

THE UNIVERSITY OF CALGARY

HOME RANGE AND HABITAT USE IN A DENSE POPULATION OF

RED-TAILED HAWKS

BY

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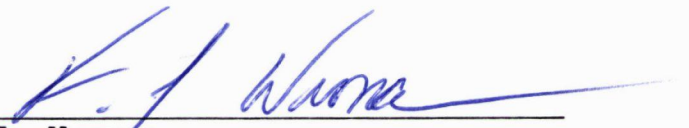
THE UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "HOME RANGE AND HABITAT USE IN A DENSE POPULATION OF RED-TAILED HAWKS", submitted by Brian J. Sevick in partial fulfillment of the requirements for the degree of Master of Science.



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ABSTRACT

The breeding density of raptors is usually limited by food or nest-sites. A study area immediately southwest of Calgary, Alberta, supporting a dense population of Red-tailed Hawks (Buteo jamaicensis) was thought to contain abundant food and nest-sites. This study attempted to determine the importance of food to this population.

Density of territorial hawks was the highest recorded in North America. Breeding pair densities exceeded all known values except one. Rates of nonbreeding (failure to lay eggs) were high in both 1984 and 1985. The cause of nonbreeding could not be determined.

Red-tailed Hawks spent most of their time perched. Flight activity (display, agonistic, "other") was restricted to mid-day and afternoon periods. Temperature, wind velocity and precipitation intensity had significant effects on activity patterns. Flight activity decreased and perching increased over the nesting cycle for both breeding and nonbreeding hawks.

Hawks defended exclusive three-dimensional home ranges. Peaks in utilization distributions were associated with nests and with perching areas that offered vantage points. These perches appeared to serve a territorial

advertisement function. Few significant differences were seen in area of home ranges between breeding and nonbreeding pairs. Home range areas decreased over the nesting cycle.

Richardson's ground squirrels (Spermophilus richardsonii) were the predominant prey and were captured from perches. More attempts to capture prey were made in the morning and midday periods than in afternoon and evening periods. Success rates declined over the course of the day.

Burrow counts identified pasture as the important source of Richardson's ground squirrels. Significantly more prey-capture attempts were made in pasture and hayfield habitats than expected. Prey abundance within habitats had little effect on time spent within habitats. Few habitat preferences were evident and territory size was not adjusted to the amount of food available.

Food or nest-sites do not appear to limit the density of Red-tailed Hawks on the study area. Resources necessary for survival and successful reproduction (including food) are contained in a minimum fixed amount of space. This space is at a premium and may limit breeding density. Competition for space is manifested in the form of territoriality.

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CHAPTER ONE

INTRODUCTION

The Red-tailed Hawk (Buteo jamaicensis) is one of the most abundant and widely-distributed species of raptor in North America. On the northern Great Plains these hawks have appeared to increase both their numbers and their range since early settlement (Houston and Bechard 1983). These increases are attributed to a suppression of range fires, which has resulted in a concomitant increase in the number and size of stands of trees. More potential nest-sites and, consequently, greater numbers of breeding Red-tails are assumed to be the end result. Before this population trend can be evaluated, an understanding of how Red-tailed Hawk population densities are regulated must be gained.

The breeding density of raptors is normally limited by food or nest-sites, whichever is in shorter supply (Newton 1976, 1979). Limited resource availability results in competition and ultimately limits breeding density. There are several lines of circumstantial evidence for limitation by competition for food resources (Newton 1979). First, large raptors, depending on large, sparsely-distributed

prey, breed at lower densities than smaller raptors which depend on smaller and more numerous prey. Second, local differences in breeding density are associated with local differences in food abundance. Third, cyclical fluctuations in breeding density are linked with cyclical fluctuations in food. Fourth, sudden and long-term changes in breeding density are associated with corresponding changes in food.

Several lines of circumstantial evidence for limitation by competition for nest-sites are also available (Newton 1979). First, low breeding densities occur in areas that are low in nest-sites, but otherwise suitable. Second, increases in breeding density are associated with provision of artificial nest-sites. The links between breeding density and food and nest-sites suggest limitation, but cannot be considered conclusive (Newton 1979).

Other habitat features may limit breeding density. The ultimate limiting resource may vary from one situation to another (Village 1983a). Few studies have investigated how raptors relate to their underlying habitat. More work in this area would further our understanding of which resources are important and might be limiting.

Availability of perch sites may limit breeding densities of Red-tailed Hawks. They are important to

breeding birds for several reasons. Perches that offer views of both territory and nest are preferred and allow the detection of intruders (Santana C. et al. 1986, Santana C. and Temple 1988). Foraging perches may also be limiting. Red-tailed Hawks forage mainly from perches, and the number and arrangement of perches in a territory likely determines foraging success, and ultimately reproductive success (Janes 1984a).

Territorial behavior might also be presumed to limit breeding density. Instead, territoriality probably adjusts breeding densities to the resources available (Newton 1979), serving as a proximate factor influencing breeding density (Newton 1976, Davies 1978, Village 1983a). Territorial behavior has more of a direct effect on breeding dispersion patterns than on absolute densities (Nilsson et al. 1982). Resource availability, rather than competition for resources, is probably the ultimate factor determining the breeding density of raptors

Both breeding and nonbreeding adult birds of prey must be considered when examining limitation of breeding density. Population regulation in raptors concerns territorial birds that lay eggs and rear young, as well as those that hold territories, yet do not lay eggs (Newton 1979). Failure to lay eggs should be carefully assessed in raptor population studies (Postupalsky 1974). Nonbreeding

birds compete for resources throughout the breeding season and their numbers are limited in the same manner as breeding birds.

In the area immediately south of Calgary, Alberta, breeding densities of Red-tailed Hawks are greater than most areas in North America (Rothfels and Lein 1983). The area supports dense populations of Richardson's ground squirrels (Spermophilus richardsonii) and numerous stands of trees provide ample nest-sites (Rothfels 1981). In another area of southern Alberta, Schmutz et al. (1980) showed that food was superabundant and not being competed for. Food and nest-sites did not appear to be limiting the breeding population in either study.

The study of the behavioral ecology of Red-tailed Hawks immediately south of Calgary, form the basis of this thesis. The limitation of breeding density by competition for resources is of particular interest. It is an extension of the work of Schmutz (1979) and Rothfels (1981) who proposed that space, not food or nest-sites, was limiting the population density of breeding Red-tailed Hawks. They hypothesized that this space is necessary to perform nesting activities without disturbance. In this study, I attempted to determine how the high nesting density is achieved, by examining how the hawks relate to

their underlying habitat. The role of food and space were of particular interest.

