1977) to the extent that population utilization functions must have some constancy for species adjacent on the resource axes to respond to their neighbors' harvesting. Thus, there is danger in assuming that body sizes, foraging behaviors, or habitat differences in Accipiter have resulted from or may be used as a measure of competitive intensity. However, some aspects of the ecological relationships of Accipiter and some characteristics of their habitat and prey resources give inferences into the likelihood of competition occurring among them, at least in Oregon.

Although breeding began earlier for the larger species, Accipiter co-occurred for the entire nesting period of the smaller (A. striatus) (Fig. 4). For the most part, and especially from the mid-portions of the breeding season, each is in an equivalent stage of nesting. In addition, both subregions contain two or three accipiters in the same habitat from April through August and my observations of birds

foraging in both areas indicated the lack of any horizontal partitioning of foraging habitat. Thus, within Oregon there were two or three species of Accipiter foraging for similar resources in the same habitat during the same season.

Reynolds and Wight's (1978) examination of the relative densities of nesting accipiter was not conducted over a sufficient period to provide a definite estimate of the constancy of nesting pairs from year to year. However, during 7 years of investigating nesting Accipiter in Oregon, I did not find evidence of even minor fluctuations in nest densities (with exception of A. striatus in northwestern Oregon). Despite the fact that A. striatus as well as A. cooperii had relatively low nest site reoccupancy rates from year to year, new nest sites were established in adjacent areas and overall numbers did not change appreciably. Newton et al. (1977) and Tinbergen (1941) also found some constancy in breeding numbers of Accipiter from year to year (but see McGowan (1975) for cyclic aspect of A. gentilis populations in Alaska).

Bird numbers in North American coniferous forests undergo intra-seasonal, seasonal, and annual variations. Intra-seasonal variation (here our concern is with spring and summer) arises from two sources: 1) the unsynchronized arrival and departure of nesting birds and, 2) reproduction. Seasonal variation is, of course, due to the arrival and departure of migrants and fluctuations of populations of residents. In general, bird numbers in the coniferous forests of Oregon vary as follows: numbers are relatively low in early spring (April) as only resident species are present. In late spring migrants arrive, and along with the residents, nest and fledge young by early summer. Within Oregon the highest density is probably achieved at fledging. Shortly thereafter adults and immatures of migratory species leave, and densities gradually approach the pre-nesting levels. The gradual decrease takes place during mid-to-late summer. Small mammals, in accordance with their reproductive strategies (multiple litters, early maturation and breeding of young of the year), probably increase from early summer, peaking by late summer.



Annual variation in bird numbers results from year to year fluctuations in population levels of various species composing the forest avifauna. The extent of the annual fluctuations in numbers of birds is not fully understood. Wiens (1975) compared coefficients of variation in breeding numbers from 15 studies conducted over 2-5 successive years and found densities in northern and northeastern mature coniferous forest to be "extremely stable" ( $cv = 2.2$  and  $2.3$ , respectively), but in all other forests densities ranged from intermediately to highly variable (range of  $cv = 11.4$  to  $37.2$ ). With the exception of the northern and northeastern forests, the coefficients of variation approximated values reported for rangeland habitats (Wiens and Dyer 1975). It was not clear to what extent these variations represented sampling error or the true variations in density. However, due to the screening effect of the vegetation in forested habitat and the differing degrees of conspicuousness of birds, sampling error should be greater in tall forest than in grassland situations (see Emlen 1971). Additional work is required to establish the annual stability of bird numbers in mid-latitude conifer forests in North America.

Two aspects of my data suggested that Accipiter body size and ultimately their resource utilization functions may have diverged as a result of competition. The first was the position of the utilization curves of each Accipiter on the resource spectrum. MacArthur and Levins (1967) argued that there is a theoretical limit to similarity of resource utilization (amount of overlap) beyond which coexistence is impossible and competitive exclusion results. May and MacArthur (1972), MacArthur (1972), and May (1974) suggested that this limit is approached when similar, normally-distributed utilization functions of two or more competitors have means that are displaced by about 1 standard deviation. There are, however, problems in applying this theory to my dietary data as the theory assumes the competitors have equal carrying capacities, are competing for a one-dimensional resource, and that their utilization functions have identical dispersions.

Nevertheless, mean prey sizes of A. cooperii and A. gentilis were separated by about 1 standard deviation (Fig. 17). However, mean sizes of prey of A. striatus and A. cooperii in both subregions were displaced considerably more than 1 standard deviation. The greater displacement between means stemmed from the fact that A. striatus had a capture rate 2 to 4 times that of A. cooperii. This resulted in an expanded utilization function of A. striatus relative to, and greater overlap on, the utilization function of A. cooperii. If two similar, normal utilization functions have a maximum theoretical overlap value equal to about 1 standard deviation then expanding one relative to the other (but maintaining their positions) increases the area of overlap. To maintain the theoretical degree of overlap the functions must, therefore, be displaced beyond 1 standard deviation. Difference in prey size of A. striatus and A. cooperii also corresponded to a slightly larger A. striatus to A. cooperii weight ratio (1:2.73) than for A. cooperii to A. gentilis (1:2.66). A. cooperii and A. gentilis captured nearly the same number of prey and, therefore, had similar areas under their utilization functions.

The second aspect suggesting divergence due to competition was the extent to which the combined utilization functions (summation of the curves of all species) included the entire size range of the resources at or near the proportions with which they occurred in the forests. The fit of the utilization and availability functions of Accipiter in northwestern Oregon showed this pattern well (availability of mammalian prey not included) (Fig. 18a). In eastern Oregon, however, the situation was somewhat more complicated. Here A. striatus captured most of its prey from one size class larger than peak availability (Fig. 18b). In addition, A. cooperii and A. gentilis also captured prey from the same size class. Thus, the combined utilization curve peaked one size class to the right of peak availability. However, if mammals were included, the availability curve would extend (at low levels) further to the right and produce a better fit of the two curves.

Figure 17. Mean, range and one standard deviation (thickened bars) of prey size of Accipiter in northwestern and eastern Oregon.

