

AN ABSTRACT OF THE THESIS OF

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Title: Habitat Selection by Nesting Swainson's Hawks: A
Hierarchical Approach

Abstract

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The habitat relationships of Swainson's hawks in northern California were studied at several levels of resolution: 1) distribution of hawk populations among three adjacent geographic areas, 2) density of hawk territories among landscapes within a single geographic area, 3) habitats associated with individual nesting territories, and 4) selection of foraging habitats and prey resources by individual hawks. Patterns of habitat selection observed at each level were compared to results obtained at other levels, and to temporal variations in habitat quality.

Individual Swainson's hawks exhibited strong selection for specific habitats wherein prey availability was highest, however these habitats were not found in increased

proportions in Swainson's hawk territories. Similarly, densities of Swainson's hawk territories among different landscapes did not reflect the availability of high-quality habitat; many pairs nested in marginal habitats and exhibited low reproductive success and large areas of apparently suitable habitat were unoccupied. At a larger scale, the distribution of Swainson's hawk populations was markedly dissimilar among three adjacent geographic areas with similar habitat composition.

Lack of concordance among levels of habitat selection by Swainson's hawks was explained by behavioral and environmental factors that constrain optimal habitat selection. I suggest that high temporal variability of habitats in agricultural environments, combined with site tenacity and natal site philopatry by nesting hawks, prevented the density and distribution of the hawk population from closely tracking the available habitat. Reproductive fitness, however, was strongly associated with habitat quality.

Habitat Selection by Nesting Swainson's Hawks:
A Hierarchical Approach

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TABLE OF CONTENTS

INTRODUCTION.....	1
STUDY AREA.....	8
METHODS.....	11
Validation of pellet analysis.....	21
RESULTS.....	25
Population size and structure.....	25
Nesting chronology.....	29
Level I Selection: distribution and density of populations among geographic regions.....	29
Level II Selection: distribution and density of individuals among different landscapes within a geographic region.....	30
Level III Selection: habitat characteristics of nesting territories.....	34
Level IV Selection: habitat selection by foraging individuals.....	37
Home Range Characteristics.....	40
Level V Selection: prey selection.....	41
Pellet analysis.....	41
Prey availability.....	43
Availability of prey among different habitats.....	45
Territory composition and reproductive success.....	48
DISCUSSION.....	53
Territory establishment and nest site selection.....	54
Density among geographic regions.....	54
Densities among landscapes within a geographic region.....	56

Habitat selection by foraging individuals.....	60
Constraints on optimal habitat selection.....	65
Competition.....	67
Site tenacity and environmental variability.....	68
Summary.....	72
LITERATURE CITED.....	74

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Use and availability of habitats within the combined foraging areas of of 12 radio-marked male Swainson's hawks in the Butte Valley, California, 1987 - 1989.	38
2. Seasonal variation in percentage of 4 prey species of Swainson's hawks in the Butte Valley, California, 1986 - 1989.	44

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Rates of consumption and pellet regurgitation by six captive Swainson's hawks feeding on four prey species.	19
2. Species, age class, and detectability of prey delivered to six Swainson's hawk nests in the Butte Valley, California, 1985 to 1987.	20
3. Occupancy and reproductive success at Swainson's hawk nests in the Butte Valley, California, 1986 to 1990.	26
4. Success and productivity (\pm SE) of traditional and newly-formed pairs of Swainson's hawks in the Butte Valley, California, 1986 to 1990.	28
5. Habitat composition and Swainson's hawk density and productivity on five study blocks in the Butte Valley, California in 1989.	32
6. Percent composition of habitats (\pm SE); 1) within the study area, 2) within 1 km of 68 Swainson's hawk nest sites, 3) within the foraging radius of 12 radio-marked hawks and, 4) in the home ranges of 12 radio-marked hawks in the Butte Valley.	36
7. Prey species identified from pellets collected at 59 Swainson's hawk nests in the Butte Valley, 1986 to 1989.	42
8. Relative abundances of 7 species of rodents in 8 vegetation types in the Butte Valley, California, 1987 - 1989.	47
9. Correlations of territory composition with reproductive rates at 28 Swainson's hawk nests monitored in the Butte Valley, California, 1985 to 1989.	50
10. Results of stepwise multiple regression of reproductive success on habitat composition of Swainson's hawk territories in the Butte Valley, California.	51

HABITAT SELECTION BY NESTING SWAINSON'S HAWKS:

A HIERARCHICAL APPROACH

Introduction

Describing the relationships between birds and their environments is an important focus of avian ecology. Theories relating to habitat selection and optimal foraging have been the impetus for much of current ornithological research (Cody 1985). Habitat selection is fundamental to our understanding of behavior and morphology of birds (Klopfer and Ganzhorn 1985) as well as the structure and dynamics of bird communities (Lack 1971, Cody 1974). These fields are not only interesting theoretically, but also in their application to conservation and management of populations and species. The working hypothesis for habitat selection studies has been that individuals select particular habitats to enhance or maximize their fitness (Rosenzweig 1985). A subsequent hypothesis is that through the processes of natural selection and adaptation, species or populations become 'dependent' on those habitats for long-term persistence (Ruggiero et al. 1988). Studies of avian habitat selection typically involve correlation of bird distribution or density with vegetation structure or other habitat variables (MacArthur and MacArthur 1961, Cody

1981), or by comparison of use versus availability of habitats by individuals (Johnson 1980, Thomas and Taylor 1990). There are problems with the application of these traditional approaches. Fretwell and Lucas (1969) and Van Horne (1983) describe situations where simple density-habitat quality relationships are likely to be unreliable. Correlation of bird density or abundance with habitat structure may not identify the actual resources used by the birds (Cody 1981) and changes in availability of those resources may result in unpredictable shifts in habitat selection. Connell (1980) and Wiens (1977) challenge assumptions of equilibrium between species abundance and habitat quality. In variable environments, species attributes such as longevity and site tenacity may confound correlations of bird density with habitat (Wiens 1985). Depending on study design, comparisons of use and availability of different habitats (preference studies) may circumvent problems with density - habitat quality relationships, but may be complicated by factors such as local occurrence of competitors and predators, traditional use of resources, and social behavior (Thomas and Taylor 1990). In particular, inconsistencies in methods used to assess the actual availabilities of habitats or resources frequently make preference studies difficult to interpret (Johnson 1980, Thomas and Taylor 1990).

The complexity of habitat selection by birds and the

problematic nature of studying habitat selection has led to increased recognition of ecological scale as a unifying concept in understanding habitat selection processes (Morris 1987, Karr 1983). Commonly viewed in terms of spatial and temporal variation, ecological scale includes other dimensions such as level of resolution (species - populations - individuals) (Johnson 1980), phenotypes, or age classes (Maurer 1985). In studies of habitat selection, the choice of a particular scale of observation may have a powerful influence on the conclusions that are reached (Wiens 1985). Allen and Starr (1982 p.259) stated that "the same ecological situation can yield diametrically opposed results when investigated at different scales". To reduce the effects of human bias on ecological scale, Morris (1987) proposed the use of biological definitions of scale derived from species attributes including generation time, dispersal distances and home range size. According to Wiens (1985), however, there is a basic "paradox" in selecting any particular scale of study; by studying habitat selection on a broad scale the investigator cannot perceive the individual dynamics that produce selection patterns, conversely, studies focused at the level of individual organisms may miss patterns evident at a larger scale. In addition, patterns of habitat selection observed at different scales of study may not be independent: Johnson (1980) suggested a natural ordering or hierarchy of

selection processes with each level conditional upon the level preceeding it. For example, the selection of habitats within an animal's home range is conditional upon habitat selections made when the animal established the location of its home range, which in turn is conditional upon the geographic range of the population in question (Johnson 1980).

Viewing habitat selection as a heirarchy of processes occurring at different scales can reveal patterns not evident at a single scale of observation (Allen and Starr 1982). A heirarchical approach focuses attention on the explicit definition of each level of scale studied (Allen and Starr 1982, Morris 1987), possible relationships between levels (Johnson 1980), and the appropriate metrics to measure at each level (Van Horne 1983, Morris 1987). Allen et al. (1984) deemphasized the importance of any particular scale of observation and advocated studies that incorporate multiple levels of resolution. Changing the scale at which a system is studied may change the patterns observed in the system; these changes may yield important insights into the underlying structure of the system (Allen et al. 1984).

Scales of environmental variation and avian response occur as continuous gradients (Karr 1983, Morris 1987), from which a few scales are defined for study (Morris 1987). Using spatial scale, Morris (1987) defined two levels of habitat selection: macrohabitat (area of home range) and

microhabitat (variables influencing time and energy budgets within the home range). Describing patterns of distribution of breeding birds in grassland communities, Wiens and Rotenberry (1981) classified habitat selection into three levels: geographic range, location of territories, and patterns of use. Wiens et al. (1986) also discussed the effects of temporal scale on habitat selection by breeding birds, but did not define specific scales for study.

Johnson (1980) proposed a hierarchy of selection processes including: 1) geographic range of a species or population, 2) home range location, 3) use of habitats within the home range and 4) selection of food items at feeding sites.

Morris (1987) discussed the appropriate metrics to be considered at different levels of analysis: density responses to changes in habitat scale, fitness rewards to individuals in different habitats, and allocation of time and energy by individuals in different habitats. At the level of individual behavior during short temporal scales, habitat selection is synonymous with optimal foraging (Rosenzweig 1985).

A Hierarchy Approach to Habitat Selection

In this study I examined habitat and resource selection by nesting Swainson's hawks (Buteo swainsoni) at several levels of resolution. My objectives were to identify patterns of habitat selection and describe changes in these

patterns occurring with variation in temporal and spatial scale of observation. Recognizing that the selection of any particular scale of study is an arbitrary process (Allen and Starr 1982), I used characteristics of the hawk population under study to modify the hierarchy of study scale proposed by Johnson (1980). My hierarchy consists of six levels of resolution, each with different spatial scale, population metrics, and resource metrics. The effects of temporal variation are discussed for each of these levels.

Level I addresses the distribution and density of Swainson's hawk populations within a broad geographic area (northern California). At this broad level of resolution, I compare the sizes of Swainson's hawk populations among three large basins with roughly similar landscapes. At Level II, I analyze the density and distribution of Swainson's hawk territories within a population relative to gross habitat associations within the range of the population (study area). At level III, I compare the habitat composition of Swainson's hawk territories to the availability of those habitats within the range of the study area population. At Level IV, I compare use and availability of specific habitats by individual Swainson's hawks. Use and availability of habitats were calculated for each hawk in the sample (design 3 of Thomas and Taylor 1990). Level V is the selection of prey resources by foraging Swainson's hawks. I estimated the proportion of different prey species

in the diet and the availability of each prey species in different habitats and compared the results to habitat selection patterns of foraging Swainson's hawks.