The specific objectives of this study were:

1. To determine the breeding density and success of Red-tailed Hawks on a study area south of Calgary, Alberta.
2. To characterize the social behavior of these hawks by comparing activity patterns between different stages in the nesting cycle and between breeding and nonbreeding nesting pairs.
3. To determine the relationships between territory size and breeding status, stage in nesting cycle and habitat composition of territories.
4. To examine the feeding ecology of Red-tailed Hawks near Calgary, particularly their food habits and choice of foraging habitats.
5. To relate their distribution of activity to resource abundance in various habitats.

CHAPTER TWO

STUDY AREA AND GENERAL METHODS

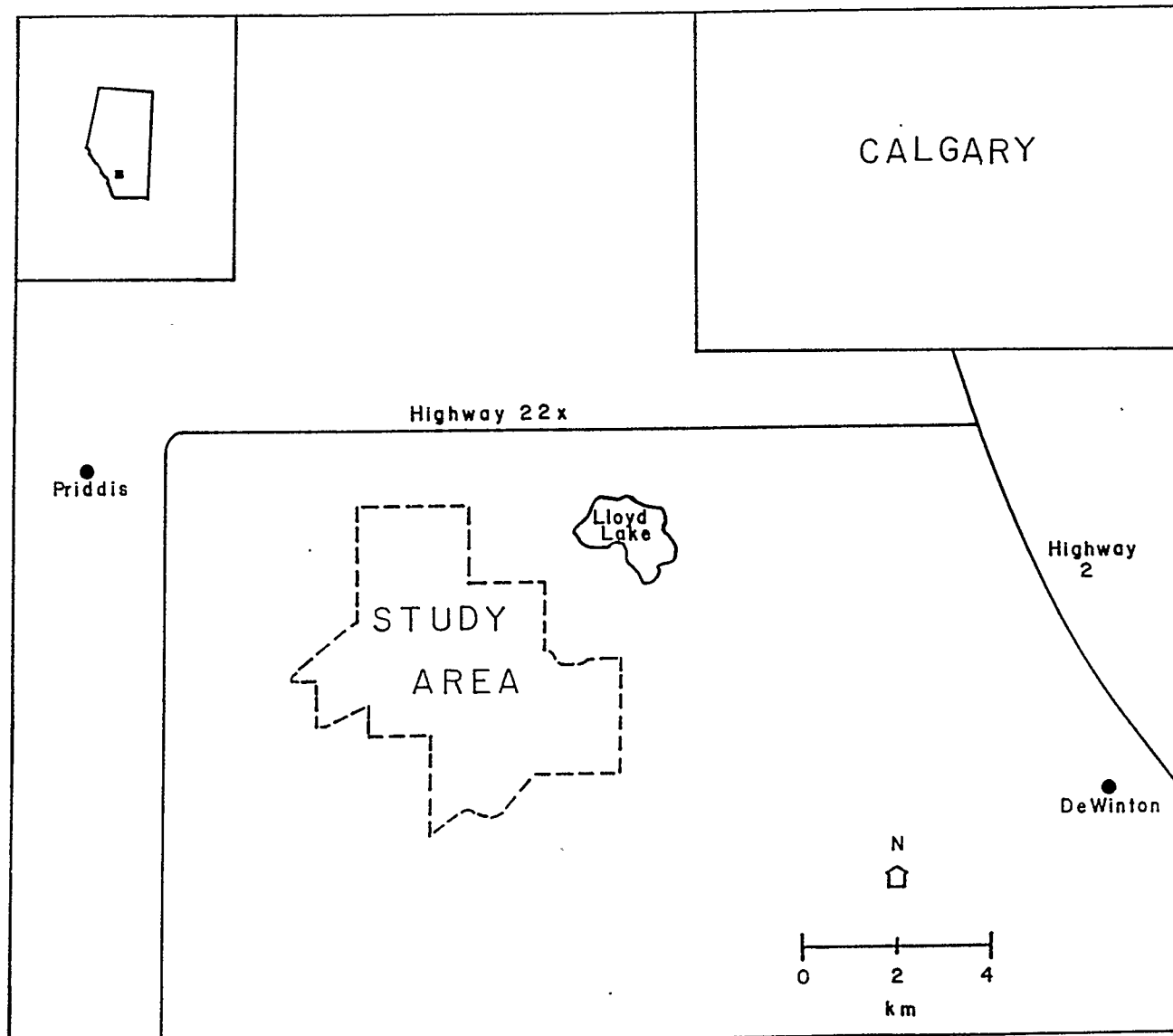
1. STUDY AREA

In April, 1984, a 26 km² block of farmland southwest of Calgary was chosen as the study area (Fig. 1), based on its high density of nesting Red-tailed Hawks and topography. A nest inventory in 1983 and work by Rothfels and Lein (1983) showed a very high nesting density in the area. Rolling hills in the area facilitated observation of hawks. Boundaries of the study area were arbitrarily chosen and were delineated by roads, trails and cutlines.

Agricultural activity in the area is predominantly ranching, with some cereal crop production. There are no "acreage" developments within the study area. Despite its close proximity to Calgary, human activity inside the study area is low. Most of the land is posted against trespassing and consequently most human activity is related to agricultural practices.

The study area lies within the Aspen Parkland Ecoregion (Strong and Leggat 1981). The area is primarily hilly grassland, with abundant wooded areas. Within these

Figure 1. Schematic map showing the location of the study area in relation to Calgary, Alberta and other geographic features.



areas, trembling aspen (Populus tremuloides) predominates, with balsam poplar (Populus balsamifera), white spruce (Picea glauca), and willows (Salix spp.) scattered throughout. Most of the agricultural land consists of pasture and hayfields. Some of the land is cultivated for various cereal crops. Farming practices in the area are fairly consistent from year to year. A more thorough description of habitat and land use is provided by Rothfels (1981).

Meteorological records are available for Calgary International Airport from Environment Canada. This allows an examination of climatic conditions found in the region for both 1984 and 1985 (Table 1). Historical norms for 1951-1980 are provided for comparison. The climate of Calgary and the study area is quite variable. The mean values provided do not reveal the variability found between days. Temperature and wind velocity approximated normal values for all months and between both years. Precipitation values appeared lower than normal in most months for both years.

2. GENERAL METHODS

General methods common to all aspects of the study are outlined in this chapter. Specific methods used in

Table 1. Meteorological data for Calgary, Alberta (Source: Environment Canada). Actual mean monthly values for 1984 and 1985 are compared to normal mean values recorded from 1951-1980.