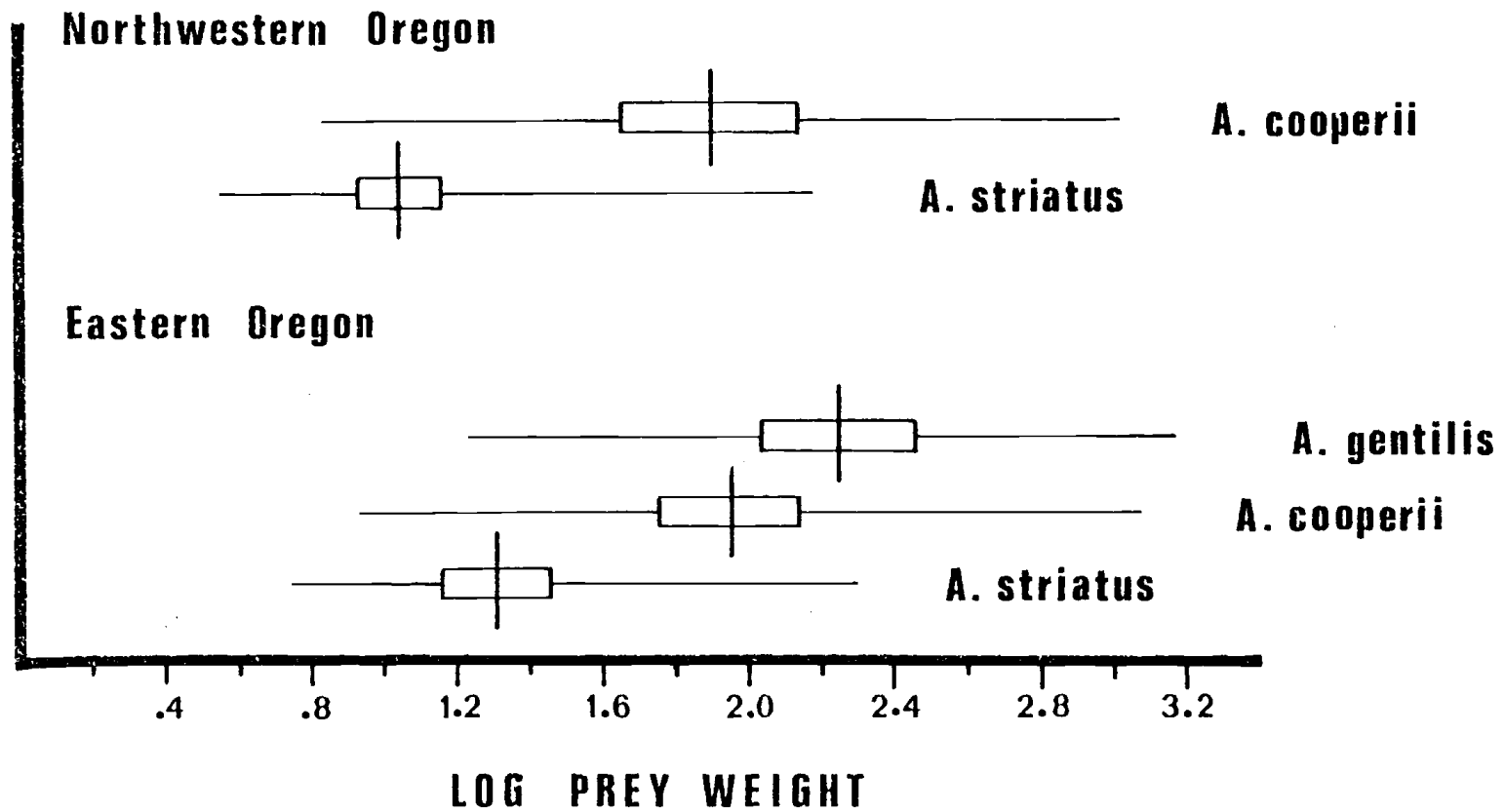
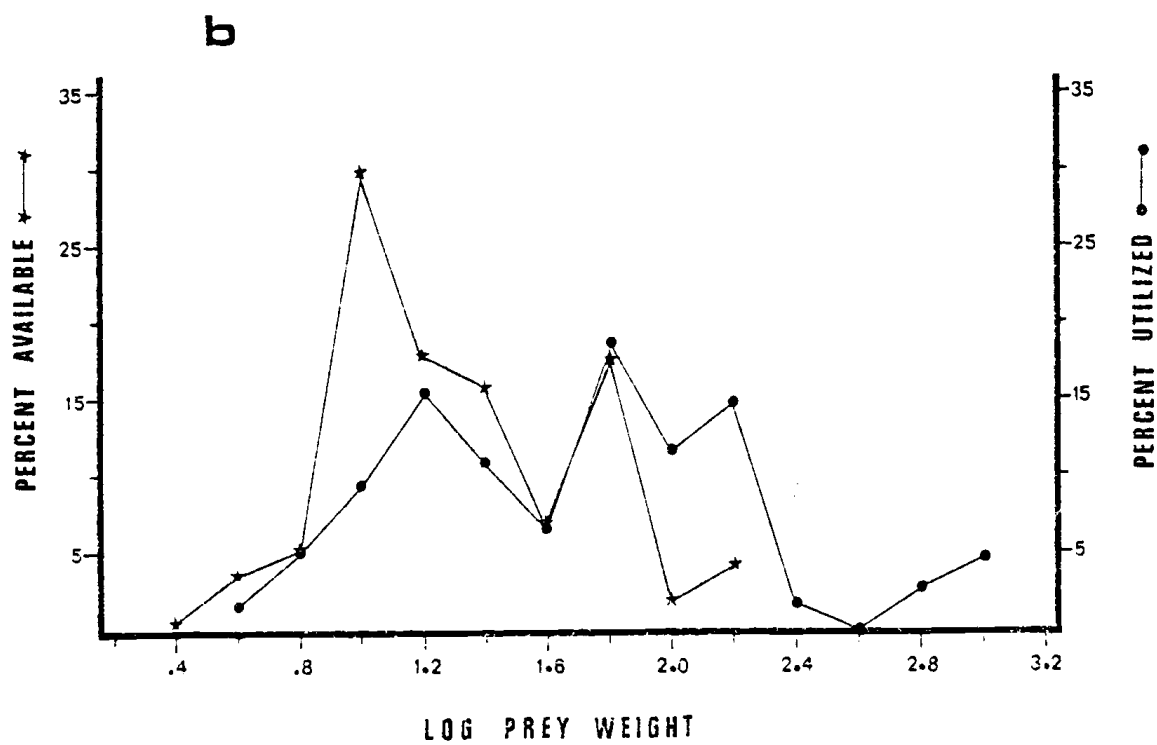
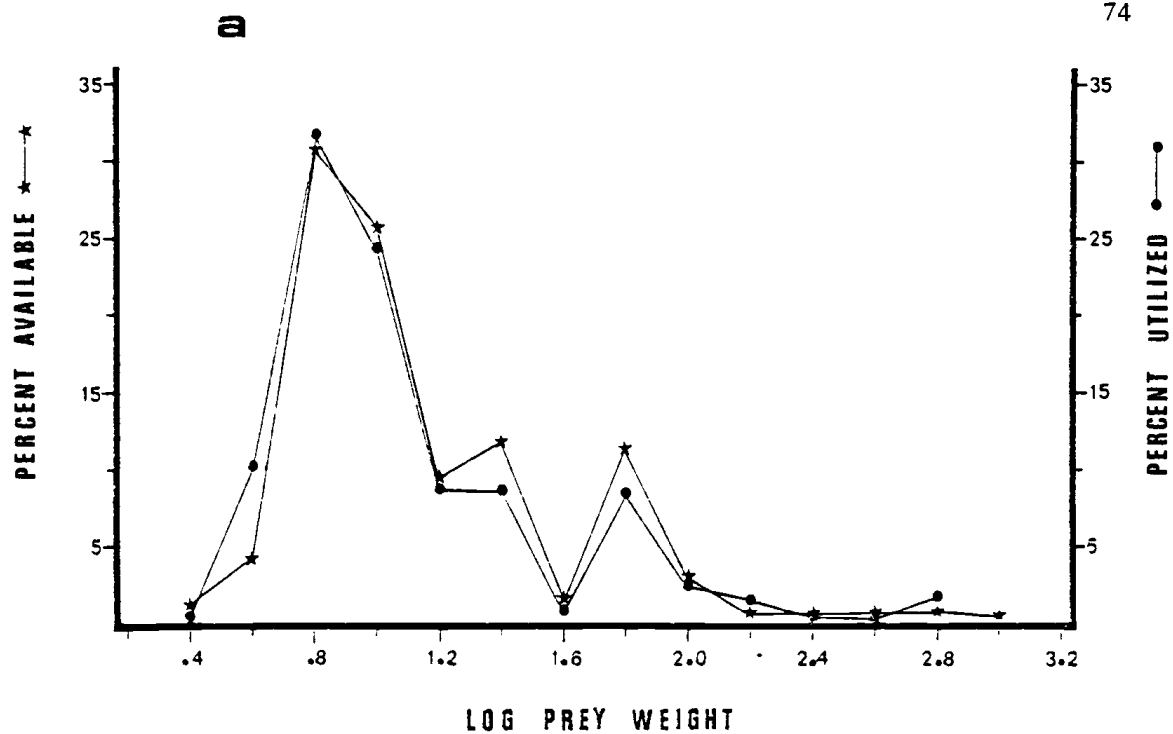


Figure 18. Total utilization curve (diets of all species combined) of Accipiter and prey availability curve (birds only) for a) northwestern and b) eastern Oregon. See text for explanation.



Finally, due to the structure of the food resource in Oregon and the nature of the predator-prey relationship, the prey of Accipiter is an ideal resource for partitioning. That is, no single Accipiter can utilize the entire size range of prey. The mobility of mammals and birds is such that large Accipiter (i.e., A. gentilis) cannot efficiently forage for small prey and, conversely, small Accipiter can not subdue prey much larger than themselves.

Thus far the discussion has been limited to the hypothesis that Accipiter body size and associated utilization functions resulted from interspecific competitive interactions during the breeding season. In fact there may be reasons to believe that body size, and ultimately niche divergence, among Accipiter may stem from competitive interactions during the winter (Fretwell 1972), or that Accipiter size may reflect the prey size availability within the winter range of each. I chose, however, to examine the ecological relationships of Accipiter during the breeding season since, 1) their ranges were known to overlap during nesting and, 2) my observations showed that whereas all species can be seen throughout the winter in Oregon, A. gentilis was closely associated with montane areas while A. striatus and A. cooperii occurred in lowland areas.

#### Partitioning of Nesting Habitat

Consistency of structural characteristics among nest sites and the relative scarcity of stands containing the "proper" structure in both subregions indicated that selection of nest sites by Accipiter was an active rather than a random process. The basic differences among nest sites of Accipiter were associated with the successional stage of the conifer stands each selected for nesting. The most characteristic aspect of sites of all species was the high degree of canopy closure relative to surrounding forests. From inside the nest sites the obvious characters were heavy shading and high trunk density. Trees comprising the nest sites of A. striatus and A. cooperii had extended trunks with many dead limbs, and the trunks of the larger

overstory trees in A. gentilis sites were often obscured by smaller understory trees (Fig. 5a,b,c).

Aside from a characteristic physical environment produced within dense conifer stands, which provide a unique nesting microenvironment (Reynolds and Meslow in prep.), the high tree and foliage density provided protection from avian predators (i.e., large owls (Bubo), crows and ravens (Corvus), and other Accipiter). Nests of A. striatus and A. cooperii were hidden in crotches of split trunks, mistle toe (Arceuthobium sp.) clumps, or closely packed, overhanging limbs. In addition, canopies were sufficiently dense to provide hiding cover and protection for fledglings. Finally, since smaller accipiters arrived on the breeding grounds later than large species, they could further reduce the risks of predation by choosing sites sufficiently distant from sites already occupied by potential predators.

Partitioning of nesting habitat by Accipiter in Oregon probably stemmed from a species' specific selection of stand structures that provided microhabitats required by different physiologies, behaviors, and ecologies associated with the body size of each species. Given the structural similarities of nest sites of A. striatus and A. cooperii in both subregions and the dissimilarities between sites of these species and those of A. gentilis, competition for nest sites might be greatest among the two smaller species. However, only twice during this study did an Accipiter occupy a nest site used previously by another; A. cooperii usurped a site of A. striatus and a site in an unusually young forest stand abandoned by A. gentilis was occupied the following year by A. cooperii.

Differences among nest sites in northwestern and eastern Oregon were attributable to the floristics and associated histories of the forest stands involved; northwestern Oregon nest sites were dominated by Douglas-fir while those in eastern Oregon were dominated by white fir and ponderosa pine. Since Douglas-fir stands in western Oregon tend to be even-aged and to have fast growth rates (Franklin and Dyrness 1973), nest sites in this subregion had relatively tall trees of uniform height, diameter, and spacing. In contrast, trees in nest



sites of A. striatus and A. cooperii in eastern Oregon were true fir (Abies) and pine and tended to be of various heights, diameters, spacing, and the sites themselves had somewhat less canopy closure (Reynolds and Meslow in prep.).

### Partitioning of Food

Several studies of birds and their diets have demonstrated positive correlations of prey size with predator size (Hespenheide 1971, 1975; Diamond 1975), and this relationship holds for a variety of Accipiter species (Storer 1966; Meng 1959; van Beusekom 1972; Opdam 1975). The prey size to predator size relationship does not, however, account for the difference in the sizes of prey taken from different taxonomic groups (e.g., birds and mammals) by Accipiter. To what extent do size preferences within prey taxons affect the partitioning of food among Accipiter?

Root (1967), MacArthur (1958), Gibb (1954) and others have shown that birds co-occurring in the same habitat may reduce competition by restricting feeding activities to different parts of trees or to different layers of the forest. To what extent do co-existing Accipiter partition food by foraging at different heights within the forest? If Accipiter forage within the same zone do they utilize different tactics to search for and capture members of different foraging guilds? To examine these questions I examined niche breadths, and niche overlaps of Accipiter in each of these dimensions and attempted to determine the interrelationships of these dimensions of their food niche.

Prey Size Dimension. For the analysis of the prey size relationships among Accipiter I calculated niche width indices with respect to prey size for each species in both study areas (Table 10). With the exception of A. striatus in eastern Oregon, as Accipiter size increased niche width also increased. Although A. striatus captured prey from fewer categories (9), its greater niche width resulted from a more equal utilization of the size categories within its prey size

Table 10. Niche width with respect to prey size in diet of Accipiter in northwestern and eastern Oregon.