In Levels I through V, I examine habitat selection at progressively finer levels of resolution, using hawk density, nest site location and habitat use to indicate resource preference. At level VI, I assess the effects of habitat selection on reproductive success, a measure of fitness. Evaluation of fitness of individuals nesting in different habitats, when compared with measures of habitat selection, may serve to validate the observed patterns of habitat selection or allow identification of constraints on optimal habitat selection.

STUDY AREA

The extreme northcentral portion of California is composed of three adjacent large basins; the Shasta Valley, Butte Valley and the southern Klamath Basin. Roughly similar in size, the Shasta and Butte Valleys are separated by a narrow (ca. 18-km wide) strip of the southern Cascade Mountains. Steep escarpments of the Modoc Plateau divide the Butte Valley from the larger Klamath Basin. These three basins are included together in the Modoc Plateau region of the California Sagebrush Steppe Ecological Province (Barbour and Major 1977) and the Basin and Range Physiographic Province (Franklin and Dyrness 1973). This study focused primarily on the non-forested floor of the Butte Valley, ranging from 1,280 m to 1,340 m in elevation and occupying approximately 415 km². of the basins 1,883 km² area. The topography, soils and vegetation of the Butte Valley are typical of the Basin and Range Physiographic Province (Franklin and Dyrness 1973). The climate is characterized by warm, dry summers and cold, snowy winters. Mean annual precipitation, largely snow, is 27.94 cm. During this study, annual precipitation ranged from 34.47 cm in 1986 to 16.90 cm in 1988.

Prior to settlement in the mid-1800s, the native vegetation in the Butte Valley was dominated by four habitats, alkaline wetlands, perennial grasslands, pine woodland and sagebrush steppe (U. S. Government Land Office

1874, Merrill 1957). Dominant plant communities included saltgrass (Distichilis sp.) and basin wildrye (Elymus cinereus) in lowlands, bigsage (Artemesia tridentata) and bluebunch wheatgrass (Agropyron spicatum) in drier sites, and Ponderosa pine (Pinus ponderosa) and Idaho fescue (Festuca idahoensis) in upland areas (Franklin and Dyrness 1973, Barbour and Major 1977). Field notes from land surveys (U. S. Government Land Office 1874) and settlers' journals attest to the general abundance of grasses and wetlands in the valley.

Grazing by cattle and sheep, and invasion by exotic grasses resulted in the virtual elimination of perennial grass-dominated habitats from the Butte Valley in the early 1900s, and favored dense stands of bigsage and rabbitbrush (Chrysothamnus spp.) with cheatgrass (Bromus tectorum) as an understory (Franklin and Dyrness 1973). Fire suppression and grazing permitted the invasion of the valley floor by western juniper (Juniperus occidentalis), which had previously been restricted to hillsides and rocky outcrops (Burkhardt and Tisdale 1976). The establishment of agriculture in the valley resulted in clearing and cultivation of pine woodlands and mesic grasslands. Wetlands were drained for cultivation, and all perennial streams were diverted for irrigation.

Presently, grazed sagebrush steppe comprises about 21% of the floor of the Butte Valley and juniper woodland covers

22% (Table 6). Wetlands and seasonally flooded areas occupy about 5% of the valley. The remaining 53% supports several varieties of cultivated crops. The proportion of each crop-type grown varies annually, but irrigated alfalfa (Medicago sativa) is generally dominant (35% of cultivated area), followed by grains (30%) and potatoes (5%). In recent years increasing numbers of fields have been abandoned, accounting for 30% of cultivated area in 1987. Depending on soil type and crop last grown, these fields are colonized by cheatgrass and exotic weeds such as Russian thistle (Salsola kali) and tumbled mustard (Symbrissum sp.). Poor soil structure and wind erosion frequently limit natural revegetation, resulting in xeric, sparsely vegetated areas.

METHODS

I estimated the size and distribution of the Swainson's hawk population in the Butte Valley by conducting a systematic survey of the entire valley floor each year from 1987 to 1989. The open, flat terrain and high road densities in agricultural portions of the valley enabled me to use trucks to survey large areas. Sage-steppe areas were searched on foot as well as from vehicles. Limited visibility in juniper woodland habitats required me to watch these areas from a distance, recording flight patterns of hawks until a nest area was revealed. In addition to making regular searches, I followed any foraging hawk of unknown origin until it returned to its nest site. My survey effort was concentrated during the period of courtship and nest-building (mid April through late May) when hawk pairs were most visible, although new nests were located as late as August. Deserted nests were included in the sample if they showed evidence of use during the present year (Postupalsky 1974, Steenhof and Kochert 1982). The results of partial surveys made each year from 1983 to 1986 provided a map of established territories to check and allowed me to concentrate searches in previously unsurveyed areas. Nests of red-tailed hawks (Buteo jamaicensis) were also recorded during surveys. Each nest site was plotted on 1:24,000 aerial photographs. Intensive surveys for Swainson's hawks

nesting in the adjacent Klamath Basin were conducted by P.H. Bloom and S. Hawks (Bloom 1980, Risebrough et. al. 1989). I surveyed the Shasta Valley each year from 1985 to 1987.

Nest contents were inspected about one week after the mean hatching date of June 16. During this first nest visit I recorded the number of nestlings and unhatched or broken eggs, identified any fresh prey remains in the nest and collected regurgitated pellets. These procedures were repeated during two subsequent nest checks made in early July and early August. Guidelines suggested by Fyfe and Olendorff (1976) were followed to minimize disturbance to nesting hawks and their young. Terminology proposed by Postupalsky (1974) was used to define nesting success and productivity of Swainson's hawk territories. To control bias associated with survey timing and differential detectability of failed breeding attempts (Steenhof and Kochert 1982), I used only data from known traditional pairs (pairs for which I had >1 year of data) to calculate annual nest success and productivity. Territories were classified as occupied if at least 1 adult was observed repeatedly during the early nesting season. A pair was considered to have attempted to breed if a nest was constructed or new material was added to an existing nest. I considered a breeding attempt to be successful if > 1 nestling survived to four weeks of age. Territorial pairs that did not attempt to breed were included in the same category as

failed attempts.

The extent and distribution of different habitats were mapped over the entire study area each year from 1987 to 1989. I used 1986 aerial photographs (1:24,000) as base maps, updating them each year with data collected during field mapping. The valley was classified into 11 habitats, including coverage of four agricultural crops, two sage-steppe types, abandoned fields, pastures, unmanaged grasslands, wetlands and juniper woodland. The clear boundaries of past and present agricultural fields and other properties permitted high accuracy in habitat delineation. I categorized the density of nest sites (trees > 3 m in height) in each square kilometer of the valley as low (1 to 5 trees/km²), moderate (6 to 19 trees/km²) or high (>20 trees/km²).

The habitat classification process resulted in a map of the valley which depicted five geographic areas or blocks with differing predominant habitats. These blocks were used as subplots within the study area. I computed the percent coverage of each habitat in each block, and counted the number of one-km² plots in each category of tree density. Densities of nesting hawks were expressed as number of pairs per 100 km² in each block. Nests within 0.5 km of a block boundary were given a value of 0.5 in that block and 0.5 in the adjacent block.

I compared the habitats used by nesting Swainson's

hawks to the habitat composition of the study area (Level III Selection). I measured the percent coverage of each habitat within a 3.14-km² circle (2-km diameter) surrounding the nest site. I used three measures of territory size to determine the size of the analysis area, (1) mean distance between nearest neighbors (60 sites) in this study was 2.04 km: one-half of this distance gives a radius of one km, (2) mean foraging distance of radio-marked male Swainson's hawks was 0.917 km, approximately the radius of the circle, and (3) mean home range size for 12 radiomarked male hawks was 4.05 km² -- including an outlier of 28.8 km². The mean proportion of each habitat within all Swainson's hawk territories was compared to the actual proportions of those habitats in the entire Butte Valley.

I used radio telemetry to locate foraging adult male hawks and monitor their habitat use. Two females tracked in a pilot study had foraging ranges entirely within the ranges of their mate, and made fewer foraging trips. I used a mist-net (6 X 3 m, mesh size 10 cm) with a live great horned owl (Bubo virginianus) as a decoy to trap adult hawks at the nest site (Hamerstrom 1963). Trapped males were fitted with backpack-mounted transmitters weighing 19.5 to 22.0 g (2.5 percent of mean body weight for males). In addition, all adult hawks trapped were marked with individually numbered plastic legbands and U.S. Fish and Wildlife Service lock-on bands.

To determine home range area and habitat use, I followed each radio-marked male from dawn until dusk one day per week. I attempted to keep the bird in direct view, recording all behaviors in narrative form, during the entire observation period. Birds were regularly lost to view during periods of high-altitude soaring, but were relocated when they resumed foraging or returned to the nest. While monitoring foraging bouts, I paid close attention to detecting prey capture attempts and recording the habitat where the attempt was made. A prey capture attempt was defined as a dive from a perched or flying position, stall with loss of altitude, or actual ground strike. I recorded bird locations and associated habitat on 1986 aerial photographs (1:13,000). Home range sizes were computed with the Minimum Convex Polygon (MCP) technique (Southwood 1966 p.262), using at least 200 locations (20-minute intervals) per bird and deleting the outermost 5% of locations as outliers. I felt that for the objectives of this study, MCP performed better than more sophisticated statistical techniques that emphasized the nest area and loafing perches. Home range estimates made using MCP are "strongly influenced by peripheral fixes" (Kenward 1987 p.170), and include large areas that are rarely used by the animal. The high mobility and nest-centered foraging movements of Swainson's hawks, however, resulted in a large proportion of foraging activity being represented by peripheral fixes.

The large "unused" areas traversed by a bird as it flies to a foraging site may be important components of the energetic costs of using a particular home range.

To describe habitat selection by foraging male Swainson's hawks (Level IV Selection) I compared use and availability of habitats within an analysis area surrounding the nest site of each radioed-marked male hawk. I defined available habitat as the habitats within a circle, centered on the nest, with radius equal to the distance to the outermost point used in constructing the home range (95% MCP). I considered this larger area to approximate the potential foraging area of each male hawk, placing less emphasis on previous habitat-selection choices made during home range establishment. Johnson (1980:69) suggested that home range location may be influenced by habitat and warned that "comparing usage values to the availabilities within the home range ... may well be misleading". For Level IV Selection, use values were the proportion of prey capture attempts made by each bird in each habitat during approximately 80 hours of monitoring. Availability values were percent coverage of each habitat within the foraging radius of each hawk. I compared these values with the Chi-Square/ Bonferroni Confidence Interval method (Neu et. al. 1974, Byers et al. 1984).