Month	Mean Daily			Total			Mean Wind		
	Temperature			Precipitation			Velocity		
	(°C)			(mm)			(km/h)		
	1984	1985	Norm	1984	1985	Norm	1984	1985	Norm
April	5.4	5.3	3.3	15.5	23.9	32.6	16.3	19.4	18.1
May	8.7	11.8	9.4	65.8	21.9	48.7	17.9	16.8	18.2
June	13.8	13.1	13.5	73.0	40.9	89.4	16.4	17.3	17.0
July	17.4	18.4	16.4	24.6	53.2	65.4	15.9	16.0	14.9
August	17.4	14.4	15.2	16.4	66.2	55.4	15.5	21.3	14.4

investigating nesting success, activity patterns, home range and territory size, habitat and prey preferences are described and discussed in the appropriate chapters.

All nests in the study area were located by an intensive inventory throughout the 1983 breeding season, and by spring searches in 1984 and 1985. Prior to leaf-out, stick nests suitable for use by Red-tailed Hawks were identified and plotted on an aerial photo mosaic map. Many of the nest-sites were known from previous work in the area (Rothfels 1981). Others were spotted from vehicles using binoculars and 15-45x telescopes. Because of accessibility and visibility problems, some had to be located through searches on foot. Disturbance during nest checks was minimized by following procedures outlined by Fyfe and Olendorff (1976) and Call (1978). No close or prolonged approaches were made until after hatching.

After locating all suitable stick nests, an attempt was made to determine the reproductive status of each breeding territory using the criteria of Postupalsky (1974). Monitoring of nest status continued throughout the breeding season. Species observed using nests included Red-tailed Hawks, Great Horned Owls (Bubo virginianus), Swainson's Hawks (Buteo swainsoni), and Common Ravens (Corvus corax).

All active raptor nests were visited and climbed at least once after eggs were presumed to be hatched. Food remains found at the nests were recorded. Brood size and age of nestlings were determined during these visits. Nestling age was estimated by taking measurements of the 4th primary (Petersen and Thompson 1977, Torrance 1984, Bechard et al. 1985). All nestlings were eventually banded with U. S. Fish and Wildlife Service aluminum leg bands prior to fledging. Approximate fledging dates of Red-tailed Hawks were determined by nest checks or during behavioral observations.

Detailed behavioral observations of adult Red-tailed Hawks were made from mid-April to mid-August in 1984 and 1985. Observations on movement, activity, habitat use, and foraging behavior were made on 15 and 16 territorial pairs in 1984 and 1985, respectively. Both breeding and nonbreeding pairs were selected for study. Where possible, data were collected for the entire breeding season. To maintain equal sampling of non-breeding and breeding territories, and because of failures during incubation, some territories were dropped or added for observation midway through the breeding season. At any given point in the study, 12 pairs of birds were under observation. Information was obtained for the incubation, nestling, and fledgling stages of the nesting cycle for breeding birds.

Selection of territories was based primarily on the ease with which the territory could be observed. Open hillsides or surrounding roads and trails facilitated this process and were highly desirable. Contiguity with other territories and the presence of individually-recognizable birds were other selection criteria.

Within a pair, a bird that was not involved in nest-related activities (incubation, brooding, feeding young and nest vigilance) was normally observed. Because females are usually involved in these nest-related activities (Petersen 1979), the bird selected was usually the male.

The study required individual recognition of the hawk(s) belonging to a particular territory. In all three years of the study an attempt was made to mark adults with colored, numbered, patagial markers (Wallace et al. 1980, Young and Kochert 1987). Dho-ghaza nets (Clark 1981), using mounted Red-tailed Hawks or Great Horned Owls as lures (McCrary 1981, Bechard 1982), were used to trap adult hawks. Bal-chatri traps (Berger and Mueller 1959) baited with Richardson's ground squirrels were also used to capture adults. Both of these techniques met with limited success. All nestlings were also marked with patagial tags just prior to fledging. A combination of patagial marking, plumage characteristics, sexual dimorphism, and especially

behavior did allow identification of hawks belonging to a given territory.

Territorial pairs were observed from hillsides overlooking nesting territories. All territories were observed for 2 hours once every 2 days on a schedule which varied to sample all times of the day. The observations were divided temporally into four periods. These were: Period 1 (early morning, before 1030), Period 2 (midday, 1030 to 1430), Period 3 (afternoon, 1431 to 1830), and Period 4 (evening, after 1830). Locations of hawks were estimated visually every two minutes during the two-hour period and plotted directly on an aerial photo mosaic map (1:10,785). The behavior of the birds was also recorded at each interval according to predetermined categories. Weather conditions were recorded at the beginning and end of each observation period. The sets of location data provided the boundaries and sizes of territories and home ranges for each of three nesting cycle phases. The behavioral information allowed a comparison of activity budgets.

Major habitat categories were delineated on the aerial photo mosaic map of the study area. The habitats were categorized as:

1. Woods: any clump or expanse of trees or bush evident on the aerial photo mosaic map and known to still exist.

2. Pasture: areas presently or previously (within 1 year) grazed by livestock (mainly cattle). Most vegetation was short and the areas were not cutlivated during the study period.

3. Hayfield: areas where grasses or legumes were grown. They were usually cut once and sometimes twice per year for hay. A few of these fields were ploughed and reseeded at intervals of several years.

4. Cropland: cultivated fields in which cereal grains were planted.

5. Fallow: cultivated fields where no crop was planted. Vegetation was sparse as the fields were normally turned over several times during the spring and summer.

6. Other: any areas that did not fit into any of the above categories.

Habitat types were determined in 1983 and later confirmed by periodic inspections in 1984 and 1985 to record changes associated with agricultural practices. The area of each habitat was determined using a digitizer tablet and associated computer programs. Habitat type for each location observation was later determined from the labelled aerial photo mosaic map. When this information

was compared to habitat availability, habitat selection and preference could be established.

Indices of prey abundance in various habitats were obtained by counting the number of active burrows of Richardson's ground squirrels (signs of recent digging) and "fresh" mounds of northern pocket gophers (Thomomys talpoides) (Reid et al. 1966) along transects. This information was used to determine if habitat preference was associated with food abundance. The habitat type and prey species of all prey capture attempts were also recorded to investigate this relationship.

CHAPTER THREE

BREEDING DENSITY, CHRONOLOGY AND SUCCESS

INTRODUCTION

To confirm that high breeding densities of Red-tailed Hawks were present on the study area, a thorough evaluation of all sections of the breeding population was necessary. This involved locating and monitoring all members of the population throughout the breeding season. Additional information on breeding chronology and breeding success was gained in this process, permitting an examination of the effects of high density on chronology and reproductive success.