	Predator	Log-weight Category														Number	Niche Width
		3	4	5	6	7	8	9	10	11	12	13	14	15	16		
NORTHWESTERN	<u>A. striatus</u>	.5	12.6	39.2	29.2	9.1	7.5	.5	1.0	-	.5	-	-	-	-	9	3.72
	<u>A. cooperii</u>	-	.7	1.8	3.6	9.3	8.9	9.6	36.3	12.1	4.6	3.6	-	8.9	.7	12	5.40
EASTERN	<u>A. striatus</u>	-	3.4	10.3	20.7	28.4	18.1	10.3	5.2	1.7	1.7	-	-	-	-	9	5.50
	<u>A. cooperii</u>	-	-	.9	-	8.0	8.8	3.5	35.4	13.3	22.1	2.7	.9	2.7	1.8	11	4.78
	<u>A. gentilis</u>	-	-	-	-	1.8	1.4	2.8	19.7	24.8	26.1	3.7	.5	4.6	14.7	10	5.13

range. Niche width values from untransformed data (1.01 and 3.68 for A. striatus and A. cooperii in northwestern Oregon, and 1.26, 4.27, and 6.43 for A. striatus, A. cooperii and A. gentilis in eastern Oregon) were closer to expected values of consumers whose prey are distributed log-normally (demonstrating the importance of resource scaling when calculating such things as niche breadth). With a log-normally distributed prey resource (Fig. 6 and 7), the smaller hawk (A. striatus) will have a shorter search time and alternatively a relatively restricted diet, while larger hawks (e.g., A. gentilis) which feed on rarer items, have longer search times and must capture from a wider range of food size. The different search times explain why the utilization functions of Accipiter become symmetrical and of equal width when plotted logarithmically. Additionally, because Accipiter body sizes are energetically and physically constrained by prey size (discussed above), the symmetry of utilization functions on the log scale explains why Accipiter (and frequently other consumers with similarly structured resources) have body sizes that tend to differ by a constant multiple on an arithmetic scale (MacArthur 1972; Hutchinson 1959).

Maximum prey size increased proportionally with increasing Accipiter size and was probably limited by the ability to subdue larger prey. However, minimum prey size did not vary proportionally to Accipiter weight. On the small end of the food size spectrum, A. striatus was limited by availability, smaller birds and mammals did not occur in Oregon forests. Thus, A. striatus had a utilization function somewhat truncated on the left (Fig. 11). Since A. cooperii and A. gentilis were capable of taking small birds and mammals, it was not surprising that their utilization curves trailed to the left. However, because of greater mass, larger Accipiter need more food to meet their energetic demands. As a result, they should forgo the pursuit of small prey unless situations arise (e.g., young or inexperienced prey) where the cost of pursuit is sufficiently small. 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 8). Since heavier bodied hawks have greater striking power (Goslaw 1971; Storer 1966), the prey weight to predator weight ratios were expected to increase with Accipiter size. However, the power gained by size in A. gentilis was counteracted by its being a prey size generalist in a region of the resource spectrum where prey availability is low and truncated on the right. That is, A. gentilis must be large to maximize its prey size range but, due to the numerical distribution of prey size available, its mean prey size is decreased.

Prey Taxa Dimension. Taxonomic composition of the diet of Accipiter was examined by calculating niche width from the proportions of prey taken in each taxon (Table 11). Here again the same pattern found in the prey size dimension holds; increased niche width with increased body size of Accipiter.

In both subregions each Accipiter captured significantly different mean weights of prey (Table 7), and each differentially used the two major taxa - birds and mammals (Fig. 9). A. striatus had more small birds available to it than small diurnal mammals. In addition, this hawk foraged primarily in the upper canopy zone, and, as a consequence, did not encounter smaller mammals. Preferred prey sizes of the larger Accipiter were to the right on the prey size axes resulting in reduced encounters of birds and increased encounters of mammals of preferred size. Thus, as Accipiter body size increased, greater numbers of larger mammals were taken, counteracting the decline in frequency of birds. Difference in mean mammal versus mean bird weights in the diets of Accipiter (Fig. 19) may reside in the relative difficulty of capture of the two major taxa - mammals, being slower and limited to fewer planes of escape, may be easier to capture. However, larger mean mammal weights may simply reflect the availability of fewer mammal species (i.e., the size-frequency distribution for mammals was more discrete than for birds) and the fact that most mammals were larger than most birds. For example, Steller's Jay (Cyanocitta stellerii), 106.6 g, and American Robin

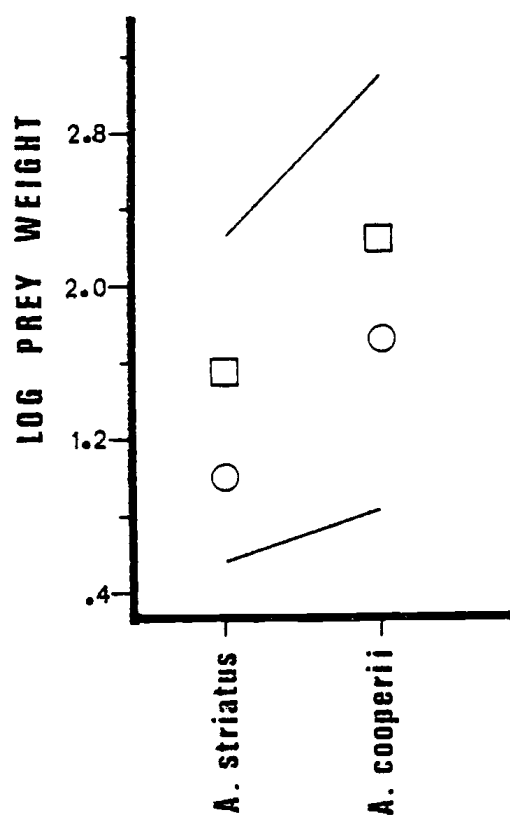
Table 11. Taxonomic composition of the diet of Accipiter in northwestern and eastern Oregon.

		Predator	Taxonomic Category <sup>a/</sup>																										#	Niche Width
NORTHWESTERN			PH	ST	PI	TY	CR	PA	SI	CE	TG	TU	SY	B	ST	P	I	TH	F	RE	SC	SY	EU	TA	N	MI				
	<u>A. striatus</u>	-	-	-	9.5	-	13.1	12.6	12.1	4.0	5.5	8.0	-	-	17.1	-	-	-	14.1	-	-	-	-	-	-	-	10	8.54		
	<u>A. cooperii</u>	1.1	1.1	5.7	-	14.6	-	1.4	-	-	21.0	-	1.4	1.4	1.4	4.3	1.4	14.2	1.8	1.4	8.2	7.8	2.5	3.9	-	18	9.31			
EASTERN			TE	PH	CO	ST	CA	PI	TY	CR	PA	SI	CE	TU	SY	P	TH	F	SY	LE	EU	GL	TA	S	SP	N				
	<u>A. striatus</u>	-	-	-	-	-	11.2	7.8	-	7.0	4.3	2.6	11.2	3.5	3.5	10.3	34.5	-	-	-	-	1.7	-	-	-	11	5.85			
	<u>A. cooperii</u>	1.8	-	-	2.7	1.8	7.1	-	8.9	-	-	-	10.6	-	-	2.7	9.7	2.7	-	24.8	-	2.7	-	-	17.7	2.7	13	7.65		
	<u>A. gentilis</u>	3.7	4.6	3.2	1.4	-	9.6	-	16.5	-	-	-	11.0	-	-	-	2.3	1.4	11.0	5.1	6.9	6.0	2.3	10.6	1.4	16	11.24			

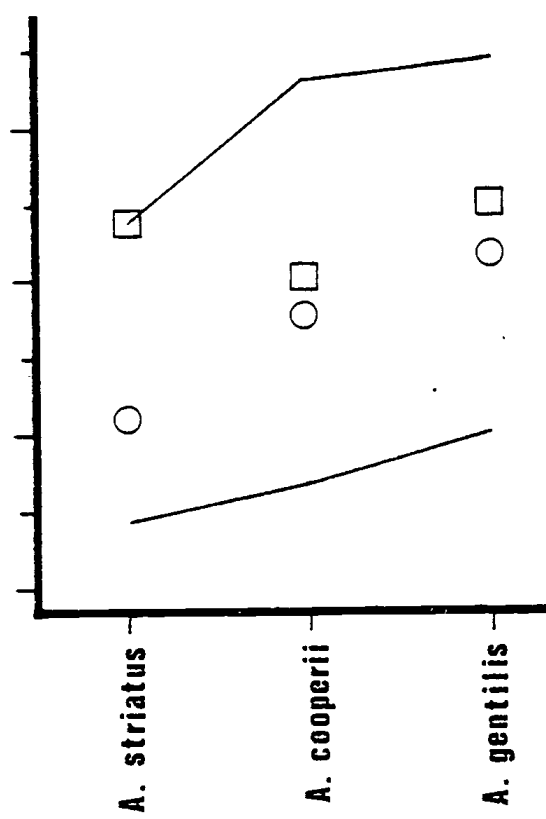
<sup>a/</sup> See Figure 16 legend for key to key to taxa.

Figure 19. Relationship of Accipiter body size to prey size range, mean bird, and mean mammal size captured. Circles represent mean bird size and squares represent mean mammal size.

Northwestern Oregon



Eastern Oregon



(Turdus migratorius), 81.2 g, were the largest of the most common birds in Oregon forests while the smallest mammals commonly captured were Eutamias sp., 67.5 g. Additionally, for all species of mammals comprising more than 5% to the diet of the hawks in both subregions (with the exception of Eutamias), each was larger than 160 g (Appendix 1 and 2).

Prey Zone and Guild Dimension. To determine the extent of differences in the diets that were attributed to foraging in different zones and the utilization of various foraging tactics among Accipiter, prey were grouped into 15 categories; 5 height zones and their inclusive prey foraging guilds (Table 12). Examining guilds on a zone basis allowed for maximum niche differences among each Accipiter; all possible tactics per zone were considered.

With the exception of A. gentilis, niche width with respect to zone and tactic increased with increased Accipiter size (Table 12). The pattern was associated with the inter-dependence of the prey size, prey guild, and foraging zone dimensions. Small birds tended to be foliage gleaners, trunk gleaners or hawkers (warblers, nuthatches, and flycatchers), and occurred mostly in the mid- to upper-canopy portions of the forests. As a result, A. striatus, a prey size specialist, was necessarily a zone and guild specialist. In contrast, most large birds and mammals tended to be ground-searchers, foliage-gleaners, or guild generalists, and due to their greater weight, were associated with the ground or were zone generalists. Thus, A. gentilis was a zone and guild specialist. On the other hand, since A. cooperii captured birds and mammals intermediate in size, each of which had representatives in all the zones and guilds, A. cooperii was a zone and guild generalist.