To assess prey selection by nesting Swainson's hawks (Level V), I analyzed regurgitated pellets collected at each nest site from 1986 to 1988. Pellets collected during three annual nest checks were dated, dried and stored frozen until analysis. To identify prey species, I compared bones, teeth, hair and feathers in pellets to specimens in the Oregon State University Vertebrate Museum. Grasshoppers were enumerated by counting the number of mandibles in each pellet (Johnson et al. 1987). Results were expressed as percent frequency and percent biomass of each prey species. For biomass calculations, I used weights from specimens captured in this study and from Steenhof (1983). Analysis of falconiform pellets has several potential biases including overrepresentation of large prey items (Bond 1936, Wakely 1978), bone digestion (Marti 1987) and differential detectability of some prey species (Errington 1930, 1932). I used two complementary prey analysis techniques to check the accuracy of our pellet analysis data. I fed known quantities of various prey species to six captive Swainson's hawks and recorded the proportion of each prey item eaten and their detectability in the resultant pellets (Table 1). In addition, I recorded the feeding behavior of adult and nestling hawks during 180 hours of observation made at six nest sites (30 hrs per nest) between 1985 and 1987. Species, size class and proportion consumed were recorded for 127 prey items brought to the nest during observations

(Table 2). These data were used to calculate correction factors to adjust the raw data from pellet analysis.

Table 1. Rates of consumption and pellet regurgitation by six captive Swainson's hawks feeding on four prey species.

species	age class	N	percent consumed	mean # pellets
<u>Spermophilus beldingi</u>	juv.	12	91	1.0
<u>S. beldingi</u>	adult ¹	7	63	2.3
<u>S. beldingi</u>	adult ²	5	43	2.0
<u>Microtus montanus</u>	adult	20	100	1.0
<u>Peromyscus</u> spp.	adult	20	100	0.7
<u>Lepus californicus</u>	adult	4	68	2.5
<u>L. californicus</u>	juv.	4	68	2.0

¹ lean adult squirrel (200 - 230 g).

² fat, late season squirrel (approx. 300 g).

Table 2. Species, age class and detectability of prey delivered to six Swainson's hawk nests in the Butte Valley, California, 1985 to 1987.

Species	age class	N	% in remains ¹
<u>Spermophilus beldingi</u>	juvenile	6	17
<u>S. beldingi</u>	adult ²	12	100
<u>S. beldingi</u>	adult ³	6	100
<u>Microtus montanus</u>	adult	64	11
<u>Thomomys mazama</u>	adult	14	43
<u>Lepus californicus</u>	adult	2	100
<u>L. californicus</u>	juvenile	5	100
<u>Sylvilagus nuttalli</u>	adult	2	100
<u>S. nuttalli</u>	juvenile	2	50
unid. rodent		20	20
unid. bird		8	75

¹ percent of individual prey items that could be identified from uneaten remains in the nest approximately 8 hr after delivery.

² denotes lean adult squirrel (200 - 230g), ³ denotes large, fat squirrel (approx. 300g).

Validation of pellet analysis

Small prey such as deer mice (Peromyscus spp.) and juvenile montane voles (Microtus montanus) were eaten whole and were frequently under-represented in pellets (Table 1). Hawks eating a single deer mouse did not regurgitate a pellet until they had fed again. Larger prey such as adult voles and juvenile Belding's ground squirrels were eaten entirely and represented by a single pellet per individual prey item. Adult ground squirrels were partially eaten. The fat content of adult ground squirrels increased rapidly in June prior to estivation. Swainson's hawks rejected this fat while feeding, resulting in consumption rates of only 40 percent of large, fat squirrels. Adult Belding's ground squirrels were divided into more than one meal or divided among nestling and adult hawks, resulting in \geq two pellets produced per squirrel. I used this information to calculate correction factors that were applied to the raw data from pellet analysis. I assumed that few juvenile ground squirrels (< 150 g) were taken by nesting Swainson's hawks. The hawks were not feeding young until late June and early July, at which time the young squirrels were nearing adult weight (200 g). I used data from observations made at six nest sites to estimate the proportion of squirrels in the remaining two size classes (Table 2). Corrected number of individuals was equal to the count from pellet analysis/ 2

pellets per individual. Corrected biomass was equal to: [N (total squirrels) x proportion in age class x average weight x proportion consumed] / number of pellets per individual. I used a similar correction on the weights of black-tailed jackrabbits (Lepus californicus) and Nuttall's cottontails (Sylvilagus nuttalli); the observed distribution of size classes x proportion eaten / observed number of pellets per individual. I assumed the proportion of each adult cottontail consumed to be similar to that of juvenile black-tailed jackrabbits.

Total squirrel biomass =

$$\frac{N (0.25) (170g)}{1.0 \text{ pellet}} + \frac{N (0.50) (230g) (0.63)}{2.0 \text{ pellets}} + \frac{N (0.25) (300g) (0.40)}{2.3 \text{ pellets}}$$

Total jackrabbit biomass =

$$\frac{N (0.65) (450g) (0.68)}{2 \text{ pellets}} + \frac{N (0.35) (1450g) (0.68)}{2.5 \text{ pellets}}$$

Total cottontail biomass =

$$\frac{N (0.50) (200g) (0.68)}{2.0 \text{ pellets}} + \frac{N (0.50) (700g) (0.68)}{2.0 \text{ pellets}}$$

The need for these correction factors was reinforced by observations made at nest sites. Smaller prey were swallowed whole, and several might be eaten during the

course of a day. Larger prey such as ground squirrels were left in the nest and consumed by > 1 hawk, resulting in more than one pellet per individual prey item. The heads, skins and large bones of larger prey accumulated in the nest and were strongly overrepresented in prey remains.

Prey availability

I compared relative abundance of small mammals in 8 habitats each year from 1986 to 1989, using 2 sampling techniques to estimate relative abundance: livetraps and burrow counts. I set 120- X 380-m (4.56-ha) grids of 100 Sherman livetraps baited with a mixture of rolled oats and peanut butter and placed at 15-m intervals in each habitat three times annually: once each in May, June and July. Traps were checked every 12 to 24 hours for 3 days (1986, 1987, 1989) or 5 days (1988) for a total of 22,400 trap-nights. All habitats were sampled simultaneously or within 3 days of each other. Results were expressed as percent of total captures per species per habitat. I counted active burrows of Belding's ground squirrels (Spermophilus beldingi) and Mazama pocket gophers (Thomomys mazama) along transects in each habitat type. Counts were made by walking slowly along a compass bearing, counting fresh mounds within 2 m on either side of the observer. Each habitat received at least 3 km of transect sampling. Results were expressed as numbers of burrows (per species) per 100 m and in percent of total counts per habitat,

adjusted for unequal transect length.

I compared the habitats within Swainson's hawk territories to a measure of fitness (reproductive output) to determine if fitness varied with habitat quality. I calculated mean annual productivity (total # young/# years) for a sample of 28 territories for which we had at least three consecutive years (mean = 4) of reproductive data. The sample included territories in all habitats in approximately the same proportion as the general population. Habitat composition within a circle (1-km radius) surrounding each nest was used to represent the composition of each territory. I used Linear Regression to compare hawk productivity to individual habitat variables, and Stepwise Multiple Regression to evaluate the combined effects of all habitats.

All tests of statistical significance were performed at $\alpha = 0.05$. Proportional data were arcsine transformed prior to testing. Mean values in the text are presented with standard errors (\pm S.E).

RESULTS

Population size and structure

I located 68 individual Swainson's hawk territories in the Butte Valley study area between 1986 and 1990 (16.6 pairs per 100 km²). The proportion of territories occupied in a given year ranged from 85% in 1989 to 94% in 1986 (Table 3). Fluctuations in annual occupancy rates were caused by abandonment of traditional territories and by new pairs attempting to establish territories in previously unoccupied areas. Swainson's hawks occupying the Butte Valley during the breeding season were almost exclusively adults of breeding age; I observed only 2 individuals in subadult plumage during the study. Nonterritorial adult 'floaters' were also rare. I was able to track most adults back to their territories during the early part of the nesting season. Failed breeding attempts resulted in congregation of nonterritorial adults in prime foraging areas late in the nesting season. The timing of their appearance and the high frequency of color-marked individuals in the population enabled me to distinguish failed breeders from nonbreeding floaters.

I observed 208 breeding attempts by Swainson's hawks between 1986 and 1990. Nesting success varied annually, ranging from 58% in 1989 to 87% in 1986 (Table 3). Mean productivity for all nest attempts was 1.8 ± 0.2 young/year

Table 3. Occupancy and reproductive success at Swainson's hawk nests in the Butte Valley, California, 1986 to 1990.

year	traditional territories checked	percent occupied	percent successful	mean number fledged ¹
1986	33	93.9	87.0	2.0 ± 0.27
1987	33	86.5	78.1	1.7 ± 0.23
1988	37	84.8	71.8	1.8 ± 0.22
1989	46	88.1	57.7	1.3 ± 0.18
1990	59	86.8	79.7	2.0 ± 0.19
All years	208	88.0	74.9	1.8 ± 0.13

¹ mean number of young per occupied territory (± SE)

(Table 3). Nesting failure typically resulted from loss of nestlings (51% of failures), followed by failure to lay eggs (24%), failed incubation (17%) and incomplete nest building (8%). Nestling losses that resulted in nest failure were caused by predation by great horned owls ($n = 5$) or golden eagles (*Aquila chrysaetos*) ($n = 2$), windstorms ($n = 3$), and human disturbance ($n = 3$). I attributed the remaining 11 cases to starvation and subsequent fratricide between siblings in food-stressed nests. Twelve percent of successful nests experienced reductions in brood size resulting from fratricide, starvation and unknown causes.

I color-banded 86 breeding adult Swainson's hawks in the Butte Valley between 1984 and 1990 and recorded the locations of marked individuals each year. Swainson's hawks exhibited relatively high territory fidelity; 83% of marked individuals returned to the same territory the following year and 62% were still present on the original territories 6 years after banding. I observed territory shifts by 16 individuals; in each case the bird moved to an adjacent territory < 3 km from the previous years' site. Territory fidelity had a strong influence on reproductive success. In 124 nesting attempts where the identity of both pair members was known, traditional pairs exhibited significantly higher nest success and productivity than pairs consisting of one or more new pair members (two-tailed t -test, $p < 0.05$) (Table 4.)

Table 4. Success and productivity (\pm SE) of traditional and newly-formed pairs of Swainson's hawks in the Butte Valley, California, 1986 to 1990.

pair status	N	percent successful	mean productivity
traditional pair	128	85.9	2.2 \pm 0.04
new female	10	80.0	1.8 \pm 0.09
new male	11	54.5	0.7 \pm 0.23
new pair	18	22.2	0.5 \pm 0.29

During this study we banded 326 nestling Swainson's hawks in the Butte Valley; Peter H. Bloom banded an additional 35 young between 1979 and 1984. Of these, 18 were later trapped as breeding adults in the Butte Valley (mean age = 5.7 ± 0.6 years) and color-marked. Eleven of these marked individuals, resighted in 1990, ranged from 4 to 11 years old (mean = 7.9 ± 0.7 years). Distance of dispersal from natal site to breeding site averaged 8.1 ± 0.5 km ($n = 18$).