In the past, comparative studies of breeding raptors and their reproductive success have been difficult because of different methods of censusing, different criteria of evaluation, and different terminologies employed in reporting findings (Postupalsky 1974). These problems have been addressed and standards are now available (Postupalsky 1974, Steenhof 1987). A thorough breeding study should include an assessment of the breeding status of all members of the population (Newton 1979, Steenhof 1987). To achieve

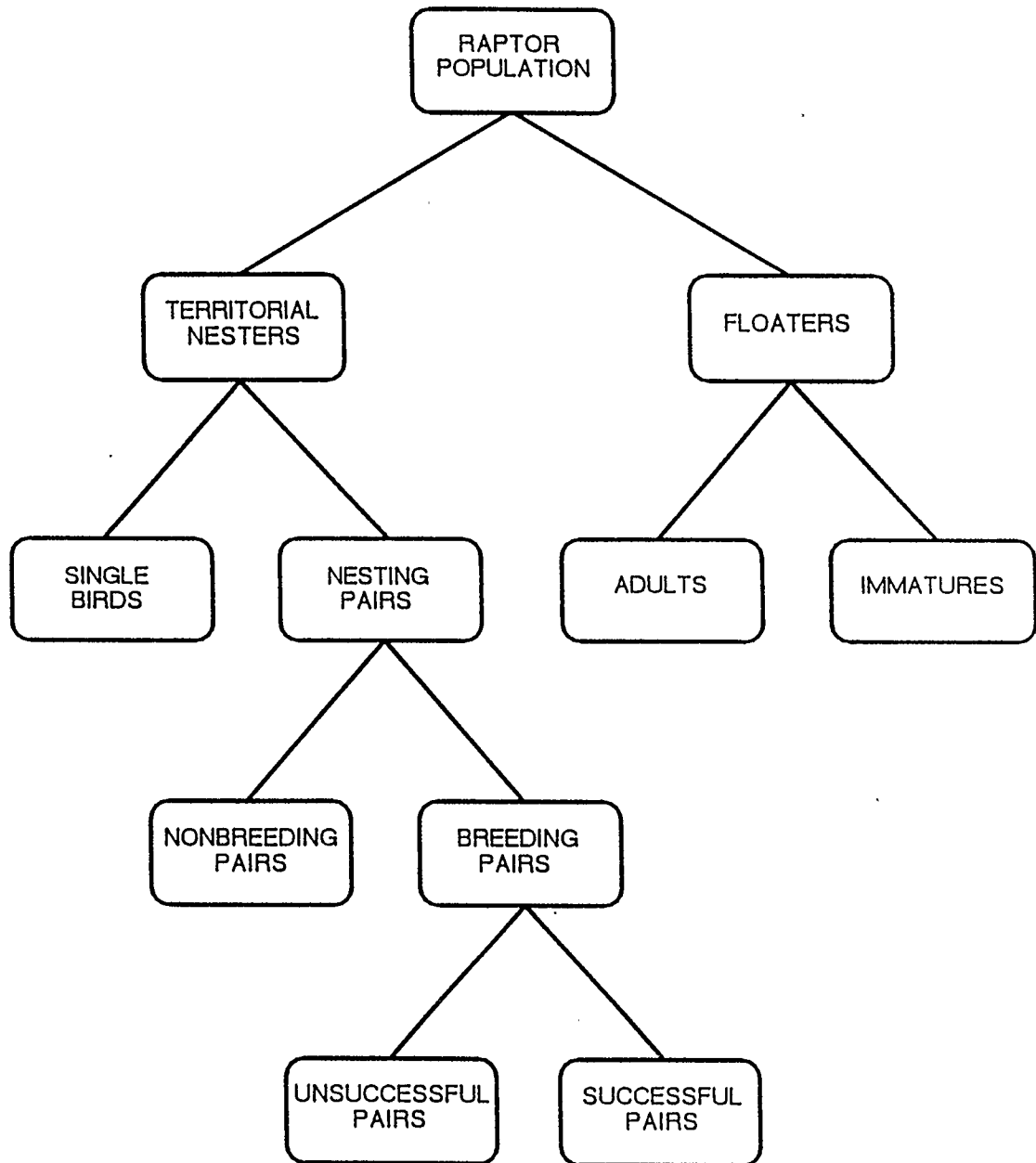
this, an understanding of how the population is organized is required.

Steenhof (1987) has provided a useful breakdown (Fig. 2). Breeding populations of raptors consist of territorial nesters and floaters. Floaters are not associated with any nesting territory and can be either adult or immature birds. Territorial nesters are single birds or nesting pairs that are associated with nesting territories. Nesting pairs include both nonbreeding and breeding pairs. Breeding birds are recognized by observations of eggs, an incubating adult, or fresh eggshell fragments. Breeding pairs can be either successful or unsuccessful. Success is defined by the production of one or more young that reach fledging age.

Productivity of a population should be calculated on the basis of all nesting pairs (Postupalsky 1974, Steenhof 1987). Determination of the extent of nonbreeding (failure to lay eggs) is considered crucial for the proper assessment of a population (Brown 1974, Postupalsky 1974, Newton 1979). Nonbreeding has not been measured, or has been inadequately reported, in many studies of raptor populations.

In view of the importance of surveying all segments of the population, it was an objective of this study to document the breeding density, the extent of nonbreeding,

Figure 2. Division of a raptor population into segments based on reproductive status (Redrawn from Steenhof 1987).



the breeding chronology, and the reproductive success of the population of Red-tailed Hawks on the study area.

METHODS

The procedures for locating breeding territories were described in Chapter 2. Each breeding territory contained at least one stick nest and often one or more alternate nests. To determine the density of the raptor population, the distribution of individuals in various reproductive segments of the population throughout the study area was determined. Monitoring of birds was carried out continuously throughout the breeding season to detect changes in reproductive status.

Territorial nesters were identified by various behavior patterns: they showed preference for areas around nest-sites (see Chapter 5), defended and displayed in the area (see Chapters 4 and 5), copulated in the area, and built and repaired nests. Nests being utilized by nesting pairs were identified by the presence of green sprigs of vegetation "decorating" the nest (Bohm 1978). Decoration continued throughout the season for both breeding and nonbreeding nesting pairs. Both breeding and nonbreeding nesting pairs tended to focus their nesting activities on only one nest within the territory.