No clear pattern emerged when standardized niche widths of Accipiter in the three dimensions were compared within eastern Oregon, but in northwestern Oregon niche width in the prey size dimension was the narrowest, while the zone-guild dimension was the broadest (Table 13). Perhaps more significant was the fact that niche width in



Table 12. Foraging zone and prey guild composition of diets of Accipiter in northwestern and eastern Oregon.

Predator		Foraging Zone <sup>a/</sup> and Guild <sup>b/</sup>															#	Niche Width
		1			2			3			4	5						
		GS	FG	G	GS	FG	G	TG	FG	H	AI	GS	FG	H	AI	G		
NORTHWESTERN	<u>A. striatus</u>	-	-	11	-	14	1	25	25	10	-	8	6	-	-	2	9	5.64
	<u>A. cooperii</u>	19	3	1	5	6	15	5	2	2	-	11	11	-	-	21	12	7.28
EASTERN	<u>A. striatus</u>	-	-	5	1	2	1	17	28	8	1	27	5	2	-	4	12	5.15
	<u>A. cooperii</u>	27	-	1	1	1	9	2	4	3	-	13	27	1	2	10	13	5.42
	<u>A. gentilis</u>	35	-	-	-	-	14	3	9	2	-	11	13	-	-	14	8	5.00

<sup>a/</sup> 1, ground-shrub; 2, shrub-canopy; 3, canopy; 4, aerial; 5, generalist.

<sup>b/</sup> GS, ground searcher; FG, foliage gleaner; TG, trunk gleaner; H, hawk; AI, aerial insectivore; G, generalist.

Table 13. Standardized niche width [ $B_s = (B-1)(n-1)$ ] with respect to prey size, prey taxon, and foraging zone and prey guild in northwestern and eastern Oregon.

Location	Species	Niche Dimension		
		Size	Taxon	Zone-Guild
Northwestern	<u>A. striatus</u>	0.21	0.33	0.33
	<u>A. cooperii</u>	0.34	0.36	0.45
Eastern	<u>A. striatus</u>	0.35	0.21	0.30
	<u>A. cooperii</u>	0.29	0.29	0.32
	<u>A. gentilis</u>	0.32	0.45	0.29

all dimensions was nearly equal between study areas and among species.

When calculating the MacArthur and Levins (1967) dietary overlap measure ( $\alpha$ 's) the usual procedure is to determine the use of a particular resource category by each species relative to its use of the other categories; that is, to proportionalize the use (i.e.,  $\sum U_{iH} = \sum U_{jH} = 1.0$ ) of each dimension (MacArthur and Levins 1967). However, proportionalizing equalizes the area under the utilization curves of each competitor, an undesirable characteristic if two consumers have different capture rates. Since the smaller Accipiter had greater capture rates (Fig. 13), I calculated  $\alpha$  values from the actual number of prey in each size class ( $\alpha_n$ ) captured in both subregions during 112 days (see above) ( $\alpha$  values from the proportionalized utilization ( $\alpha_u$ ) are presented for comparison) (Table 14). When compared to  $\alpha_u$ , the  $\alpha_n$ 's demonstrated a greater asymmetry of overlap between species pairs; the Accipiter with the higher capture rate had greater overlap on its neighbors' utilization function.

Comparing  $\alpha_n$ 's among all species combinations showed that overlap was consistently lowest in prey size dimension (6 cases) and lowest in the taxon and zone-guild dimension in one case each. Interestingly the lowest value ( $\alpha_{cg}$ ) occurred in the taxon dimension; A. cooperii and A. gentilis captured birds and mammals of about the same size (Fig. 11b), but tended to take different taxa (Fig. 16). Thus we see a possible case of niche complementarity (Schoener 1974); food resources of A. gentilis were less abundant, requiring them to forage as prey size generalists. This strategy resulted in greater overlap with A. cooperii in the size dimension and requires, at least theoretically, the partitioning of another dimension - in this case prey taxon.

Overlap values ( $\alpha$ 's) for prey size, prey taxon, and prey zone and guild can be combined to estimate the overall differences in prey utilization among coexisting Accipiter. If the proportions of different food sizes taken were the same in all foraging heights or in

Table 14. Niche overlap ( $\alpha$ ) with respect to prey size, prey taxon, and foraging zone and prey guild in northwestern and eastern Oregon.

Location	Interaction	Niche Dimension					
		Size		Taxon		Zone-Guild	
		$\alpha_u$	$\alpha_n$	$\alpha_u$	$\alpha_n$	$\alpha_u$	$\alpha_n$
Northwestern	$\alpha_{sc}$	0.14	0.04	0.31	0.07	0.18	0.07
	$\alpha_{cs}$	0.21	0.96	0.33	1.37	0.44	1.27
Eastern	$\alpha_{sc}$	0.37	0.23	0.33	0.24	0.16	0.22
	$\alpha_{cs}$	0.32	0.56	0.43	0.58	0.22	0.65
	$\alpha_{cg}$	0.81	0.86	0.54	0.46	1.33	1.01
	$\alpha_{gc}$	0.87	0.82	0.79	0.93	0.74	0.83
	$\alpha_{sg}$	0.16	0.11	0.19	0.12	0.28	0.24
	$\alpha_{gs}$	0.15	0.25	0.36	0.57	0.22	0.60

all prey taxa then the resource dimensions are independent and the total overlap in all dimensions is a product of the  $\alpha$ 's in each dimension (May 1975, Cody 1974). However, overlap in prey type of Accipiter correlated strongly with overlap in prey taxon and both were correlated to the zone-guild dimension (Fig. 20) indicating the dimensions were interdependent. When interdependent, the arithmetic mean ("summation  $\alpha$ ," Cody 1974) of the  $\alpha$ 's in each dimension is an estimate of the total multidimensional overlap. The combined unproportionalized  $\alpha_n$ 's (Table 15) have a greater range of values (0.06-1.20) than the values from the proportionalized utilization ( $\alpha_u$ 's) (0.21-0.89), demonstrating that overlap measures from proportionalized utilization may greatly underestimate  $\alpha$ 's.

One problem of "natural experiments" such as my attempt at elucidating the ecological relationships of different combinations of competitors in different areas is attributing differences in resource use to competition or to differences in the resources (Connell 1975). Some aspects of the food of A. striatus and A. cooperii in northwestern and eastern Oregon warrant discussion. The avifauna of eastern Oregon forests had about one half the density and species as that in northwestern Oregon forests. In addition, the size-frequency distribution of birds in eastern Oregon was shifted somewhat toward larger birds (compare Figures 6 and 7). However, eastern Oregon had a greater density and number of species of small mammals. Utilization of a larger mean size of birds by A. striatus and A. cooperii in eastern Oregon to a large degree reflected the differences in size frequency of birds there. However, increased utilization of mammals (53.1%) by A. cooperii in eastern Oregon was intriguing. Other studies of the food of A. cooperii in North America indicated that this hawk captured an equivalent percentage of mammals as in northwestern Oregon (Storer 1966, 17%; Meng 1959, 18%; Duncan 1966, 33%; Hamerstrom and Hamerstrom 1951, 15%). Further, while A. cooperii in eastern Oregon captured larger birds but smaller mammals and in different proportions than A. cooperii in northwestern Oregon, mean prey size and coefficient of variation around the mean in both areas

Figure 20. Comparisons of dietary overlap in 3 dimensions of food niche ( $\alpha_{\text{taxon}}$  to  $\alpha_{\text{zone-guild}}$  to  $\alpha_{\text{size}}$ ; and  $\alpha_{\text{zone-guild}}$  to  $\alpha_{\text{taxon}}$ ). The near linear relationships indicate that these are not independent dimensions of the niche.  
■ - northwestern, ● - eastern Oregon.

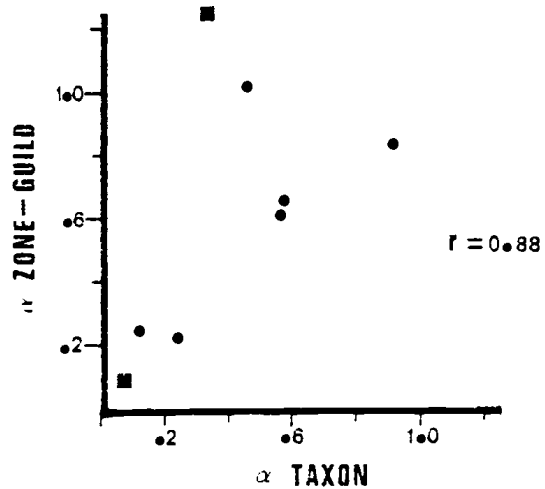
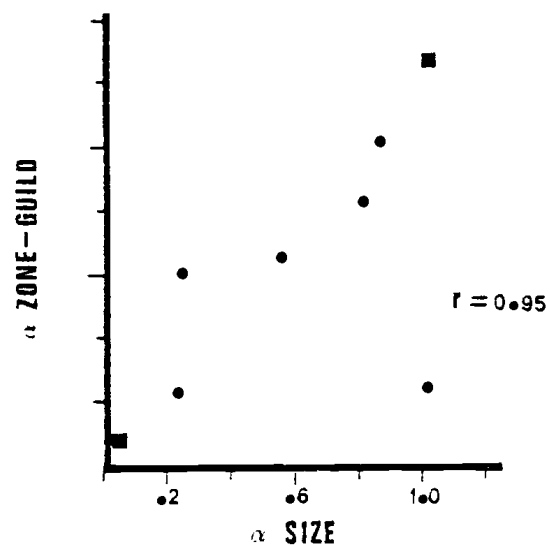
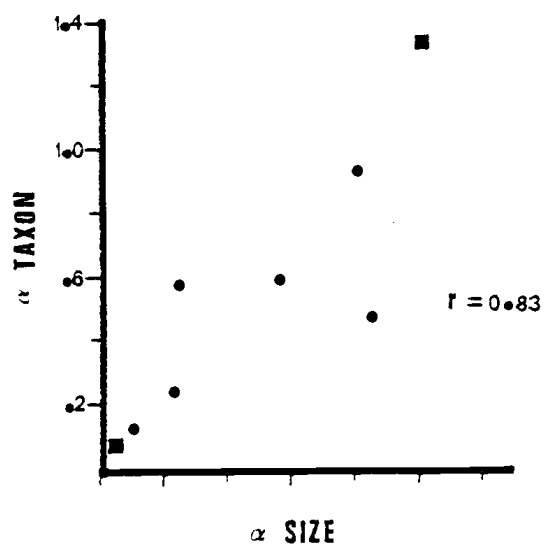


Table 15. Total  $\alpha$ 's ( $\alpha$  summation) for all dimensions of the food niche in northwestern and eastern Oregon.