Nesting Chronology

In each year of the study, migrating Swainson's hawks began arriving in the Butte Valley during the first week of April and most traditional pairs were on their territories by April 20. In 91% of successful nest attempts, incubation began between May 8 and May 18. Of 16 clutches completed after May 20, only 4 were successful. Young hawks typically fledged between July 28 and August 8. Migration from the valley was usually complete by September 5 (range = Sept. 2 - 11). Swainson's hawks were present in the valley for 154 ± 6 days each year.

Level I Selection: Distribution and density of populations among geographic regions.

The basic habitats represented in the Shasta Valley, Butte Valley and lower Klamath Basin were similar. Each

area contained pastureland, hay crops, sagesteppe and juniper woodland. The Shasta Valley supported a higher proportion of pastureland than the other basins, whereas the Butte Valley and Klamath Basin contained relatively more sagesteppe and intensive agriculture.

The size and stability of Swainson's hawk populations differed dramatically among the three basins. In repeated surveys over 4 years, I identified only 1 traditional Swainson's hawk territory in the Shasta Valley. P.H. Bloom (1980) surveyed the Klamath Basin and estimated a density of 22.7 pairs per 100 km² in 1979. Since then, however, the population has declined by approximately 50% and exhibits low reproductive success (Risebrough et al. 1989). Comparing 1979 and 1986 USDA Soil Conservation Service aerial photographs, I found no dramatic changes in relative proportions of different types of habitats during the period of population decline. The Butte Valley supported 16.6 pairs per 100 km² in 1990. This population appeared to be stable or slowly increasing.

Level II Selection: Distribution and density of individuals among different landscapes within a geographic area.

To examine Level II habitat selection I compared densities of nesting Swainson's hawks among different landscapes in the Butte Valley. Habitat variables and hawk

densities showed considerable variation among the five landscape blocks (Table 5). The 2 blocks containing the greatest proportion of cultivated land, Cedar Mt. and Ball Mt., had similar proportions of alfalfa, grain and juniper woodland, but differed in the intensity of farming practices. Deeper soils and slightly higher precipitation on the Ball Mt. block provided favorable conditions for agricultural production, resulting in greater intensity of rodent control, insect control, and crop rotation. Much of the Cedar Mt. block consisted of shallow, sodic soils which were marginal for cultivation. Nearly 20% of this block was abandoned farmland. The Sage block consisted almost entirely of heavily-grazed sagesteppe vegetation with widely scattered junipers. The Mt. Hebron block was dominated by dense juniper woodland and dryland pasture. Suitable nest trees, largely western junipers, were well-distributed on all but the Meiss Lake block. The Ball Mt. block supported a higher abundance of deciduous trees such as poplars (Populus spp.), elms (Ulmus spp.), and willows (Salix spp.), that may have been less suitable as nest sites for Swainson's hawks. The margins of the Meiss Lake and Ball Mt. blocks supported ponderosa pine forest, whereas the Cedar Mt. block was surrounded by juniper woodland.

Densities of nesting Swainson's hawks differed significantly among blocks ($X^2 = 13.75$, $df = 4$, $P = 0.01$) (Table 5). The Sage, Meiss Lake, and Ball Mt. blocks had

Table 5. Habitat composition and Swainson's hawk density and productivity on 5 study blocks in the Butte Valley, California in 1989.

	Meiss	Cedar	Ball	Hebron	Sage
	Study block				
Area (km ²)	52.0	141.1	66.3	72.8	74.6
Habitat	Percent Coverage				
alfalfa	1.6	29.9	22.4	1.4	0.0
abandoned	1.4	19.7	6.9	7.2	1.3
grain	14.9	19.1	18.9	7.4	3.0
potatoes	0.0	2.6	11.1	2.6	0.0
sagesteppe	0.0	7.9	0.7	0.0	60.7
rabbitbrush	1.2	0.0	0.9	0.8	32.2
juniper	0.0	12.1	14.2	60.8	1.8
grass	30.7	3.1	0.4	4.9	0.0
pasture	0.7	5.4	15.4	14.8	0.0
wetland	49.5	0.0	1.5	0.0	0.0
tree dispersion/1	31.8	87.1	61.0	99.8	93.4
tree density 2/	1.9(-)	31.2(+)	2.3(-)	16.5(0)	10.7(-)
productivity 3/	1.71	1.79	2.00	1.61	0.81

1/ percent of 100 ha blocks with at least 3 trees.

2/ pairs per 100 km².

3/ total number young produced/ total nest attempts (# attempts).

Symbols indicate values significantly greater (+) or less (-)

than study area (Chi square/ Bonferroni Confidence Interval, $p < 0.05$).

fewer territories than the population mean (Chi Square/Bonferroni, $p < 0.05$); only the Cedar Mt. block contained more territories than expected. Estimation of densities in each block was complicated by edge effects--pairs that nested in a block but utilized foraging habitat in an adjacent block. Over 60% of Swainson's hawk pairs on the Sage and Mt. Hebron blocks nested < 1 km of the block boundary and were frequently observed in the adjacent block. Conversely, most nests in the Cedar Mt. and Ball Mt. blocks were located in the interior.

Temporal changes in the proportion or distribution of habitats were not detected on the Sage, Ball Mt., or Meiss Lake blocks between years of this study. On the Cedar Mt. and Mt. Hebron blocks, acreage of alfalfa and grain declined by 11% as marginal fields were abandoned or planted to annual rye grass (Conservation Reserve status). This trend was particularly pronounced in the Mt. Hebron block, where virtually all of the alfalfa present in 1985 had been abandoned or converted to dryland pasture by 1990. Annual densities of nesting Swainson's hawks were stable in all but the Sage and Ball Mt. blocks. The number of interior pairs on the Sage block declined from 7 in 1984 to 2 in 1990. I did not locate any Swainson's hawk territories in the Ball Mt. block between 1985 and 1987. In 1988 a new pair established a territory on the northern boundary of the Ball Mt. block and was successful in 1989 and 1990. In

1990, another new pair began defending a site in the interior of the Ball Mt. block, but did not build a nest.

Productivity of Swainson's hawk nests was similar among the Cedar Mt., Ball Mt., Mt. Hebron and Meiss Lake blocks. Hawks nesting within the Sage block produced only about half the number of young per nesting attempt as did hawks on the other blocks (Table 5).

Level III Selection: Habitat characteristics of nesting territories

Mean habitat composition of 68 Swainson's hawk territories (1-km circles) was similar overall to the composition of the Butte Valley study area (Table 6). Juniper woodland was disproportionately more abundant within territories (two-tailed t -test, $P = 0.013$), whereas the proportions of alfalfa, abandoned fields, sagesteppe, potatoes, and grainfields did not differ from the study area as a whole (P values in Table 6). The proportions of perennial grassland, grazed pastures and rabbitbrush were somewhat lower on territories than in the study area ($P = 0.04-0.07$), however the low overall abundance and uneven distribution of these habitats made this comparison difficult to interpret. Territories averaged $31 \pm 4.0\%$ active agriculture, compared with 34% for the entire Butte valley.

Ninety-six percent of the Swainson's hawk territories (1-km radius) in the Butte Valley also contained ≥ 1 red-tailed hawk nest site ($\bar{x} = 1.5 \pm 0.1$): 44% had 2 or more.

Table 6. Percent composition of habitats (\pm SE): 1) within the study area, 2) within 1 km of 68 Swainson's hawk nest sites, 2) within foraging radius of 12 radio-marked hawks and, 4) within the home ranges of 12 radio-marked hawks in the Butte Valley.

habitat	Percent coverage			
	study area	1-km circle	foraging radius	home ranges
alfalfa	15.4	16.3 \pm 2.20 (0.15)	20.5 \pm 4.01 (0.29)	33.1 \pm 6.86 (0.02)
abandoned	13.3	14.7 \pm 2.82 (0.13)	21.1 \pm 4.37 (0.18)	19.0 \pm 6.42 (0.39)
sagesteppe	20.7	18.4 \pm 3.70 (0.13)	14.6 \pm 4.65 (0.35)	13.0 \pm 6.06 (0.23)
rabbitbrush	6.9	3.5 \pm 1.55 (0.07)	11.5 \pm 4.11 (0.36)	8.3 \pm 5.32 (0.79)
potato	2.3	2.6 \pm 0.87 (0.70)	6.7 \pm 3.31 (0.25)	3.7 \pm 2.64 (0.59)
grain	13.0	14.8 \pm 2.71 (0.15)	13.4 \pm 2.91 (0.86)	14.9 \pm 3.34 (0.57)
juniper	14.7	24.6 \pm 3.70 (0.01)	9.5 \pm 3.48 (0.17)	5.7 \pm 2.84 (0.01)
grassland	5.9	3.1 \pm 1.04 (0.04)	1.5 \pm 1.61 (0.01)	1.0 \pm 0.95 (0.01)
pasture	9.7	1.5 \pm 0.60 (0.05)	1.9 \pm 2.03 (0.01)	0.9 \pm 0.69 (0.01)

P-values from comparison of means with study area (two-tailed t -test) are given in parenthesis.

Level IV Selection: Habitat selection by foraging individuals

I recorded 947 prey capture attempts by the 12 male Swainson's hawks that were radio marked in this study. Comparing the distribution of foraging attempts among the habitats within the foraging radius of each male, I found that habitats used for foraging differed from their availability ($X^2 = 1469.8$, $df = 8$, $P = 0.001$). The Bonferroni confidence intervals identified habitats selected or avoided by the foraging hawks (Fig. 1). Foraging Swainson's hawks selected alfalfa and grass more than expected based on availability ($P < 0.001$). Abandoned fields and rabbitbrush communities were used slightly less than expected ($P = 0.02$ and 0.06 , respectively); all other habitats were used significantly less than expected ($P < 0.01$).

Of the habitats available to foraging Swainson's hawks in this study, alfalfa was strongly selected by 9 of the 12 males, whereas 3 birds used it in proportion to its abundance. In these 3 cases, alfalfa occurred in small patches ($< 5\%$) at the extreme edge of the foraging radius where competition and energetics would likely constrain use. Grassland habitat occurred in small proportions on 6 ranges and was strongly selected for by the 3 males whose ranges contained $< 5\%$ alfalfa. Males did not select grass if their foraging ranges contained $> 10\%$ of alfalfa.