Nesting pairs showing signs of incubation were classified as breeding. In most cases, direct observations of nests by telescope allowed the detection of incubation and the assignment to either breeding or nonbreeding status. Observation of two paired birds perched away from the nest for long intervals in cold temperatures (during the normal incubation period) indicated nonbreeding status. If nests could not be observed directly by telescope, nest trees were climbed to confirm nonbreeding status in early June (when breeding birds were already in the nestling stage of the nesting cycle). Earlier visits were not made in order to avoid disturbing the birds, which may cause nest abandonment (Fyfe and Olendorff 1976, Steenhof and Kochert 1982).

Observations with telescopes, climbs late in the nestling stage, and observations of fledglings near the nest were used to determine the success of breeding pairs. Successful pairs had at least one young reach the fledgling stage (Postupalsky 1974, Steenhof 1987). Actual observations of fledged young were used to assign success status rather than a minimum fledging age calculated from growth measurements (Steenhof 1987).

An attempt was made to assess the floater population of Red-tailed Hawks on the study area. Hawks not associated with any nesting territory were recorded during

regular surveys of the study area and while making behavioral observations. Adults as well as subadults were identified. Immatures are readily distinguishable from adults by tail plumage (Clark and Wheeler 1987). Immatures have brown or reddish-brown tails. Second-year birds have tails with mixed brown and red feathers. Adults have red tail feathers.

The reproductive chronology of Red-tailed Hawks was determined both by direct observations and from estimated nestling ages. Chronologies were developed only for those pairs under intense observation. Estimates based on nestling age were confirmed by behavioral observations for these birds.

Nestlings were aged by taking measurements of the fourth primary, as described by Bechard et al. (1985). Ages were calculated for each nest visit. A 31-day incubation period (Bent 1937, Wiley 1975), and a 45-day nestling period (Wiley 1975) were used in conjunction with the nestling ages to develop chronologies.

Five measures of reproductive success were calculated. Percent success rates (percentage of pairs producing at least 1 fledgling) were calculated for both nesting pairs and breeding pairs. Mean numbers of fledged young per nesting pair, per breeding pair, and per successful pair were also calculated for each year.

RESULTS

A. NESTING DENSITY

In both 1984 and 1985, Red-tailed Hawks bred at high densities on the study area, and nests were relatively evenly distributed (Fig. 3 and 4). Nonbreeding pairs outnumbered breeding pairs in 1984, while the reverse occurred in 1985 (Table 2). Density of nesting pairs on the study area was 1.02 pairs/km² in both years. Density of breeding pairs was 0.47 pairs/km² in 1984 and 0.55 pairs/km² in 1985.

No single territorial individuals were observed in either year. A small number of floaters, including both adult and subadult birds, appeared to be present on the southern edge of the study area in both years. Apart from these floaters, only 3 other subadults were seen on the study area in two years. None were marked with patagial tags, indicating that they were not local offspring. They were chased off territories and were never present for more than one day. One adult that had been marked as a fledgling in 1983 was seen in the area for a few days in 1985, associated with the floater group.

Figure 3. Nest-sites and breeding status of territorial pairs in 1984. Filled circles represent breeding pairs and open circles represent nonbreeding pairs. Pairs under behavioral observation are indicated by squares. Dashed line indicates the boundary of the study area.

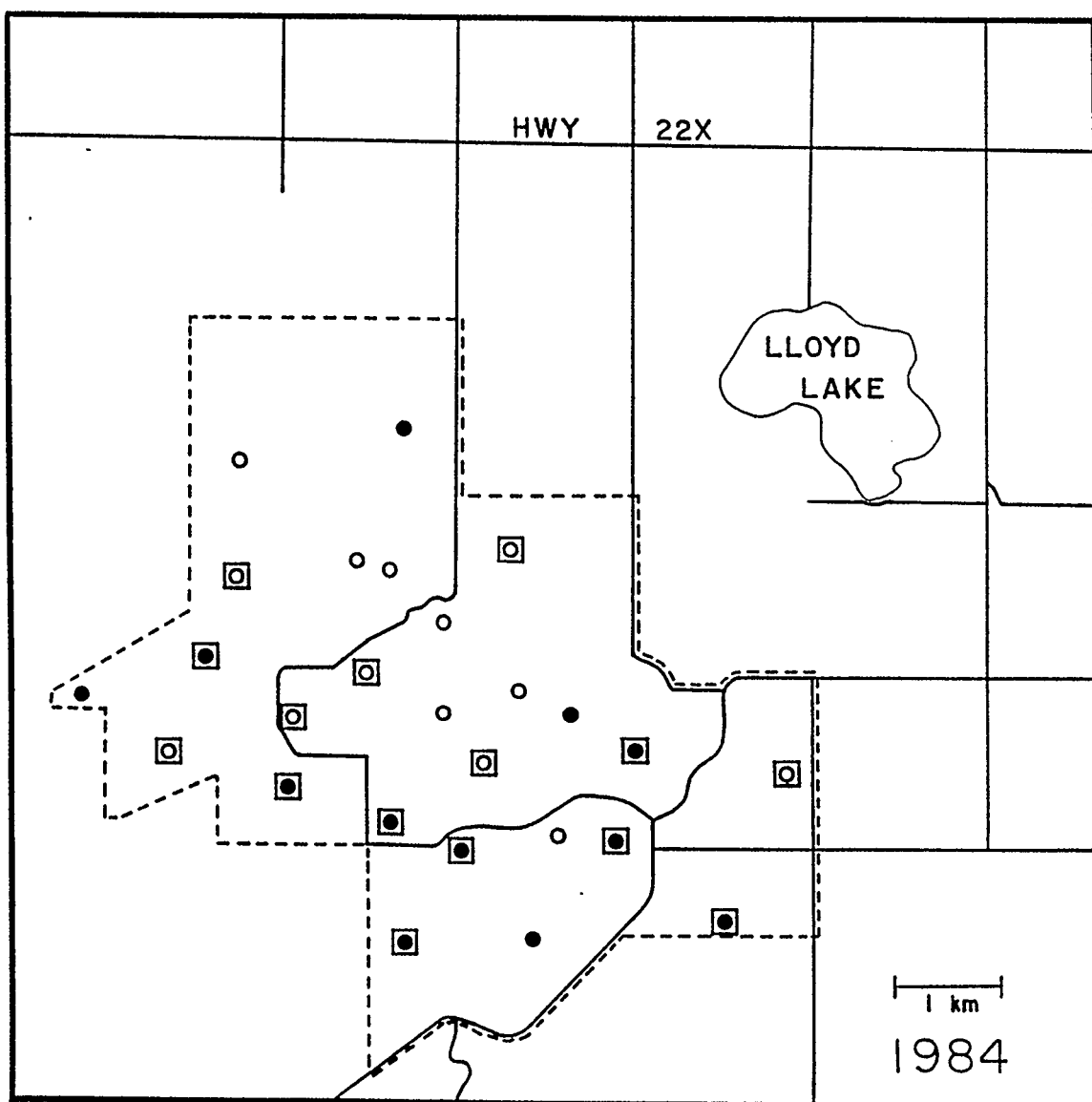


Figure 4. Nest-sites and breeding status of territorial pairs in 1985. Filled circles represent breeding pairs and open circles represent nonbreeding pairs. Pairs under behavioral observation are indicated by squares. Dashed line indicates the boundary of the study area.