Location	Interaction	Proportional $\alpha$ 's	Unproportional $\alpha$ 's
Northwestern	$\alpha_{sc}$	0.21	0.06
	$\alpha_{cs}$	0.33	1.20
Eastern	$\alpha_{sc}$	0.29	0.23
	$\alpha_{cs}$	0.32	0.60
	$\alpha_{cg}$	0.89	0.78
	$\alpha_{gc}$	0.80	0.86
	$\alpha_{sg}$	0.21	0.16
	$\alpha_{gs}$	0.24	0.47



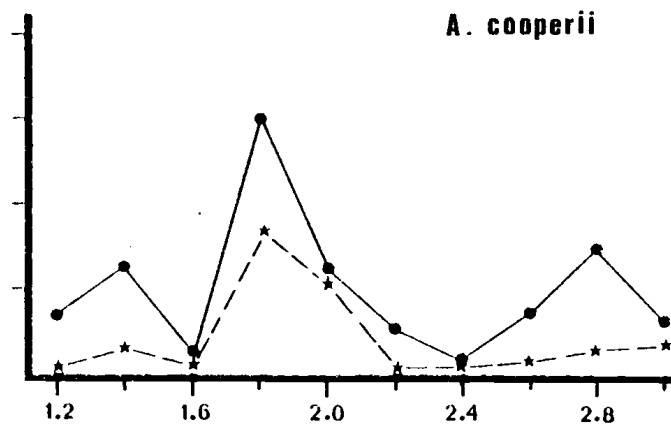
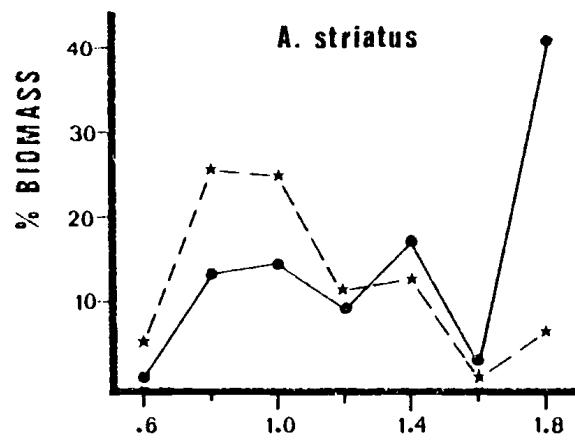
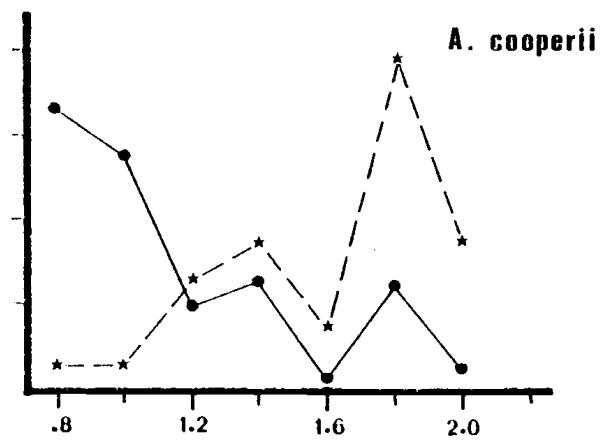
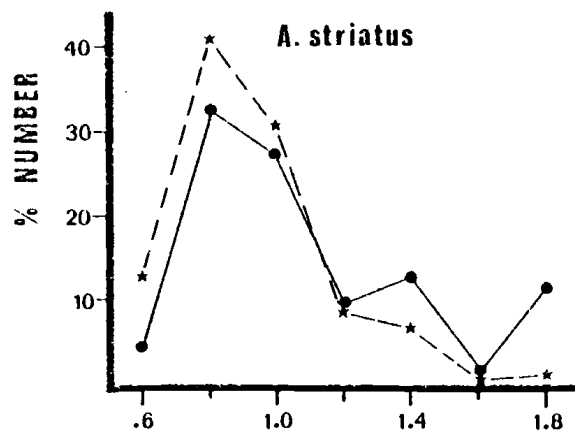
were nearly identical (Table 7). Thus, the location and shape of the utilization curves on the resource spectrum of A. cooperii in both study areas were nearly identical, despite the different resource levels and compositions.

Finally, niche breadth for Accipiter in both study areas contradicts an important prediction of most optimal foraging models: as food resources become less abundant, whatever the cause, consumers should include a larger variety of prey in their diet, i.e., broaden their food niche (for a review of this topic see Pyke et al. [1977]). Reduced availability of prey and the expected prey depressing effect of the combined harvesting of the three species should have, accordingly, resulted in greater niche width in eastern than in northwestern Oregon. However, the causal relationship of the niche shifts of Accipiter in Oregon were confounded by the differences in the resources and competitive regimes in the subregions.

#### Accipiter Foraging Strategies

Due to the location of Accipiter utilization curves on the log-normally distributed prey resource, foraging of each species is subject to different time and energy constraints and each, therefore, should employ a different strategy. Principal among these were the opposing specialist (pursuers) and generalist (searchers) strategies in the prey size dimension. Additionally, smaller Accipiter (A. striatus) foraged as prey number maximizers (i.e., captured prey from size classes within their prey size range in the same proportion with which they occurred) whereas larger species (A. cooperii) foraged as prey biomass maximizers (i.e., captured larger prey items at a frequency higher than they occurred in the environment). To demonstrate this, I plotted the percent number of birds available within the prey size range of both A. striatus and A. cooperii and the percent number in the diet of each hawk. Next the fit of each curve was compared to two similarly derived curves of biomass available and biomass taken (Fig. 21) (for a similar treatment in fish see Griffiths

Figure 21. Percent availability and utilization curves of Accipiter in northwestern Oregon. (Upper) percent number in diet vs. percent number of prey available for A. striatus and A. cooperii. (Lower) percent biomass in diet vs. percent of biomass of prey available for A. striatus and A. cooperii. Note that A. striatus utilization best fits the numbers curve while A. cooperii best fits the biomass curve. Availability -----; utilization -----.



LOG PREY WEIGHT

1975). (Since Accipiter diets consisted of few mammals in northwestern Oregon only data from this subregion were plotted.) For A. striatus the best fit occurred in the "numbers model," and for A. cooperii the best fit occurred in the "biomass model."

An examination of the different foraging strategies elucidated some of the apparently adaptive correlates that accompany the apportionment of the various duties among the sexes associated with nesting in Accipiter. During the entire nesting period males were the principal foragers of nesting pairs (see also Tinbergen 1942; Snyder and Wiley 1976; Reynolds 1972). Within Falconiformes size dimorphism reaches an extreme in Accipiter; males are as much as 50% smaller than females (Storer 1966). Within the genus size differences between males and females increases from a minimum in A. gentilis to a maximum in A. striatus (Storer 1966). Paralleling the size difference is an increased inability of males to sufficiently cover the eggs and males of the smaller species contribute little to incubation (Hald-Mortensen 1974). Females assumed all or nearly all the incubation and brooding but began foraging late in the nestling period (see also Snyder and Wiley 1976; Tinbergen 1942; Schnell 1958).

Numerous authors (Snyder and Wiley 1976; Amadon 1975; Balgooyen 1976; Reynolds 1972; Hald-Mortensen 1974; Brown and Amadon 1968; Cade 1960; Earhart and Johnson 1970; Mosher and Matray 1974; Storer 1966) considered the adaptive correlates of size dimorphism in birds of prey and several hypotheses have resulted. Most of these associate larger female size with an adaptive behavioral dominance over males, better brooding capabilities, and nest defense. However, several (Balgooyen 1976; Mosher and Matray 1974; Reynolds 1972) view reduced male size to be adaptive in that it increases foraging efficiency. Reynolds (1972) hypothesized that smaller hawks have a reduced energetic cost of transport over larger individuals; relegating foraging to smaller males would result in an overall energy savings (greater kcals delivered to the nest). Balgooyen (1976) elaborated on this theme in the American Kestrel (Falco sparverius) and Mosher and Matray (1974) offer experimental evidence for this view. Reynolds (1972), in

addition to the energy savings, attributed reversed size dimorphism and the differential roles of the sexes to an increased foraging efficiency of smaller males arising from the log-normal distribution of prey size and abundance; since smaller prey are more abundant, smaller males have a high rate of encounter with optimally-sized prey and, ultimately, a more predictable prey delivery rate.

As noted earlier, the utilization functions of smaller Accipiter were located to the left on the prey size axes. Associated with this position was a difference in foraging strategy; the smaller the hawk the greater the time spent pursuing rather than searching for prey. That is, the smaller the hawk the more it foraged as a prey numbers maximizer or a time minimizer. By increasing its capture rate and decreasing its travel time (smaller home range) the small species minimized the time between prey deliveries to the nest. Minimizing time between prey deliveries is especially important when young are small and have low resistance to food deprivation.

On the other hand, for large Accipiter, a shift toward smaller males results in only a minor increase in encounters of optimally-sized prey. Here, male size should decrease to the point where increases in encounter rates of optimal prey are balanced by a concomitant decrease in prey size range - they must remain prey size generalists. That is, in the larger species (i.e., A. gentilis) males should approximate female size. Species intermediate in size (A. cooperii) should display an intermediate degree of sexual size differences.

Energy savings due to the reduced cost of transport in smaller males adds to the adaptiveness of reversed size dimorphism in Accipiter, but does not account for the decreasing degree of dimorphism as Accipiter size increases (Storer 1966). By this hypothesis alone, large Accipiter, since they forage over larger home ranges and spend more time searching than the smaller species, should show the greater degree of dimorphism.

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## APPENDIX

Appendix 1. Weights, activity zones, and foraging guilds of birds, mammals, and reptiles and densities of birds and mammals in the conifer forests of northwestern and eastern Oregon.