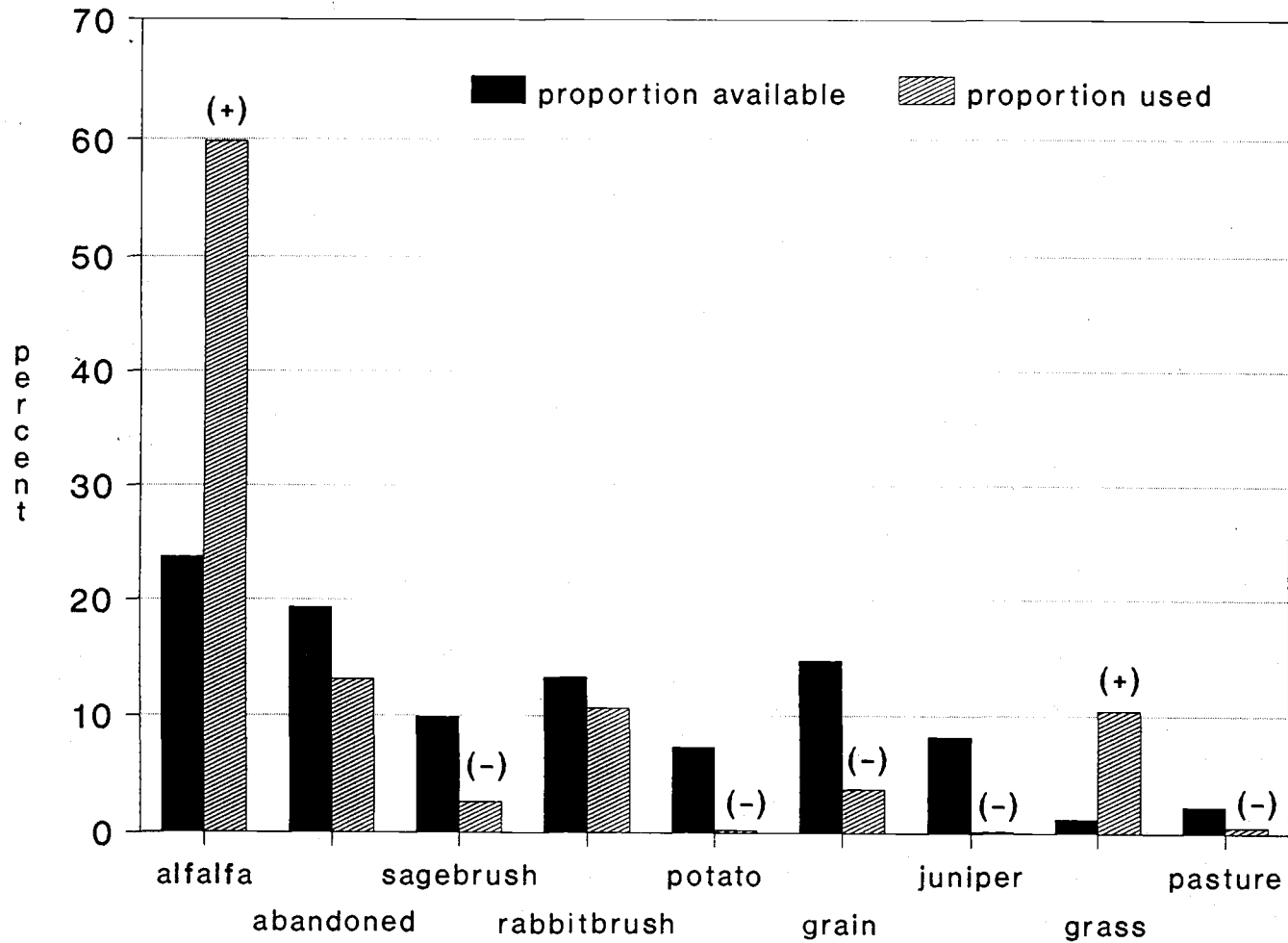


Figure 1. Use and availability of habitats within the combined foraging areas of 12 radio-marked Swainson's hawks in the Butte Valley, California, 1987 - 1989. Symbols indicate values higher (+) or lower (-) than expected based on availability (Chi-Square/ Bonferroni Confidence Interval, $P < 0.05$).

Habitat selection by foraging male Swainson's hawks was strongly affected by temporal variation in weather conditions, vegetation structure and plant moisture content. Although some of this variation was caused by seasonal patterns of climate and plant growth, cultural practices were often the dominant habitat variable in agricultural areas.

During the course of each day, consistent, well-defined patterns in local weather conditions affected the foraging behavior of nesting male hawks. Mornings (0530 - 0900 hrs) tended to be cool and windless. With few exceptions, the radio-marked hawks remained perched near the nest tree or foraged from low perches within 0.5 km of the nest during this time period. Hawks that nested at sites surrounded by non-preferred habitats such as sage-steppe or abandoned fields typically foraged in these habitats in the early morning. Temperatures usually increased rapidly after mid-morning, reaching a maximum of 29.4 - 35.0 C shortly after 1100 hrs. Higher temperatures and subsequent development of thermals and afternoon winds were associated with longer movements to selected foraging habitats by the hawks. Mean foraging distance for 12 radio-marked Swainson's hawks was greater after 1100 hrs ($\bar{x} = 1.62 \pm 0.33$ km) than before 1100 hrs ($\bar{x} = 0.21 \pm 0.06$ km) (two-tailed t test, $P=0.003$).

Patterns of habitat selection by radio-marked Swainson's hawks seemed related to seasonal trends in vegetation density and height. In agricultural habitats, these trends were regulated by cultural practices such as crop rotation and harvest schedules. Plant heights in alfalfa fields were cyclic; growth from approximately 3 cm

to 60 cm typically required 30 days, at which time the fields were harvested, reducing plant height to 3 cm. Fields typically were cut 2 - 4 times per year. Use of alfalfa fields by foraging Swainson's hawks closely followed these cycles; 93% of use occurred during harvest activity and prior to the plants attaining 9 cm in height. Alfalfa fields over 25 cm in height were rarely used by foraging Swainson's hawks. Use of grain fields by radio-marked hawks followed a similar pattern; 86% of use occurred early in the season when plant heights were < 20 cm. After this time the plants formed a closed canopy and grain fields were not used as foraging habitat by the hawks. Grain fields were rarely harvested during the Swainson's hawk nesting season, however in 3 instances fields were harvested early and each received heavy post harvest use by radio-marked Swainson's hawks.

Home Range Characteristics

The proportion of individual habitats within the home ranges used by the 12 radio-marked Swainson's hawks differed from the overall study area (Table 6). Swainson's hawks home ranges included higher proportions of alfalfa and less juniper woodland, perennial grassland and pasture than the overall study area (two-tailed t test, P values in Table 6). Mean habitat composition of home ranges of 12 radio-marked Swainson's hawks was similar to the composition of the corresponding foraging-radius based analysis areas (Table 6), differing only in coverage of alfalfa. Alfalfa was significantly more abundant on home ranges than within foraging radii (one-tailed t -test, $P = 0.03$).

Home ranges of the 12 radio-marked hawks varied in size

from 69 to 2,884 ha. Home range size was positively correlated with the distance from the nest to the nearest alfalfa field ($r_s = 0.80$, $df=12$, $P=0.008$, Spearman Rank Correlation). Home range size was negatively correlated with the proportion of alfalfa within the analysis area ($r_s = -0.74$, $df=12$, $P=0.01$). The three largest home ranges (1,005-2,884 ha) corresponded to nest sites located within the interior of the Sage and Mt. Hebron blocks, from 3-6 km from cultivated fields. Centered at the nest site, foraging movements of these male Swainson's hawks typically produced linear home ranges, with alfalfa fields forming the outer margins of the range. Nest sites with abundant alfalfa nearby were associated with smaller, more circular home ranges.

Level V Selection: Prey Selection

Pellet Analysis

I identified 2,074 individuals of at least 27 vertebrate taxa and 14,077 invertebrate prey items representing three insect families in 1,347 pellets (Table 7). Mammals (13 species) accounted for 88.7% of vertebrate prey numbers and birds (12 species) accounted for 10.7%. Belding's ground squirrels, *Mazama* pocket gophers and montane voles made up 83.3% of vertebrate prey numbers and 80.1% of vertebrate prey biomass. Grasshoppers (*Dissoteira* spp.) were an important numerical component of the prey taken by Swainson's hawks but contributed little to total

Table 7. Prey species identified from pellets collected at 59 Swainson's hawk nests in the Butte Valley, California, between 1986 and 1989.

Species	individuals		biomass	
	N	%	g	% total
<u>Spermophilus beldingi</u>	328	15.8 ^b	21193	14.9 ^a
<u>Microtus montanus</u>	1265	61.0	69575	48.8
<u>Thomomys mazama</u>	134	6.5	20100	14.1
<u>Peromyscus</u> spp.	54	2.6	1026	0.7
<u>Lepus californicus</u>	26	1.2 ^b	8398	5.9 ^a
<u>Sylvilagus nuttalli</u>	11	0.5 ^b	1683	1.2 ^a
other mammal (7 sp.)	19	1.0	2095	1.7
Total mammal	1840	88.7	124370	87.3
<u>Euphagus cyanocephalus</u>	30	1.4	1950	1.3
unidentified sparrow	169	8.1	5070	3.7
other bird (10 sp.)	24	10.8	5259	3.8
Total avian	223	10.7	12279	8.6
Total reptile	11	0.5	1577	1.1
grasshopper (Acricidae)	14043	^c	4213	2.9
Total insect	14077		4225	2.9

^a denotes values corrected for juvenile body weights and uneaten proportions of large prey items.

^b denotes values corrected for multiple pellets produced from single large prey items.

^c numbers of individual insects not included in analysis.

prey biomass. Species composition of prey varied widely among individual Swainson's hawk nests, however the overall proportions of prey species taken seemed similar between groups of nests in different habitat blocks; suggesting that the hawks were selecting specific prey species.

Prey Availability

Availability of prey, in terms of both abundance and vulnerability to avian predators, varied temporally and among habitats. Seasonal variability in the availability of prey exerted a strong influence on prey selection by Swainson's hawks in the Butte Valley (Fig. 2). Belding's ground squirrels exhibited dramatic changes in availability during the spring and summer. Adult squirrels emerged from hibernation in February and March and juveniles typically appeared above ground in April. In late June most squirrels were of adult weight and began accumulating fat in preparation for estivation (Morton 1975). By early-to mid-July few squirrels were visible above ground. Thus during the period of peak nutritional demand by nestling Swainson's hawks, an important food resource became unavailable. Belding's ground squirrels made up a large proportion of the diet of the hawks during courtship, nest-building and incubation, but were rarely seen in pellets collected after July 1.