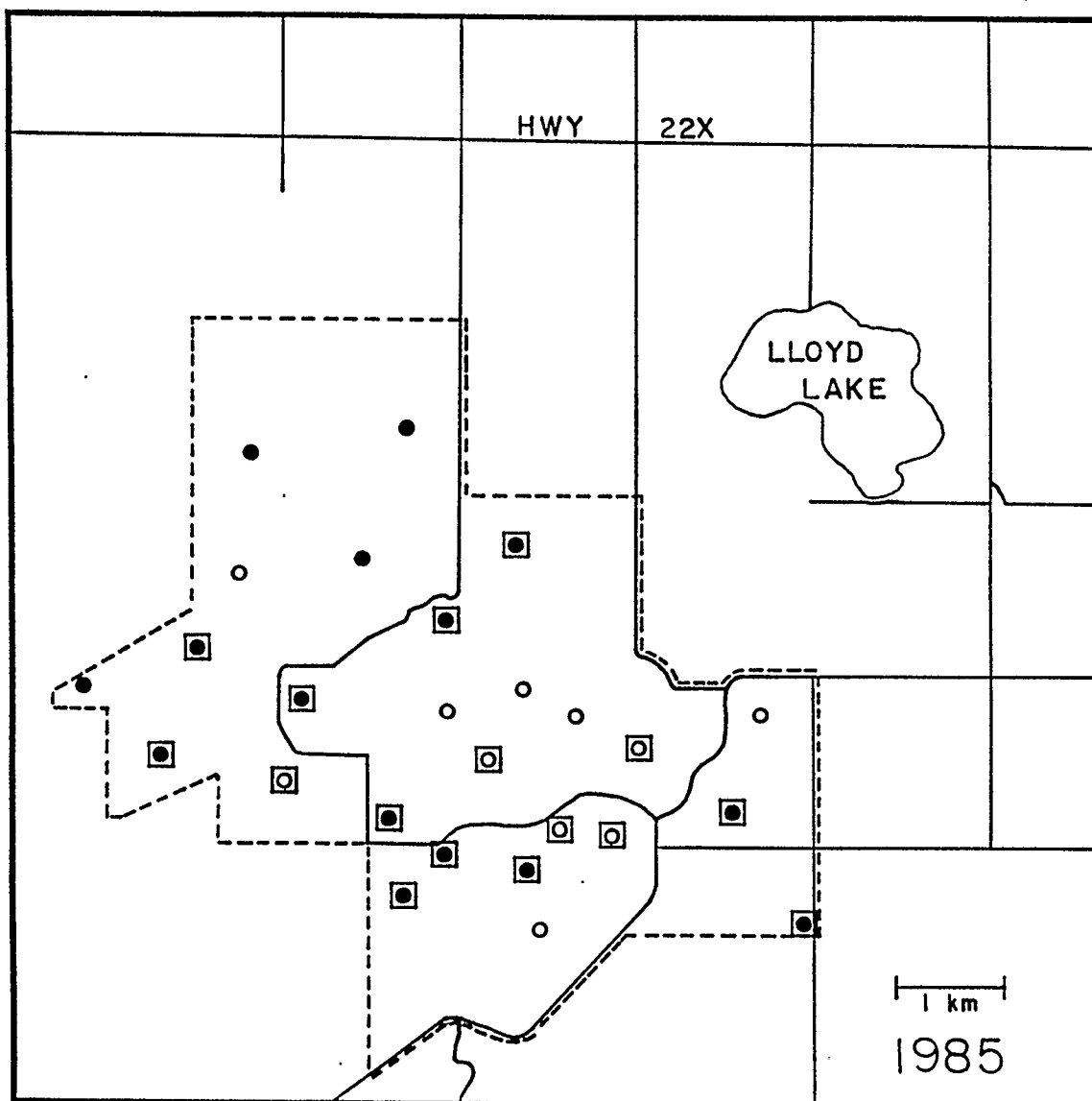


Table 2. Numbers of territorial Red-tailed Hawks on the study area.

Reproductive Status	Numbers Of Pairs	
	1984	1985
Nesting pairs	26	26
Nonbreeding	14	11
Breeding	12	15
Unsuccessful	2	1
Successful	10	14

B. REPRODUCTIVE CHRONOLOGY

The reproductive chronology of breeding Red-tailed Hawks on the study area is found in Table 3. Red-tails (including some previously marked birds) were present on nesting territories in early April of each year. Exact arrival dates for unmarked birds could not be determined because of the presence of migrants. Observations of marked birds showed that some hawks did not arrive until the end of April in both years. Greater numbers of marked and unmarked Red-tailed Hawks in early April of 1985 than in 1984 suggest that arrival times were earlier for this year.

The period over which eggs were laid was greater in 1985 (21 days) than in 1984 (9 days). Laying began earlier in 1985 than in 1984. The latest laying date was the same in both years. The assumed 31-day incubation and 45-day fledgling periods were well-supported by direct observations of nests and fledglings.

Departure dates were difficult to determine and appeared quite variable. Territories appeared to break down in mid-August with the arrival of migrants and the departure of some resident birds. A few marked and individually recognizable hawks were present in the vicinity of their territories until mid-September of each year.

Table 3. Reproductive chronology of breeding Red-tailed Hawks on the study area (N = 7 for 1984, and N = 10 for 1985).

Mean date (Range)		
	1984	1985
Laying date (1st egg)	May 4 (Apr 30-May 9)	Apr 28 (Apr 18-May 9)
Hatching date (1st egg)	Jun 4 (May 31-Jun 9)	May 29 (May 19-Jun 9)
Fledging date (earliest in brood)	Jul 19 (Jul 15-Jul 24)	Jul 13 (Jul 3-Jul 24)

C. REPRODUCTIVE SUCCESS

The reproductive success of territorial pairs on the study area varied between years (Table 4). Both measurements of success rates were higher in 1985 than in 1984. The number of young fledged was greater in 1984 than in 1985 when measured on a per successful pair basis. When measured on a per territorial pair basis, more young were fledged in 1985 than 1984.