Species	Weight (g)	Source	Zone <sup>1</sup>	Guild <sup>2</sup>	Density (per 40 ha)				
					Northwestern Oregon		Eastern Oregon		
					Mannan 1977	Anderson 1970	Total	This study	
<hr/>									
FAMILY Anatidae									
Mallard <u>Anas platyrhynchos</u> combined	1150.0	Kortright 1942	1	1	-	-	-	-	
FAMILY Falconidae									
Kestrel <u>Falco sparverius</u>	144.0	Craighead & Craighead 1956	3	4	-	-	-	-	
FAMILY Accipitridae									
Cooper's Hawk <u>Accipiter cooperii</u> combined	368.0	Storer 1955	3	4	-	-	-	-	
male	295.0	Storer 1955	3	4	-	-	-	-	
female	441.0	Storer 1955	3	4	-	-	-	-	
Sharp-shinned Hawk <u>A. striatus</u> combined	135.0	Storer 1955	3	4	-	-	-	-	
male	99.0	Storer 1955	3	4	-	-	-	-	
female	171.0	Storer 1955	3	4	-	-	-	-	
Goshawk <u>A. gentilis</u> combined	977.5	Storer 1955	3	4	-	-	-	-	
male	818.0	Storer 1955	3	4	-	-	-	-	
female	1137.0	Storer 1955	3	4	-	-	-	-	
FAMILY Tetraonidae									
Blue Grouse <u>Dendragapus obscurus</u>	1050.0	Blackford 1958	5	1	1	-	1	-	
Ruffed Grouse <u>Bonasa umbellus</u>	619.0	Bump et al. 1947	1	1	-	4	4	-	
unidentified grouse	834.5		5	1	-	-	-	-	
FAMILY Phasianidae									
California Quail <u>Lophortyx californicus</u>	139.0	Brush 1965	1	1	-	-	-	-	
Mountain Quail <u>Oreortyx pictus</u>	243.9	Kilgore 1961	1	1	-	4	4	-	
Ring-necked Pheasant <u>Phasianus colchicus</u>	1246.0	Robertson 1958	1	1	-	-	-	-	
FAMILY Charadriidae									
Killdeer <u>Charadrius vociferus</u>	82.4	Hartman 1955	1	1	-	-	-	-	
FAMILY Columbidae									
Band-tailed Pigeon <u>Columba fasciata</u>	406.0	Kilgore 1961	5	3	2	-	2	-	

## Appendix 1. Continued.

Species	Weight (g)	Source	Zone <sup>1</sup>	Guild <sup>2</sup>	Density (per 40 ha)			
					Northwestern Oregon		Eastern Oregon	
					Mannan 1977	Anderson 1970	Total	This study
Rock Dove <u>Columba livia</u>	376.7	O.S.U. Museum	5	1	-	-	-	-
Mourning Dove <u>Zenaidura macroura</u>	120.0	Hartman 1955	1	1	-	-	-	-
FAMILY Strigidae								
Screech Owl <u>Otus asio</u>	172.0	Craighead & Craighead 1956	3	4	-	-	-	-
Pygmy Owl <u>Glaucidium gnoma</u>	67.4	Earhart & Johnson 1970	3	4	2	-	2	-
Great Horned Owl <u>Bubo virginianus</u>	1505.0	Craighead & Craighead 1956	3	4	-	-	-	-
Long-eared Owl <u>Asio otus</u>	245.0	Craighead & Craighead 1956	3	4	-	-	-	-
Saw-whet Owl <u>Aegolius acadicus</u>	83.0	Earhart & Johnson 1970	3	4	-	-	-	-
FAMILY Caprimulgidae								
Common Nighthawk <u>Chordeiles minor</u>	57.8	Norris & Johnson 1958	5	5	-	-	-	1
FAMILY Apodidae								
Vaux's Swift <u>Chaetura vauxi</u>	15.4	Collins 1971	4	5	-	-	-	1
FAMILY Trochilidae								
Rufous Hummingbird <u>Selasphorus rufus</u>	3.8	Lasiewski 1963	2	3	7	6	7	1
FAMILY Picidae								
Common Flicker <u>Colaptes auratus</u>	148.8	Kilgore 1961	5	1	3	1	2	2
Pileated Woodpecker <u>Dryocopus pileatus</u>	282.0	O.S.U. Museum	3	2	1	1	1	-
Lewis' Woodpecker <u>Asyndesmus lewis</u>	106.0	Bock 1970	3	4	-	-	-	-
Yellow-bellied Sapsucker								
<u>Sphyrapicus varius</u>	45.9	Kilgore 1961	3	2	3	-	3	4
Williamson's Sapsucker								
<u>Sphyrapicus thyroideus</u>	50.0	Bock 1970	3	2	-	-	-	-
Hairy Woodpecker <u>Dendrocopos villosus</u>	68.0	Hartman 1955	3	2	10	12	11	13
Downy Woodpecker <u>D. pubescens</u>	28.2	Baldwin & Kendeigh 1938	3	2	-	11	11	-
White-headed Woodpecker								
<u>D. albolarvatus</u>	58.0	Bock & Lynch 1970	3	2	-	-	-	-
<u>Dendrocopos</u> spp.	48.3		3	2	-	-	-	-
Black-backed Three-toed Woodpecker								
<u>Picoides arcticus</u>	69.3	Grinnell et al. 1930	3	2	-	-	-	1
FAMILY Tyrannidae								
Western Kingbird <u>Tyrannus verticalis</u>	42.0	Grinnell et al. 1930	3	4	-	-	-	-
Hammond's flycatcher								
<u>Empidonax hammondi</u>	9.5	Kilgore 1961	3	4	-	-	-	-

## Appendix 1. Continued.

Species	Weight (g)	Source	Zone <sup>1</sup>	Guild <sup>2</sup>	Density (per 40 ha)			
					Northwestern Oregon		Eastern Oregon	
					Mannan 1977	Anderson 1970	Total	This study
Dusky Flycatcher <u>E. oberholseri</u>	10.1	Collins & Bradley 1971	2	4	-	-	-	-
Western Flycatcher <u>E. difficilis</u>	10.0	Collins & Bradley 1971	3	4	-	-	-	-
Empidonax spp.	9.8		3	4	84	33	59	10
Western Wood Pewee								
Contopus sordidulus	12.8	Collins & Bradley 1971	3	4	2	20	11	1
Olive-sided Flycatcher								
Nuttallornis borealis	34.5	Kilgore 1961	3	4	-	2	2	-
FAMILY Hirundinidae								
Violet-green Swallow								
Tachycineta thalassina	15.7	R. Stewart pers. com.	4	5	-	-	-	-
FAMILY Corvidae								
Gray Jay Perisoreus canadensis	74.6	Salt 1957	5	6	4	2	3	2
Steller's Jay Cyanocitta stelleri	106.6	Kilgore 1961	2	6	15	18	17	2
Scrub Jay Aphelocoma coerulescens	72.3	Hartman 1955	2	6	-	6	6	-
unidentified jay	89.4		2	6	-	-	-	-
Black-billed Magpie Pica nuttalli	173.5	Linsdale 1937	5	6	-	-	-	-
Common Raven Corvus corax	1410.0	Craighead & Craighead 1956	5	6	2	-	2	-
Common Crow Corvus brachyrhynchos	479.0	Baldwin & Kendeigh 1938	5	6	1	-	1	-
Clark's Nutcracker								
Nucifraga columbiana	133.8	Grinnell et al. 1930	3	3	-	-	-	1
FAMILY Paridae								
Black-capped Chickadee								
Parus atricapillus	11.2	Baldwin & Kendeigh 1938	2	3	-	7	7	-
Mountain Chickadee P. gambeli	11.4	Behle 1956	3	3	-	-	-	14
Chestnut-backed Chickadee P. rufescens			3	3	33	79	56	-
Parus spp.	10.6		3	3	-	-	-	-
Common Bushtit Psaltriparus minimus	5.9	Collins & Bradley 1971	2	3	-	1	1	-
FAMILY Sittidae								
White-breasted Nuthatch								
Sitta carolinensis	22.0	Baldwin & Kendeigh 1938	3	2	-	5	5	4
Red-breasted Nuthatch S. canadensis	10.3	Kilgore 1961	3	2	8	42	25	7
FAMILY Certhiidae								
Brown Creeper Certhia familiaris	8.4	Harrman 1955	3	2	20	44	32	4

Appendix 1. Continued.

Species	Weight (g)	Source	Zone <sup>1</sup>	Guild <sup>2</sup>	Density (per 40 ha)			
					Northwestern Oregon		Eastern Oregon	
					Mannan 1977	Anderson 1970	Total	This study
FAMILY Troglodytidae								
House Wren <u>Troglodytes aedon</u>	10.5	Baldwin & Kendeigh 1938	2	3	-	5	5	-
Winter Wren <u>T. troglodytes</u>	8.9	Kilgore 1961	1	6	62	24	43	-
Bewick's Wren <u>Thryomanes bewickii</u>	9.3	Collins & Bradley 1971	2	3	-	4	4	-
FAMILY Turdidae								
Robin <u>Turdus migratorius</u>	81.2	Kilgore 1961	5	6	5	2	4	29
Varied Thrush <u>Ixoreus naevius</u>	79.3	R. Stewart pers. com.	5	6	13	-	13	-
Hermit Thrush <u>Hylocichla guttata</u>	26.3	Kilgore 1961	1	6	16	10	13	5
Swainson's Thrush <u>H. ustulata</u>	25.0	Kilgore 1961	1	6	12	-	12	-
<u>Hylocichla</u> spp.	25.6	Kilgore 1961	1	6	-	-	-	-
Western Bluebird <u>Sialia mexicana</u>	27.9	R. Stewart pers. com.	5	4	-	-	-	-
Townsend's Solitaire <u>Myadestes townsendi</u>	31.7	Kilgore 1961	5	6	-	-	-	1
FAMILY Sylviidae								
Golden-crowned Kinglet <u>Regulus satrapa</u>	5.6	Kilgore 1961	3	3	39	12	26	9
Ruby-crowned Kinglet <u>R. calendula</u>	5.9	Collins & Bradley 1971	3	3	-	-	-	1
<u>Regulus</u> spp.	5.7		3	3	-	-	-	-
FAMILY Bombycillidae								
Cedar Waxwing <u>Bombycilla cedrorum</u>	33.5	Hartman 1955	5	6	-	-	-	-
FAMILY Sturnidae								
Starling <u>Sturnus vulgaris</u>	74.5	Baldwin & Kendeigh 1938	5	1	-	-	-	-
FAMILY Vireonidae								
Hutton's Vireo <u>Vireo huttoni</u>	11.2	Root 1967	3	3	1	10	6	-
Solitary Vireo <u>V. solitarius</u>	14.4	Collins & Bradley 1971	3	3	-	2	2	-
Warbling Vireo <u>V. gilvus</u>	11.9	Collins & Bradley 1971	3	3	3	1	2	6
FAMILY Parulidae								
Orange-crowned Warbler <u>Vermivora celata</u>	8.2	Collins & Bradley 1971	2	3	-	6	6	-
Yellow Warbler <u>Dendroica petechia</u>	8.9	Collins & Bradley 1971	2	3	-	4	4	7
Audubon's Warbler <u>D. coronata</u>	10.4	Collins & Bradley 1971	3	3	-	-	-	-
Black-throated Gray Warbler <u>D. nigrescens</u>	7.9	Collins & Bradley 1971	3	3	2	-	2	-



Appendix 1. Continued.