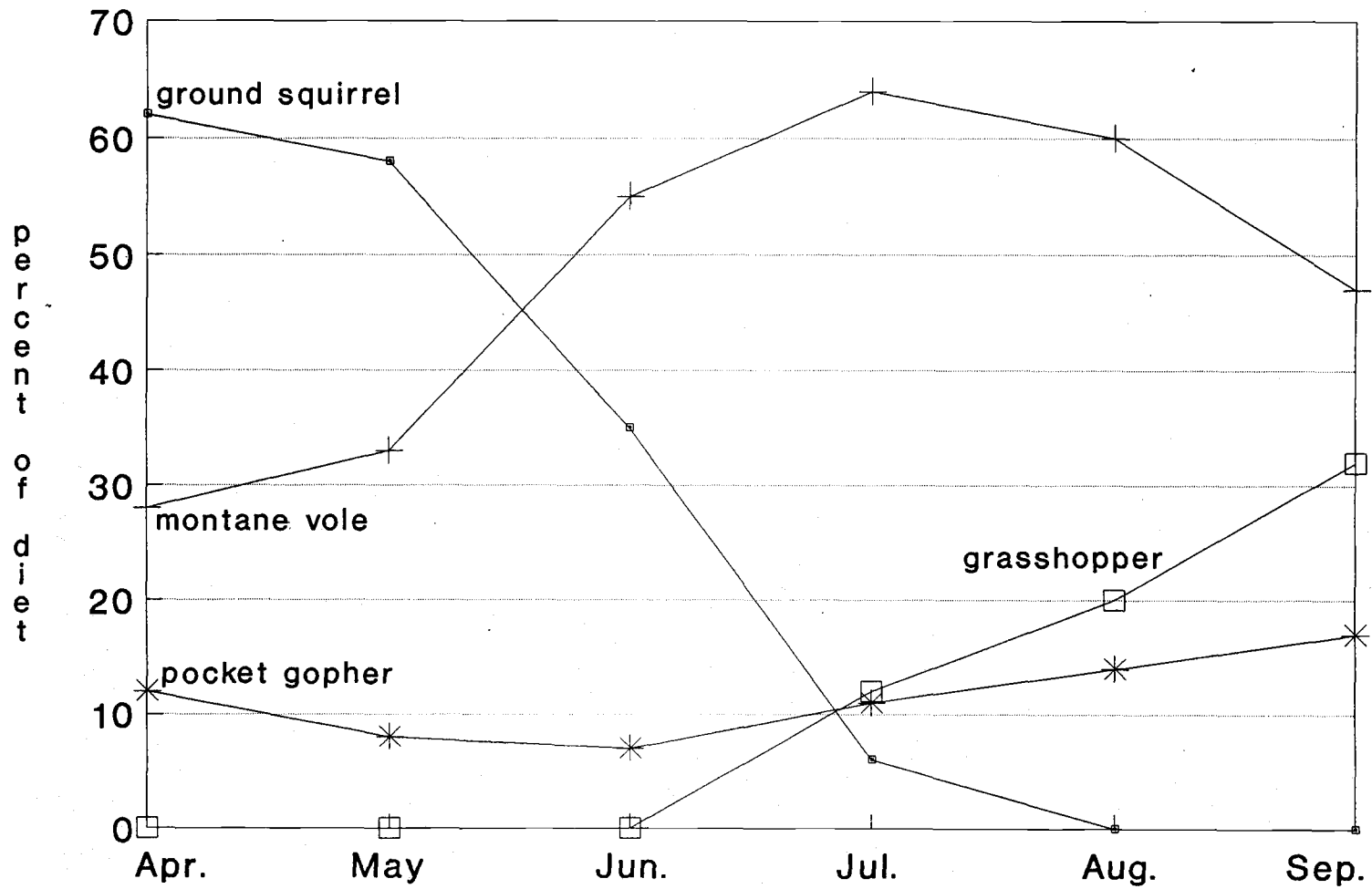


Figure 2. Seasonal variation in percentage of 4 prey species of Swainson's hawks in the Butte Valley, California, 1986 - 1989.

Availability of grasshoppers was restricted to the later part of the Swainson's hawk nesting season. Incapable of flight, immature grasshoppers generally remained in vegetation until late July, when large swarms formed in agricultural areas. Grasshopper swarms rising on thermals in the afternoons attracted large numbers of adult and recently fledged Swainson's hawks. The hawks captured the insects from the air at the rate of 2-6 per minute. We did not detect grasshoppers in hawk pellets collected prior to mid-July, however, pellets collected in August and September were often composed entirely of grasshopper parts (Fig. 2).

Availability of prey among different habitats

Analysis of data from livetrapping and burrow counts suggested a strong correlation between the primary prey of Swainson's hawks and certain types of habitats (Table 8). Relative abundances of montane voles, Belding's ground squirrels, and Mazama pocket gophers were significantly greater in alfalfa fields than other habitats (Bonferroni Z statistic $P < 0.05$). Pocket gophers and voles were also more abundant in perennial grass habitats ($P < 0.05$). Pocket gophers were the only small mammal commonly detected in grazed pastures. Small mammal captures were divided into two guilds: agricultural associates (Belding's ground squirrel, Mazama pocket gopher, montane vole) and sagesteppe

associates (Heteromyids, least chipmunk, deermice). Common in most habitats, deer mice were the most abundant small mammal in the sample (82% of total captures).

Table 8. Relative abundances of 7 species of rodents in 8 vegetation types in the Butte Valley, California, 1987 - 1989.

Species ¹	N	Percent of total captures by species							
		rabbit brush	sage	alfalfa	grain	grass	abandon fields	pasture	potato
<u>Peromyscus</u> spp.	2568	15.6+ ²	24.7+	11.6	16.7+	11.9+	10.4-	3.5-	5.6-
<u>Microtus montanus</u>	275	4.0-	0.4-	48.0+	3.3-	40.4-	0.0-	3.3-	0.7-
<u>Thomomys mazama</u>	837	2.7-	0.2-	35.1+	3.8-	28.2+	0.0-	29.7+	0.1-
<u>Dipodomys californicus</u>	121	44.6+	45.4+	0.0-	4.1-	2.5-	3.3-	0.0-	0.0-
<u>Spermophilus beldingi</u>	1884	10.6	2.5-	52.9+	4.7-	10.2	8.2-	8.6-	2.1-
<u>Perognathus parvus</u>	48	58.3+	41.7+	0.0-	0.0-	0.0-	0.0-	0.0-	0.0-
<u>Tamias minimus</u>	125	28.8+	71.2+	0.0-	0.0-	0.0-	0.0-	0.0-	0.0-

¹ Other species captured in low numbers were Lemmys curtatus (21), Mus musculus (9), Neotoma albigula (2) and Reithrodontomys megalotis (12).

² Symbols indicate values higher (+) or lower (-) than expected (Bonferroni Z Statistic, p = 0.05).

Territory composition and reproductive success

The fitness of nesting Swainson's hawks was influenced by the habitat composition of nesting territories. Three variables: rabbitbrush (%), sagesteppe (%), and distance to nearest alfalfa were strongly correlated with productivity (Table 9). Only alfalfa (%), had a significant positive correlation with productivity ($r = 0.48$, $P = 0.01$). The correlation of productivity and alfalfa was weakened by the effects of 4 adjacent territories with high proportions of abandoned fields and relatively high productivity. This group of territories was within 1.2 - 1.4 km of a large expanse of alfalfa with no resident Swainson's hawk territories. Removal of the 4 territories from this regression resulted in a new correlation coefficient of 0.65 ($P = 0.01$). Distance to nearest alfalfa was more strongly correlated with productivity ($r = -0.60$, $p = 0.01$) than was % alfalfa within a territory, suggesting that foraging energetics may be an important factor in determining the reproductive potential at a territory. Nest sites > 1.3 km from alfalfa fields showed significant reduction in reproductive success (two-tailed t -test, $P = 0.01$). Despite the strong avoidance of juniper woodland by foraging Swainson's hawks (Fig. 1), I found a slight positive correlation between juniper woodland (%) and nest productivity. Over 57% of the nest sites in this sample

were located at the edge of juniper woodland, emphasizing the overriding influence of nest site availability on habitat selection.

Results of stepwise multiple linear regression analyses differed depending on whether distance factors were included among the model variables (Table 10). Inclusion of distance factors resulted in a model in which abandoned fields (%), rabbitbrush (%), and distance to alfalfa explained 70% of the variability in productivity. Abandoned fields were not significantly correlated with other habitat variables ($P > 0.05$) and were positively associated with reproductive success ($r = 0.420$, $p < 0.05$). Although abandoned fields were avoided by foraging Swainson's hawks (Fig. 1), such fields typically occurred in close proximity to alfalfa, a preferred foraging habitat. Distance to alfalfa was strongly correlated with sage-steppe (%) ($r = 0.62$, $p < 0.05$) and alfalfa (%) ($r = -0.78$, $p < 0.05$) and was selected in stepwise regression analysis because it was a better predictor of productivity. Juniper trees used for nesting were often associated with remnant patches of sage-steppe habitat within agricultural areas; over 50% of the territories included some sage-steppe habitat. Percent rabbitbrush was not significantly correlated with other habitat variables ($-0.35 > r > 0.17$, $P > 0.05$) and was negatively associated with productivity ($r = -0.57$, $P = 0.01$).

Table 9. Correlations of territory composition with reproductive rates at 28 Swainson's hawk nests monitored in the Butte Valley, California, 1985 to 1989.

measure	r	p<
alfalfa (%)	0.477	0.01
abandoned fields (%)	0.420	0.05
sagesteppe (%)	-0.538	0.01
rabbitbrush (%)	-0.572	0.01
potatoes (%)	0.064	0.75
grain (%)	0.307	0.10
grass (%)	-0.122	0.50
distance to alfalfa (km)	-0.595	0.01

Table 10. Results of stepwise multiple regression of reproductive success on habitat composition of Swainson's hawk territories in the Butte Valley, California.

model variables	partial R ² (P)	full R ² (P)
distance to alfalfa (km)	0.354 (0.001)	
abandoned fields (%)	0.176 (0.010)	0.698 (0.01)
rabbitbrush (%)	0.168 (0.004)	
rabbitbrush (%)	0.327 (0.004)	
sage-steppe (%)	0.199 (0.001)	0.600 (0.01)

Using only the proportions of each habitat on each territory as independent variables, stepwise multiple regression selected a model in which sage-steppe (%) and rabbitbrush (%) accounted for 60% of the variability in reproductive success (Table 10). Sage-steppe and rabbitbrush habitats were avoided by foraging Swainson's hawks (Fig. 1) and had a strong negative correlation with productivity.

Productivity of traditional Swainson's hawk nests was not correlated with the proximity of red-tailed hawk nests ($r_s = 0.23$, $df = 27$, $P = 0.01$, Spearman Rank Correlation).

DISCUSSION

The patterns of habitat selection observed in nesting Swainson's hawks varied depending on the scale of investigation used. Other studies yielded similar conclusions for passerine birds in shrub-steppe habitats (Wiens and Rotenberry 1981) and small mammals (Morris 1987). At coarser levels of resolution, the distribution and densities of nesting Swainson's hawks were not significantly associated with habitats that were strongly preferred at finer scales; also, Swainson's hawk territories did not differentially include optimal foraging habitats. In addition, temporal variation in habitat selection patterns observed within particular levels of investigative scale meant that conclusions derived at each scale were dependant on the time frame used in measuring habitats and hawk responses. Seasonal changes in vegetation structure and prey availability, and subsequent shifts in habitat use patterns by Swainson's hawks, were detected only at the finest levels of resolution.