DISCUSSION

The regular spacing of nesting territories of Red-tailed Hawks on the study area is typical of areas where food and nest-sites are uniformly distributed (Newton 1979). Observations on the return of marked birds on this study site supports nest-site fidelity in this population. Janes (1984b) has also found that territorial pairs often occupy the same territories in consecutive years. This means that some pairs of hawks changed breeding status between years and may only lay eggs every second year. More observations of marked birds over a longer time period would be necessary to further investigate this phenomenon.

Densities of territorial Red-tailed Hawks on the study area are the highest recorded in North America (Table 5).

Table 4. Reproductive success of nesting pairs of Red-tailed Hawks on the study area as calculated per territorial pair (A), per breeding pair (B), and per successful pair (C).

Sample sizes as given in Table 2.

Year	Success Rate(%) (A)	Success Rate(%) (B)	Mean No. Fledged (A)	Mean No. Fledged (B)	Mean No. Fledged (C)
1984	39	83	0.7	1.5	1.8
1985	54	93	0.9	1.5	1.6

Table 5. Densities of nesting pairs of Red-tailed Hawks from
breeding populations in various North American locations.

Pairs/km ² Mean;(Range; Number of years)	Location	Source
1.02 (1.02-1.02; 2)	Alberta	This study
0.45 (0.42-0.47; 2)	Alberta	Rothfels and Lein 1983
0.37 (0.35-0.39; 2)	Wyoming	Craighead and Craighead 1956
0.24 (0.23-0.25; 4)	Wisconsin	Petersen 1979
0.19 (1)	New York	Hagar 1957
0.14 (0.11-0.16; 2)	Wisconsin	Orians and Kuhlman 1956
0.04 (0.02-0.13; 3)	Michigan	Craighead and Craighead 1956
0.12 (0.11-0.12; 2)	Montana	Johnson 1975
0.03 (0.02-0.03; 4)	Utah	Smith and Murphy 1973

Comparative densities are provided for all known studies where values included nonbreeding territorial pairs. Much regional variation across North America is noticeable. Breeding pair densities also exceed all known values except, perhaps, that of Fitch et al. (1946) who reported an "approximate" density of 0.77 pairs/km². They did not state whether this value was a breeding pair or a nesting pair density.

Traditional explanations would suggest these population densities were due to the availability of food and nest-sites (Newton 1979). The role of these variables will be assessed in following chapters.

The high densities may be due, in part, to thorough searching methods. Only after repeated searches on foot, and constant vigilance was I confident that all territories had been identified. More customary road searches would have failed to identify several nests and territorial pairs. I estimate that I would have located approximately 75% of the total number of nests and territorial pairs, using more traditional searching methods. Intensive surveys are not always practical, but they do give the best estimates of actual densities.

This study documented the abundance of all segments of the population. Nonbreeding (nonlaying) territorial pairs were included in the density estimates as suggested by

Brown (1974), Postupalsky (1974) and Newton (1979). These nonbreeding hawks occupied and defended nesting territories (see Chapters 4 and 5). They interacted with breeding birds and competed with them for resources. Thus their inclusion in density estimates for this population seems justified.

Red-tailed Hawks on the study area exhibited a high rate of nonbreeding in both years, higher than reported for other areas in North America (Table 6). The high rate of nonbreeding on the study area in both years is puzzling. It may reflect an underestimation of the nonbreeding population in other studies or it may be a site-specific phenomenon.

It is difficult to locate and ascertain the breeding status of nonbreeding pairs. They could easily be overlooked in more limited population surveys. Only through extensive searches can the extent of this population segment be determined. Despite these problems, I feel that it is unlikely that underestimation alone can account for differences between the study site and other areas.

The possible factors contributing to a failure to lay eggs are numerous and difficult to evaluate. Postupalsky (1974) attributes nonbreeding to a variety of unspecified environmental conditions (with a possible role by

Table 6. Proportion of nonbreeding pairs in populations of
Red-tailed Hawks in various North American locations.

% Nonbreeding Territorial Pairs	Location	Source
Mean; (Range; Number of years)		
44 (42-46; 2)	Alberta	This Study
27 (22-32; 2)	Alberta	Rothfels 1981
17 (1)	Wyoming	Craighead and Craighead 1956
13 (5-21; 4)	Wisconsin	Petersen 1979
11 (1)	New York	Hagar 1957
9 (4-13; 2)	Wisconsin	Orians and Kuhlman 1956
25 (0-50; 2)	Michigan	Craighead and Craighead 1956
12 (9-14; 2)	Montana	Johnson 1975
19 (0-43; 4)	Utah	Smith and Murphy 1973

organochlorine pesticides). Newton (1979) has suggested that food shortages might result in the inability of the female to achieve the necessary body condition for successful breeding. He also suggests that building new nests, disturbance by neighbors, change of mate, ages of birds, appropriation of nest-sites by other species, delay in arrival, social interactions (especially in dense populations), and weather may also be involved.

All of the above factors may play a role in the high incidence of nonbreeding in this population. The high density of this population suggests that disturbance by neighbors and social interactions may play a role. Later arrival and a higher incidence of nonbreeding in 1984 may mean that arrival dates are also important. Observations of copulations among nonbreeding birds suggest a physiological barrier to successful laying. The inability to lay eggs may reflect poor body condition prior to, and during migration, rather than poor food conditions on the breeding grounds. The significance of these factors in accounting for nonbreeding is difficult to determine, but should be the subject of future research.

A high rate of nonbreeding might be the norm for this population. Johnson (1975) stated that high rates of nonbreeding might be characteristic of a Montana population in some years, although the cause of such occurrences were

not specified. Hansen (1987) has suggested that Bald Eagles (Haliaeetus leucocephalus) in Alaska may exhibit an endogenous long-term population cycle. When breeding habitat is saturated, nonbreeders may become so numerous that they decrease the productivity of breeders. Recruitment of nonbreeders declines and eventually the productivity of breeders increases and the cycle is renewed. Central to habitat saturation is a shortage of food. An evaluation of the possibility of a shortage of food on the study area will be given in later chapters.

The reproductive chronology of Red-tailed Hawks on the study area in both years was unremarkable except for earlier laying dates and a greater laying period in 1985 than in 1984. Both suggest that differences in arrival dates may have been a contributing factor. Individuals laying near the start of the season breed more successfully than those laying later (Newton 1979). A link between breeding success and laying dates may be present.