Species	Weight (g)	Source	Zone <sup>1</sup>	Guild <sup>2</sup>	Density (per 40 ha)			
					Northwestern Oregon			Eastern Oregon
					Mannan 1977	Anderson 1970	Total	This study
Townsend's Warbler <u>D. townsendi</u>	9.1	Collins & Bradley 1971	3	3	-	2	2	1
Hermit Warbler <u>D. occidentalis</u>	8.3	Collins & Bradley 1971	3	3	73	17	45	-
MacGillivray's Warbler <u>Gporonis tolmiei</u>	10.3	Collins & Bradley 1971	1	3	-	13	13	-
Wilson's Warbler <u>Wilsonia pusilla</u>	7.0	Collins & Bradley 1971	2	3	51	15	33	-
unidentified warbler	8.8		2	3	-	-	-	-
FAMILY Icteridae								
Western Meadowlark <u>Sturnella neglecta</u>	89.0	Lanyon 1956	1	1	-	-	-	-
Red-winged Blackbird <u>Agelaius phoeniceus</u>	61.4	Baldwin & Kendeigh 1938	1	1	-	-	-	-
Brewer's Blackbird <u>Euphagus cyanocephalus</u>	64.7	R. Stewart pers. com.	5	1	-	-	-	-
Brown-headed Cowbird <u>Molothrus ater</u>	38.7	Hartman 1955	2	1	-	3	3	9
FAMILY Thrupidae								
Western Tanager <u>Piranga ludoviciana</u>	26.9	Collins & Bradley 1971	3	3	21	35	28	4
FAMILY Fringillidae								
Black-headed Grosbeak <u>Pheucticus melanocephalus</u>	42.4	Collins & Bradley 1971	2	3	9	4	7	-
Lazuli Bunting <u>Passerina amoena</u>	13.8	Collins & Bradley 1971	2	3	-	2	2	-
Evening Grosbeak <u>Hesperiphona vespertina</u>	64.2	Kilgore 1961	3	3	55	17	36	7
Purple Finch <u>Carpodacus purpureus</u>	23.8	Kilgore 1961	3	3	-	2	2	-
Cassin's Finch <u>C. cassinii</u>	28.0	Grinnell et al. 1930	3	3	-	-	-	11
House Finch <u>C. mexicanus</u>	21.0	R. Stewart pers. com.	3	3	-	3	3	-
<u>Carpodacus</u> spp.	22.4		3	3				
Pine Siskin <u>Spinus pinus</u>	13.0	Collins & Bradley 1971	5	3	8	1	5	24
American Goldfinch <u>S. tristis</u>	11.3	Baldwin & Kendeigh 1938	2	3	-	2	2	14
Red Crossbill <u>Loxia curvirostra</u>	29.4	Kendeigh 1969	3	3	5	6	6	14
Rufous-sided Towhee <u>Pipilo erythrophthalmus</u>	39.0	Kilgore 1961	2	1	3	6	5	-
Dark-eyed Junco <u>Junco hyemalis</u>	17.6	Kilgore 1961	5	1	25	40	33	49
Chipping Sparrow <u>Spizella passerina</u>	15.0	Hartman 1955	5	1	-	3	3	16
White-crowned Sparrow <u>Zonotrichia leucophrys</u>	24.1	Collins & Bradley 1971	1	1	14	1	8	-

Appendix 1. Continued.

Species	Weight (g)	Source	Zone <sup>1</sup>	Guild <sup>2</sup>	Density (per 40 ha)			
					Northwestern Oregon			Eastern Oregon
					Mannan 1977	Anderson 1970	Total	This study
Golden-crowned Sparrow								
<u>Z. atricapilla</u>	31.0	Hartman 1955	1	1	-	-	-	-
Fox Sparrow <u>Passerella iliaca</u>	32.3	R. Stewart pers. com.	2	6	-	-	-	-
Song Sparrow <u>Melospiza melodia</u>	21.0	Hartman 1955	2	6	2	3	3	-
unidentified sparrow	20.0		2	1	-	-	-	-
MAMMALS								
FAMILY Talpidae								
shrew-mole <u>Neurotrichus gibbsii</u>	10.0	C. Maser pers. com.	1	1	-	-	-	-
broad-handed mole <u>Scapanus latimanus</u>	79.5	O.S.U. Museum	1	1	-	-	-	-
coast mole <u>S. orarius</u>	53.9	O.S.U. Museum	1	1	-	-	-	-
<u>Scapanus</u> spp.	66.7		1	1	-	-	-	-
FAMILY Leporidae								
brush rabbit <u>Sylvilagus bachmani</u>	644.0	O.S.U. Museum	1	1	-	-	-	-
mountain cottontail <u>S. nuttallii</u>	713.0	O.S.U. Museum	1	1	-	-	-	-
<u>Sylvilagus</u> spp.	678.5	O.S.U. Museum	1	1	-	-	-	-
snowshoe hare <u>Lepus americanus</u>	1118.0	O.S.U. Museum	1	1	-	-	-	-
<u>Lepus</u> spp.	1118.0	O.S.U. Museum	1	1	-	-	-	-
FAMILY Sciuridae								
Townsend's chipmunk								
<u>Eutamias townsendii</u>	89.3	O.S.U. Museum	5	3	-	-	-	-
least chipmunk <u>E. minimus</u>	36.8	O.S.U. Museum	5	3	-	-	-	-
yellow-pine chipmunk <u>E. amoenus</u>	49.3	O.S.U. Museum	5	3	-	-	-	14
<u>Eutamias</u> spp.	67.5		5	3	-	-	-	-
northern flying squirrel								
<u>Glaucomys sabrinus</u>	167.0	O.S.U. Museum	3	3	-	-	-	-
red squirrel <u>Tamiasciurus hudsonicus</u>	241.4	O.S.U. Museum	5	3	-	-	-	-
chickaree <u>T. douglasii</u>	201.4	O.S.U. Museum	5	3	-	-	-	1
western gray squirrel <u>Sciurus griseus</u>	759.0	O.S.U. Museum	5	3	-	-	-	-
golden-mantled ground squirrel								
<u>Spermophilus lateralis</u>	166.1	O.S.U. Museum	1	1	-	-	-	11
Townsend's ground squirrel								
<u>S. townsendii</u>	132.0	O.S.U. Museum	1	1	-	-	-	-

Appendix 1. Continued.

Species	Weight (g)	Source	Zone <sup>1</sup>	Guild <sup>2</sup>	Density (per 40 ha)			
					Northwestern Oregon		Eastern Oregon	
					Mannan 1977	Anderson 1970	Total	
Belding's ground squirrel <u>S. beldingi</u>	268.0	O.S.U. Museum	1	1	-	-	-	-
FAMILY Heteromyidae								
Ord's kangaroo rat <u>Dipodomys ordii</u>	55.3	O.S.U. Museum	1	1	-	-	-	-
pocket mouse <u>Perognathus</u> spp.	25.0	O.S.U. Museum	1	1	-	-	-	-
FAMILY Cricetidae								
bushy-tailed wood rat <u>Neotoma cinerea</u>	289.2	O.S.U. Museum	1	1	-	-	-	-
dusky-footed wood rat <u>N. fuscipes</u>	224.1	O.S.U. Museum	1	1	-	-	-	-
<u>Neotoma</u> sp.	256.6		1	1	-	-	-	-
deer mouse <u>Peromyscus maniculatus</u>	20.7	O.S.U. Museum	1	1	-	-	-	-
vole <u>Microtus</u> spp.	25.0	O.S.U. Museum	1	1	-	-	-	-
FAMILY Zapodidae								
Pacific jumping mouse <u>Zapus trinotatus</u>	23.7	O.S.U. Museum	1	1	-	-	-	-
FAMILY Mustelidae								
long tailed weasel <u>Mustela frenata</u>	284.1	O.S.U. Museum	1	1	-	-	-	-
REPTILES								
FAMILY Iguanidae								
western fence lizard <u>Sceloporus occidentalis</u>	10.0	R. Nussbaum pers. com.	1	3	-	-	-	-
FAMILY Anguidae								
alligator lizard <u>Gerrhonotus</u> spp.	13.0	R. Nussbaum pers. com.	1	1	-	-	-	-
FAMILY Colubridae								
garter snake <u>Thamnophis</u> spp.	50.0	R. Nussbaum pers. com.	1	1	-	-	-	-

<sup>1</sup> 1) Ground-Lower Shrub; 2) Upper Shrub Lower Canopy; 3) Upper Canopy; 4) Aerial; 5) Generalists (Ground through Upper Canopy)

<sup>2</sup> 1) Ground Searchers; 2) Trunk Gleaners; 3) Foliage Gleaners; 4) Hawks; 5) Aerial Insect; 6) Generalists

Appendix 2. Dietary composition of Accipiter in northwestern and eastern Oregon.