Patterns of habitat selection by nesting Swainson's hawks fell into two distinct but interdependent categories, (1) territory establishment and nest site selection, and (2) foraging habitat selection and subsequent home range development. The distinction between these functional levels has long been implicitly recognized (Hilden 1965),

however, most studies of Swainson's hawk ecology have concentrated on nest density within study blocks (Gilmer and Stewart 1984, Schmutz 1984, Cottrell 1981) or habitat characteristics of territories (Janes 1985, Dunkle 1977). Relatively few studies have focused on the level of foraging individuals (Fitzner 1978, Bechard 1982, Estep 1989). In this discussion I compare patterns of habitat selection among different levels of observational scale and describe the relationships between levels.

Territory establishment and nest site selection

For a migrating Swainson's hawk returning to the species' breeding range in the spring, the process of territory establishment includes the selection of a geographic region in which to settle (Level I Selection), selection of a landscape within that region (Level II Selection) and finally the selection of a specific territory and nest site within the chosen landscape (Level III Selection).

Density among geographic regions

At the regional level (Level I selection), the distribution and density of Swainson's hawk populations was not clearly associated with general habitat features. Despite the physiographic and vegetative similarities among

the Shasta Valley, Butte Valley, and Klamath Basin, Swainson's hawk populations in each area were markedly dissimilar. This lack of concordance was most noticeable between the Butte and Shasta Valleys. The Shasta Valley contained thousands of hectares of sprinkler-irrigated alfalfa bordered by western juniper (most preferred habitat of Butte Valley Swainson's hawks), yet the species did not nest there in appreciable numbers. Some of the high quality habitats in the Shasta Valley were < 40 km from traditional Swainson's hawk territories in the adjacent Butte Valley. Red-tailed hawks were abundant in most areas surveyed in the Shasta Valley, suggesting that an adequate prey base was available. The density of nesting Swainson's hawks in the Butte Valley (16.6 pr./100 km²) was comparable to densities reported in Montana (14.9 pr./100 km², Dunkle 1977; 16.0 pr./100 km², Craighead and Craighead 1956), in the Central Valley of California (16.0 pr./100 km², Estep 1989) and in Alberta (15.0 to 22.0 pr./100 km², Rothfels and Lein 1983). The situation in the southern Klamath Basin, where a relatively dense population of Swainson's hawks existed historically, is less clear. Change in habitat composition within the Klamath Basin between 1979 and 1989 does not seem of sufficient magnitude to explain the 50% decline in Swainson's hawk numbers described by Risebrough et al. (1989). The factors responsible for the dissimilarity of Swainson's hawk populations among the Shasta Valley, Butte

Valley and Klamath Basin are unclear at this level of resolution. Swainson's hawk abundance did not seem correlated with the broad habitat associations measured at this level.

Densities among landscapes within a geographic region

The distribution of Swainson's hawk territories among landscapes in the Butte Valley (Level II Selection) followed a pattern similar to that seen at the regional level. Traditional territories were clumped into specific landscapes (Cedar Mt. and Mt. Hebron blocks) whereas other landscapes with similar vegetative composition (Ball Mt. block) were sparsely occupied (Table 5). The combination of potential nest trees and preferred foraging habitats (alfalfa and perennial grassland) was widely available on the Ball Mt. and Meiss Lake blocks but were rarely used by nesting hawks. Hawks nesting in adjacent blocks, however, frequently made foraging trips into the largely unoccupied Meiss Lake and Ball Mt. blocks, suggesting that these areas contained suitable habitat. In addition, nest productivity of the few Swainson's hawk pairs nesting in the Meiss Lake and Ball Mt. blocks was similar to that of pairs in the densely populated Cedar Mt. block. The Sage block, dominated by shrub habitats typically avoided by foraging Swainson's hawks in this study, supported intermediate hawk densities, however the fitness of these pairs as measured by

nest productivity was greatly reduced (Table 10, 11). Comparing densities of nests among large study plots in Alberta, Schmutz (1984, 1987) found that densities of nesting Swainson's hawks were greater on plots with moderate cultivation (11 - 30%) than on plots with less cultivation, and that densities did not decline as cultivation exceeded 30%. Schmutz, however, differentiated only two broad types of habitats: grassland (pasture and ungrazed) and cultivated lands (hay crops, grain, row crops).

Territory location

The specific location of Swainson's hawk nest territories (Level III Selection) seemed to be based largely on the availability of suitable nest trees, resulting in the preferential inclusion of juniper woodland within territories (Table 6). This pattern contrasts with the results of Janes (1985), who found perch density (largely trees) to be among the dominant variables distinguishing Swainson's hawk territories from red-tailed hawk territories. Swainson's hawk territories were characterized by low perch density, leading Janes (1987) to conclude that increased perch densities conferred a competitive advantage to red-tailed hawks, with subsequent reduction in numbers of Swainson's hawk territories. In the Butte Valley, 53% of traditional Swainson's hawk territories contained at least 10% juniper woodland (>10 trees/ha); 44% contained over 30%

juniper woodland. Despite strong avoidance of juniper woodland by foraging Swainson's hawks, I found a slight positive correlation ($r = 0.37$, $p < 0.1$) between reproductive success and the proportion of juniper woodland on Swainson's hawk territories: this probably resulted from low nest productivity at territories located in sparsely treed sagesteppe habitats, and from hawks exploiting edges created by agricultural clearing of juniper woodland.

Swainson's hawks did not include disproportionately greater amounts of highly-selected foraging habitats (alfalfa, perennial grassland) in their territories, nor did they exclude habitats avoided by foraging hawks (potatoes, grain, sage-steppe, abandoned fields). This general lack of strong habitat selection at the territory level was also noted by Janes (1985, 1987) who concluded that vegetation structure (other than perch density) and habitats associated with prey were relatively unimportant variables in differentiating Swainson's hawk territories from those of other sympatric buteos. Despite this, Janes (1985) described a tendency of Swainson's hawks to avoid cropland (alfalfa and other cultivated crops) and to select grasslands over other habitats with greater shrub cover. At a similar level of resolution, Gilmer and Stewart (1984) found that Swainson's hawk territories contained relatively less cropland (grain, sunflower) and more hayland (alfalfa and grass hay) than in the overall study area. Pastureland,

largely native prairie, was used in proportion to its abundance.

In the Butte Valley, the availability of each habitat was affected not only by its relative abundance, but also by the distribution of potential nest trees. Extensive perennial grassland was found only in one area (Meiss Lake block), where potential nest sites were limited. Although used preferentially as foraging habitat, most perennial grassland habitat was therefore not available for inclusion into nesting territories. Pastures (grazed grasslands) and rabbitbrush, however, contained numerous scattered junipers yet were avoided by Swainson's hawks for nesting and foraging.

Differential fitness among Swainson's hawk pairs nesting in different habitats suggested that certain habitats should be preferentially included or excluded during territory establishment, but this was not the pattern observed in the Butte Valley. Despite a positive correlation of nest productivity with alfalfa (Table 10), nest territories did not contain disproportionately more alfalfa than did the study area as a whole. Sage-steppe and rabbitbrush habitats were strongly negatively correlated with nest productivity, yet were not selected against during territory establishment. Scattered junipers in sage-steppe habitats were used as nest sites by hawks that foraged in adjacent agricultural lands; in these cases nest productivity was

strongly correlated with the distance to the nearest alfalfa field. Territories in sage-steppe habitat > 0.9 km from alfalfa fields seldom were successful. Schmutz (1987) also observed decreased reproductive success at Swainson's hawk nests located over 1 km from agricultural fields, but did not differentiate between hay crops and other more intensively cultivated crops. Growth rates and fledging success of nestling Swainson's hawks in cultivated habitats (wheat, peas) studied by Bechard (1980) were less than in adjacent grazed grasslands; hay crops were not available in the area studied. Bechard attributed the reduction to lack of food and subsequent fratricide at nests in cultivated habitats. Schmutz (1987) on the other hand, suggested that prey availability may be higher in agricultural areas. The apparent inconsistency among these results may be due to differences in prey availability among the crop types studied. Intensively cultivated crops such as grains and row crops are typically poor foraging habitat (Bechard 1980, Estep 1989) whereas prey availability in haylands is high (Schmutz 1987, Estep 1989).

Habitat selection by foraging individuals

In contrast to the patterns seen at previous levels, individual foraging Swainson's hawks showed clear selection for specific habitats, and closely tracked temporal changes

in habitat structure and prey availability (Level IV and V Selection). Swainson's hawks are mobile, wide-ranging, periscopic (Rosensweig 1985) predators, potentially capable of assessing the quality of habitat patches from afar, and exploiting widely distributed patches of preferred habitat. The distribution of foraging effort by Swainson's hawks was related to prey availability, which in turn was dependant on prey density, vegetation cover density, and prey species composition within habitat patches. The primary prey of nesting Swainson's hawks (Table 8) were diurnal or crepuscular rodents (Ingles 1965; but see Wakeley 1978) of moderate body size (40 - 200g); nocturnal species and larger squirrels and lagomorphs were rarely taken. Foraging activity was concentrated in habitats wherein the availability of these prey was highest.

Among cultivated habitats, alfalfa fields supported the highest relative abundance of diurnal rodent species (Table 9), and were the preferred habitat of foraging Swainson's hawks in this study (Fig. 1). In this study, alfalfa fields were the only habitat preferentially included in the hawks' home ranges, the boundaries of which served mainly to connect each nest site with the nearest alfalfa fields. Use of alfalfa fields increased dramatically during monthly harvests that reduced vegetative height and exposed rodents to predation by hawks. Bechard (1982) also noted increased foraging by Swainson's hawks in newly-harvested cropland

(peas and wheat), and attributed the increase to higher prey availability. Caldwell (1986) proposed that avian predators may increase their prey capture success by exploiting prey that are disturbed or displaced during farming activity. In my study, foraging hawks clearly responded to harvest activity, frequently hunting behind moving machinery and perching on hay bales during harvest. As the height and density of alfalfa increased the hawks shifted their foraging to other more recently harvested fields, or to other habitats. Vegetative height-related shifts in foraging have also been reported by Martin (1984) who found that northern harriers (Circus cyaneus), switched from hunting voles in alfalfa fields to hunting lizards in sagesteppe after the alfalfa exceeded 43 cm in height. Other cultivated crops (grain and potatoes) typically were not harvested during the nesting season and were avoided by foraging Swainson's hawks; presumably the high plant cover density of these crops limits the accessibility of small mammal prey (Bechard 1982).

Vegetative structure, rodent populations and foraging use of grassland habitats were dependent on land use practices. Ungrazed grasslands had moderate vegetative height and high relative abundance of primary prey and, when available, were strongly preferred by foraging Swainson's hawks. Plant cover density in pastures grazed by livestock was extremely low, which likely caused the low abundance of

montane voles I observed in pastures (Hodgson 1972, Feldhamer 1979). Ground squirrels and pocket gophers were present in grazed pastures, but this habitat was seldom used by foraging Swainson's hawks. Abandoned fields and rabbitbrush communities were variable in vegetation structure but resembled pastures in having very low plant cover density and low relative abundance of primary prey species (Table 9). Like pastures, use of these habitats by foraging hawks was significantly less than their availability. These results seem to contrast with the findings of Southern and Lowe (1968), Wakeley (1978) and Bechard (1982), who found that foraging raptors selectively utilized habitats with low plant density irrespective of prey density. In this study, however, the high availability of prey in alfalfa fields, even after plant cover density increased post-harvest, probably outweighed the potential benefit of foraging in other open habitats with lower prey density but higher prey vulnerability..