Species	Northwestern				Eastern					
	A. striatus		A. cooperii		A. striatus		A. cooperii		A. gentilis	
	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*
BIRDS										
Mallard (Female)	-	-	-	-	-	-	1	-	2	-
Kestrel	-	-	1	-	-	-	-	-	-	-
Cooper's Hawk	-	-	-	-	-	-	-	-	1	-
Blue Grouse	-	-	-	-	-	-	1	-	5	-
Ruffed Grouse	-	-	-	1	-	-	1	-	2	-
unidentified grouse	-	-	1	-	-	-	-	-	1	-
California Quail	-	-	1	-	-	-	-	-	-	-
Mountain Quail	-	-	-	-	-	-	-	-	9	1
Ring-necked Pheasant	-	-	2	-	-	-	-	-	-	-
Killdeer	-	-	1	-	-	-	-	-	-	-
Rock Dove	-	-	1	-	-	-	-	-	-	-
Mourning Dove	-	-	1	-	-	-	-	-	7	-
Screech Owl	-	-	1	1	-	-	-	-	1	-
Great Horned Owl	-	-	-	-	-	-	-	-	1	-
Long-eared Owl	-	-	-	-	-	-	1	-	-	-
Saw-whet Owl	-	-	1	-	-	-	2	-	1	-
Common Nighthawk	-	-	-	-	-	-	2	-	-	-
Rufous Hummingbird	-	1	-	-	-	-	-	-	-	-
Common Flicker	-	-	4	1	1	-	5	1	14	1
Pileated Woodpecker	-	-	-	-	-	-	-	-	1	-
Lewis' Woodpecker	-	-	1	-	-	-	-	-	-	-
Yellow-bellied Sapsucker	-	-	3	-	2	-	-	-	1	-
Williamson's Sapsucker	-	-	2	-	2	-	-	-	1	1
Hairy Woodpecker	-	-	1	-	1	-	-	1	1	-
Downy Woodpecker	-	-	2	1	-	-	1	-	-	-

Appendix 2. Continued.

Species	Northwestern				Eastern					
	A. striatus		A. cooperii		A. striatus		A. cooperii		A. gentilis	
	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*
White-headed Woodpecker	-	-	-	-	1	-	-	-	-	-
Dendrocopos sp.	-	-	-	-	6	-	-	-	1	-
Western Kingbird	-	-	-	-	1	-	-	-	-	-
Western Flycatcher	-	-	-	-	1	-	-	-	-	-
Empidonax sp.	14	2	-	-	6	-	-	-	-	-
Western Wood Pewee	1	-	-	-	1	-	-	-	-	-
Olive-sided Flycatcher	1	1	1	-	-	-	-	-	-	-
Violet-green Swallow	-	-	-	-	1	-	-	-	-	-
Gray Jay	-	-	-	-	-	-	1	-	3	2
Steller's Jay	-	-	10	15	1	-	8	1	17	12
Scrub Jay	-	-	3	-	-	-	-	-	-	-
unidentified jay	-	1	8	4	-	-	-	-	1	-
Black-billed Magpie	-	-	-	-	-	-	-	-	1	-
Black-capped Chickadee	1	-	-	1	-	-	-	-	-	-
Parus sp.	12	4	-	-	8	-	-	-	-	-
Common Bushtit	9	-	-	-	-	-	-	-	-	-
Red-breasted Nuthatch	17	8	3	1	4	1	-	-	-	-
Brown Creeper	17	7	1	-	3	-	-	-	-	-
Winter Wren	6	1	-	-	-	-	-	-	-	-
Bewick's Wren	-	1	-	-	1	-	-	-	-	-
Robin	1	-	32	23	3	-	5	2	15	5
Varied Thrush	1	-	1	-	2	-	3	-	3	1
Hermit Thrush	2	-	-	-	-	-	-	-	-	-
Swainson's Thrush	5	-	1	-	-	-	-	-	-	-
Hylocichla sp.	1	-	1	1	6	-	1	-	-	-
Western Bluebird	-	-	-	-	2	-	1	-	-	-
Townsend's Solitaire	1	-	-	-	-	-	-	-	-	-

Appendix 2. Continued.

Species	Northwestern				Eastern					
	A. striatus		A. cooperii		A. striatus		A. cooperii		A. gentilis	
	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*
Golden-crowned Kinglet	6	10	-	-	1	-	-	-	-	-
Regulus sp.	-	-	-	-	3	-	-	-	-	-
Cedar Waxwing	-	-	1	3	-	-	-	-	-	-
Starling	-	-	4	-	-	-	-	-	-	-
Orange-crowned Warbler	1	-	-	-	1	-	-	-	-	-
Yellow Warbler	1	-	-	-	-	-	-	-	-	-
Audubon's Warbler	1	-	-	-	1	1	-	-	-	-
Black-throated Gray Warbler	9	5	1	-	-	-	-	-	-	-
Hermit Warbler	-	-	-	-	1	-	-	-	-	-
MacGillivray's Warbler	3	-	-	-	-	-	-	-	-	-
Wilson's Warbler	10	2	1	-	-	-	-	-	-	-
unidentified warbler	1	1	1	1	-	-	-	1	-	-
Western Meadowlark	-	-	1	-	-	-	-	-	2	-
Red-winged Blackbird	-	-	2	-	-	-	-	-	-	-
Brewer's Blackbird	-	-	-	1	-	-	-	-	-	-
Brown-headed Cowbird	-	-	5	3	-	-	-	-	-	-
Western Tanager	1	-	1	3	9	3	-	3	-	2
Black-headed Grosbeak	-	-	2	-	-	-	-	-	1	-
Purple Finch	-	-	-	-	-	-	1	-	-	-
Carpodacus sp.	-	-	-	-	5	-	-	-	2	-
Pine Siskin	10	1	1	-	4	-	-	-	-	-
American Goldfinch	-	-	-	1	-	-	-	-	-	-
Rufous-sided Towhee	-	-	7	5	1	-	1	-	-	-
Dark-eyed Junco	14	2	10	10	26	1	7	1	2	-
Chipping Sparrow	-	-	-	-	3	-	-	-	-	-
White-crowned Sparrow	-	-	1	-	-	-	-	-	-	-
Fox Sparrow	-	-	-	-	-	-	1	-	-	-

Appendix 2. Continued.

Species	Northwestern				Eastern					
	<u>A. striatus</u>		<u>A. cooperii</u>		<u>A. striatus</u>		<u>A. cooperii</u>		<u>A. gentilis</u>	
	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*
Song Sparrow	1	-	1	1	-	-	-	-	-	-
unidentified sparrow	-	-	1	-	-	-	4	-	3	-
unidentified bird	-	-	9	-	-	-	-	-	-	-
MAMMALS										
shrew-mole	-	-	1	-	-	-	-	-	-	-
coast mole	-	-	2	-	-	-	-	-	-	-
<u>Scapanus</u> sp.	-	-	2	-	-	-	-	-	-	-
brush rabbit	-	-	18	4	-	-	1	-	-	-
mountain cottontail	-	-	-	-	-	-	1	1	2	-
<u>Sylvilagus</u> sp.	-	-	1	-	-	-	-	-	1	-
snowshoe hare	-	-	-	-	-	-	-	-	19	-
<u>Lepus</u> sp.	-	-	-	-	-	-	-	-	5	-
Townsend's chipmunk	-	-	22	-	-	-	-	-	3	-
least chipmunk	-	-	-	-	-	-	-	-	1	-
yellow-pine chipmunk	-	-	-	-	-	-	1	-	-	-
<u>Eutamias</u> sp.	1	1	1	1	1	1	26	1	7	-
northern flying squirrel	1	-	2	-	-	-	1	-	15	-
chickaree	-	-	7	-	2	-	3	-	13	-
western gray squirrel	-	-	-	-	-	-	-	-	4	1
golden-mantled ground squirrel	-	-	-	-	-	-	20	-	17	-
Townsend's ground squirrel	-	-	-	-	-	-	-	-	2	-
Belding's ground squirrel	-	-	-	-	-	-	-	-	4	-
Ord's kangaroo rat	-	-	-	-	-	-	1	-	-	-
pocket mouse	-	-	-	-	-	-	1	-	-	-
bushy-tailed wood rat	-	-	-	-	-	-	-	-	1	-

Appendix 2. Continued.

Species	Northwestern				Eastern					
	<u>A. striatus</u>		<u>A. cooperii</u>		<u>A. striatus</u>		<u>A. cooperii</u>		<u>A. gentilis</u>	
	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*	Ad.	Young*
dusky-footed wood rat	-	-	2	-	-	-	-	-	1	-
<u>Neotoma</u> sp.	-	-	9	-	-	-	3	-	1	-
<u>Microtus</u> sp.	3	-	2	-	-	-	-	-	-	-
Pacific jumping mouse	1	-	1	-	-	-	-	-	-	-
unidentified mammal	-	-	-	-	-	-	3	-	6	-
REPTILES										
western fence lizard	-	-	3	-	-	-	-	-	-	-
alligator lizard	-	-	1	-	-	-	-	-	-	-
garter snake	-	-	1	-	-	-	-	-	-	-

\* Nestling or fledgling.



Appendix 3. Estimates of home range size among species of Accipiter.

Species	Hectares	Explanation	Source
<u>A. nissus</u>	1150	35 pairs/400 km <sup>2</sup>	Kramer 1955 (in van Beusekom 1972)
	1060	18 pairs/190 km <sup>2</sup>	Kramer 1955 (in van Beusekom 1972)
	1130	21.5 pairs/243 km <sup>2</sup>	Tinbergen 1946
	480	9 pairs/43.5 km <sup>2</sup>	Tinbergen 1946
	560	1 pair/560 ha	Tinbergen 1946
	650		Stulchen 1958 (in van Beusekom 1972)
	600-800		Kramer 1943 (in van Beusekom 1972)
	700-1200		Brull 1964 (in van Beusekom 1972)
Mean	835		
<u>A. gentilis</u> <u>gentilis</u>	2500		Kramer 1955 (in van Beusekom 1972)
	2300	14 pairs/450 km <sup>2</sup>	van Beusekom 1972
	3000	1 pair over many years	Brull 1964 (in van Beusekom 1972)
Mean	2600		
<u>A. striatus</u>	458	Estimated from 1.21 km radius of movement	This study
<u>A. cooperii</u>	204		Craighead and Craighead 1956
	3257	3.22 km radius	Brown and Amadon 1968
	230.5	0.81 km radius	Brown and Amadon 1968
	117.5	0.61 km radius	Fitch et al. 1946
	962	3.54 km radius between nests	This study (eastern Oregon)
	2375	5.51 km radius between nests	This study (northeastern Oregon)
Mean	1190		
<u>A. gentilis</u> <u>atricapillus</u>	2462	5.64 km radius between nests	This study (eastern Oregon)