Sage-steppe habitats supported high relative abundance of several species of small mammals but typically did not contain ground squirrels, voles or pocket gophers in appreciable numbers (Table 9). Most small mammal captures in sage-steppe consisted of Peromyscus and Heteromyid rodents that are nocturnal (Ingles 1965); the only diurnal species was the least chipmunk. These species were rarely recorded as prey of Swainson's hawks in this study.

Availability of potential prey in sage-steppe habitats was further reduced by the tall structure and dense cover provided by sagebrush stands (Janes 1985, Littlefield et al. 1984). In my study, foraging Swainson's hawks avoided sage-steppe even if it was the dominant habitat within the home range.

In addition to tracking temporal changes in habitat structure and prey availability related to agricultural activities, foraging Swainson's hawks also responded to changes in relative abundance and body composition of different prey species. Belding's ground squirrels were an important prey item for the hawks during courtship, nestbuilding and incubation, and may have been important in increasing body condition of hawks prior to egg-laying (Newton 1979, Janes 1985). The early-season importance of ground squirrels may be the primary factor responsible for the absence of Swainson's hawks from the Shasta Valley, which is not occupied by Belding's ground squirrels. However, the proportion of ground squirrels in the diet of Swainson's hawks in the Butte Valley declined rapidly as the nesting season progressed. The rapid accumulation of body fat by Belding's ground squirrels prior to estivation in early July (Turner 1972, Morton 1975) was associated with a high degree of wastage during consumption by Swainson's hawks in this study. Also, Kirkley and Gessaman (1990) have shown that nestling Swainson's hawks may die of dehydration

if fed diets composed of fat adult ground squirrels. The proportion of ground squirrels in the diet of the hawks in this study declined rapidly prior to the squirrels' estivation date, suggesting that the hawks were switching to prey species such as pocket gophers and voles with lower fat content (Kirkley and Gessaman 1990) (Fig. 2) while large numbers of squirrels were still available. Another significant prey shift occurred in late July when Swainson's hawks began feeding on grasshoppers; this prey resource was exploited by adult and recently fledged young and may have been an important energy source prior to migration (Johnson et al. 1987, Woffinden 1986). Aerial foraging by Swainson's hawks feeding on grasshoppers resulted in apparent reduction in habitat selectivity: hawks followed grasshopper swarms over large areas and across habitats.

Constraints on optimal habitat selection

The process of habitat selection occurs at the level of individual animals (Hilden 1965, Wiens 1985) and it is at this level of resolution that the habitat relationships of Swainson's hawks in this study are most clear. At short temporal scales, foraging Swainson's hawks closely tracked variability in prey density and vegetation structure, and

exhibited predictable preferences for specific habitats wherein energy return (prey captures) per unit of hunting effort was maximized (Royama 1970, 1971). Fitness of nesting Swainson's hawks was strongly correlated with the availability of these preferred habitats. During the nesting season, the energetic rewards of foraging in preferred habitat was constrained by nest site location and the distance to patches of preferred habitat (Orians and Pearson 1979); this relationship was reflected in the negative correlation between hawk fitness and distance to alfalfa fields. Theories of habitat selection and animal distribution (Rosensweig 1981) predict that individuals should select habitats wherein their fitness is enhanced or maximized, and the habitat composition of territories, distribution of individuals, and population density should reflect these habitat preferences. Wiens (1985) suggested that the observed patterns of habitat selection by species, populations and communities are the result of the summation of habitat choices made by individuals. Optimal habitats should contain the highest densities of individuals or territories and suboptimal habitats should be colonized only when the best habitats are saturated (Fretwell and Lucas 1969, Fretwell 1972). Within the timeframe of this study, patterns of habitat selection by Swainson's hawks nesting in the Butte Valley were not consistent with these predictions; habitat preferences exhibited by foraging individual hawks

were not expressed in the placement of nest sites or distribution of territories. Large areas of high-quality habitat were not saturated with breeding pairs, yet 22% of traditional pairs nested in marginal habitats and exhibited low reproductive success.

Lack of concordance between breeding bird density and habitat quality has been reported in many studies (Hilden 1965, Fretwell 1969, Wiens 1985) and has led to increased recognition of the importance of factors that constrain optimal habitat selection. Inter- and intraspecific competition (Lack 1946, Svardson 1949) and behavioral attributes such as site tenacity may limit the degree to which free choices are made (Cody 1985). In variable environments, population density and distribution may not track changes in habitat structure or food resources: site tenacity may intensify this effect (Wiens 1985). My data on the population structure, distribution and interspecific relationships of Swainson's hawks nesting in the Butte Valley suggested that the hawks were constrained from occupying an "ideal distribution" (Fretwell and Lucas 1969) in relation to high-quality habitat.

Competition

In studies by Janes (1985, 1987) and Rothfels and Lein (1984), sympatric Swainson's hawks and red-tailed hawks exhibited strong interspecific territoriality, maintained by

aggressive interactions. These studies and others (Craighead and Craighead 1956, Schmutz et al. 1980, Cottrell 1981) suggest that these two hawk species compete for similar prey resources and nest sites. Janes (1987) reported that red-tailed hawks dominated sites with higher perch densities and concluded that, through competitive interaction, red-tailed hawks can limit the distribution of Swainson's hawks. My observations in the Butte Valley did not support the contention that red-tailed hawks constrained Swainson's hawks from occupying any particular habitat. Although the early-nesting red-tailed hawks occasionally usurped nests used by Swainson's hawks in the previous year, the general abundance of nest sites and close spatial association between the two species suggested a low level of spatial exclusivity. Coexistence of the two species may have also been fostered by the high abundance of Belding's ground squirrels available to red-tailed hawks during their entire nesting period -- it seemed unlikely that prey availability was limiting during the spring and early summer.

Site tenacity and environmental variability

Behavioral attributes such as philopatry and natal site fidelity in breeding birds may create significant time lags in avian response to changing environmental conditions (Hilden 1965, Wiens 1985). Territory location and density of site tenacious species, particularly long-lived species,

may take years to reflect changes in habitat conditions (Wiens 1985). Habitat selection and territory establishment by individuals of these species may be exercised only once, with all subsequent breeding attempts occurring at the same territory (Cody 1985), regardless of habitat change. Densities of site tenacious species may therefore reflect habitat conditions in the past (Van Horne 1983) and be misleading indicators of present habitat suitability. Swainson's hawks are relatively long-lived (minimum 12 years, this study; 16 years, Houston and Milar 1981) and exhibit a high degree of site (territory) fidelity. Territory fidelity in this species may be partly attributable to temporal constraints on exploring or colonizing new sites (Levins 1968). Migrating Swainson's hawks arrive relatively late on the breeding grounds and must rapidly find mates and begin nesting; less than 25% of clutches completed after May 20 were successful. Reduced reproductive success at Swainson's hawk territories with one or more new pair members (Table 4) also indicates significant fitness costs associated with moving to new sites. Changes in habitat composition of territories, particularly in agricultural areas, occurred unpredictably, often on a time scale considerably shorter than a hawk's lifespan. Annual variation in the extent of cultivation or the types of crops grown within a territory had a dramatic effect on the quality of habitats available to breeding

hawks, yet territory locations were remarkably stable. Nesting hawks may have compensated for these short-term variations in habitat quality by shifting to new foraging areas, or may have experienced reduced reproductive success.

Behavioral constraints on the response of Swainson's hawk territory locations to variation in habitat quality may also explain the lack of concordance between hawk density and landscape habitat patterns. In agricultural environments, long-term changes in farming practices and crops produced result in dramatic landscape-level changes in habitat suitability. In the early 1980's, reduction of the government subsidy on milk production led to decreased production of alfalfa hay in the Butte Valley. Cultivation of alfalfa was discontinued in several areas in the valley (Mt. Hebron and parts of Cedar Mt. blocks), and was replaced with grain or abandoned fields. Conversely, acreage of alfalfa increased in the Ball Mt. block after changes in irrigation policies led to decreases in pasture and row crops. The abundance and distribution of Swainson's hawk territories in the Butte Valley prior to this study are not known, however, present densities of Swainson's hawk territories among landscapes in the Butte Valley seem more in accordance with habitat distribution patterns seen on 1969 aerial photographs than with the present habitat pattern. Habitat quality in the areas of highest hawk density (Cedar Mt. and Mt. Hebron blocks) has declined

dramatically during the past decade, whereas newly created high-quality habitat (Ball Mt. block) remains unoccupied after 12 years. Site tenacity and long lifespan exhibited by Swainson's hawks, combined with the tendency of young hawks to settle near their natal site, may result in time lags encompassing multiple generations before significant population shifts to new areas are detectable.

The persistence of hawk pairs in sage-steppe habitats in the Butte Valley may be related to subtle long-term changes in habitat characteristics due to extended drought conditions and continued grazing by livestock. Comparison of aerial photographs taken in 1949, 1979, and 1986 indicated a trend toward increased shrub dominance and reduction in grass coverage in sage-steppe habitats in the Butte Valley. Abundance of grassland-dependent prey, particularly voles, in sage-steppe habitats may have been higher in the past and supported a stable population of Swainson's hawks. This trend may help to explain the declining Swainson's hawk population reported in the Klamath Basin, where most of the territories monitored by Bloom (1980) (Risebrough et al. 1989) were in sage-steppe habitats.

Summary

The hierarchical approach used in this study highlighted the influence of study scale on the patterns of habitat selection observed, and allowed description of habitat relationships not evident at a single level of resolution. Interpretation of habitat selection patterns observed at a particular level was dependant on knowledge of selections made at another scale: use and availability of selected habitats, for example, was affected by the location of nest sites, which was largely independent of foraging habitat. These results emphasized the utility of using a stepwise approach to studies of habitat selection. Measurement of habitat selection processes occurring at finer scales (foraging and prey selection by individuals) allowed identification of temporal and spatial scales appropriate for studies of Swainson's hawks. Resources and habitat components identified as important at finer scales of resolution were compared to hawk responses such as density and distribution measured at coarser scales. Lack of concordance between these measures led to evaluation of environmental and behavioral factors that constrain habitat selection. Lack of concordance between levels of habitat selection also pointed out the importance of using appropriate response metrics in habitat selection studies (Karr 1983). Fitness of Swainson's hawk pairs was more closely correlated with habitat quality than was hawk

density. Recognition of hierarchical structure in ecological systems reveals a powerful tool for identification of the key components, organization, and interlevel relationships that are essential to understanding the underlying structure of the system.

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