Comparison of reproductive success with any other population is difficult because of inconsistency in the type of success variables reported. All suitable comparative data have been combined in Table 7. It appears that percent success rates per territorial pair in the present study are low, especially for 1984. The same holds true for mean number of young fledged per territorial pair.

Table 7. Reproductive success (Mean; range) of nesting pairs of Red-tailed Hawks from populations in various North American locations as calculated per territorial pair (A), per breeding pair (B), and per successful pair (C).

Source and Location (Number of years)	Success Rate (%) (A)	Success Rate (%) (B)	Mean No. Fledged (A)	Mean No. Fledged (B)	Mean No. Fledged (C)
This Study Alberta (2)	47; 38-54	88; 83-93	0.8; 0.7-0.9	1.5; 1.5-1.5	1.7; 1.6-1.8
Petersen 1979 Wisconsin (4)	72; 53-86	81; 67-95	1.1; 0.8-1.5	1.3; 1.0-1.6	1.5; 1.3-1.7
Orians and Kuhlman 1956 Wisconsin (2)	62; 55-68	67; 64-70	1.2; 1.0-1.4	1.3; 1.1-1.5	1.9; 1.7-2.1
Johnson 1975 Montana (2)	53; 53-53	60; 59-62	1.3; 1.3-1.3	1.5; 1.4-1.7	2.6; 2.4-2.7

Both values reflect the high rate of nonbreeding in this study. Success rates measured per breeding pair were higher than normal. This suggests that if pairs are successful in laying eggs, they are usually successful in fledging young. Other measures of reproductive success when calculated on a basis of breeding or successful pairs appear normal.

CHAPTER FOUR

DIURNAL ACTIVITY PATTERNS

INTRODUCTION

The activity budgets of Red-tailed Hawks have received little attention in the literature. Investigations of soaring (Ballam 1981, 1984) and bioenergetics (Diesel 1983) have given the subject cursory treatment. More detailed work by Howard (1977) and Soltz (1984) looked at changes in soaring, bioenergetics and territorial behavior as the nesting cycle progressed. Available studies of Red-tailed hawks indicate that daily activity patterns vary seasonally and with geographic location (Bildstein 1987).

Red-tails are well-suited for investigating activity budgets because they are conspicuous when perched or active, and remain close to the nest during the breeding season (Soltz 1984). Despite these attributes, changes in activity patterns associated with stage in the nesting cycle or breeding status have not been thoroughly investigated. It is a goal of this study to describe how the activity patterns of a dense population of Red-tailed

Hawks differ in relation to breeding status, breeding season and weather.

The high nesting density and abundant food supply in the study area may make the activity patterns of the population unique. If food is not a limiting resource, time normally spent foraging could be directed towards territorial defense. A high incidence of agonistic and display behavior associated with territoriality might be expected. Behavioral differences should also be present between nonbreeding and breeding pairs. Birds without nesting duties would have decreased food needs and should exhibit different activity patterns. Differences between hawks on the study area and other populations with lower nesting densities might also be expected.

METHODS

Intensive behavioral observations were carried out from mid-April to mid-August of 1984 and 1985. Pairs of hawks were observed for two-hour periods. Behavior was classified according to predetermined categories and recorded every two minutes during these periods. All territories were observed on a 2-day rotation, with observation times for each pair varied to sample all times of the day. Observations were made from open hillsides or

from roadsides using binoculars or 15-45x telescopes. The hawk (usually the male) not associated with nest-duties (incubation, brooding, feeding, nest vigilance) was monitored when possible. An attempt was made to relocate lost birds by scanning territories until successful or until the 2-hour observation period expired. To insure independence in statistical analysis, observations for any single territory were not included for more than one year unless breeding status changed between years. If breeding status changed, observations were included for both years.

The development of nesting chronologies for breeding nesting pairs was described in Chapter 3. Average laying, hatching and fledging dates were calculated from breeding birds and allowed the development of a chronology for nonbreeding nesting pairs. The behavior of nonbreeding hawks could then be compared to the behavior of breeding hawks on a stage basis.

The observations were divided temporally into four periods. These were: Period 1 (morning, before 1030), Period 2 (midday, 1030 to 1430), Period 3 (afternoon, 1431 to 1830), and Period 4 (evening, after 1830).

Wind speed was measured with a hand-held anemometer, and temperature was measured with a thermometer held at breast height in the shade. Wind speed and temperature were measured at the beginning and end of each observation

period which allowed average values to be calculated.

Cloud cover was visually estimated at the start and end of each period. Precipitation was monitored throughout the observation period.

Behavioral categories were developed prior to the 1984 field season. Extensive behavioral observations made in 1983 and previous descriptions (Conner 1974, Hubbard 1974, Weir and Picozzi 1975, Henty 1977, Lavers 1979, Springer 1979, Preston 1981, Ballam 1984, Barnard and Simmons 1986) assisted in the development of these categories. The behavioral categories included:

(1) Display. This category included flight activity that advertised territory ownership but which involved no aggressive interaction between owners and intruders. It could involve one or both hawks associated with a particular territory. It was directed towards mates (during courtship) or potential intruders. Display by a lone bird (usually the male) consisted of a series of dives, stalls and ascents which resulted in a roller-coaster, undulating flight display. Display by both members involved soaring. The male and female bird would soar together in interlocking spirals. Leg-lowering with talon presentation was common during this type of flight. The bird above would sometimes touch the wings or back of

the bird below. Early in spring, pairs sometimes locked talons and tumbled in the air for short distances.

(2) Agonistic. This category included all aggressive behavior associated with the presence of an intruding bird. It involved confrontations between residents and a variable number of conspecific intruders, or occasionally interspecific intruders. Interactions commonly involved two hawks (usually neighboring males), but could involve as many as 10 individuals. Stoops, direct flapping flight, and screams were directed at perched or flying intruders. Occasionally physical contact occurred. Soaring in spirals with leg-lowering was also common. Intermittent aggressive dives upon intruders distinguished this type of soaring in spirals from that seen during display. Fighting birds occasionally locked talons and tumbled short distances in the air. Altitude supremacy seemed to be the goal of aerial combatants.

(3) Other. This category included all flight activity that could not be placed in the previous categories. Most of such activity consisted of soaring by a lone bird at various altitudes. The function of this type of soaring is unknown and remains controversial (Henty 1977, Preston 1981, Ballam 1984). This category also included direct

flapping flight when no known intruder was identified. Hovering flight was also included in this category. The purpose of "other" flight was probably related to both foraging and territoriality.

(4) Perched. This category included all perched behavior.

Data were analyzed using SPSS nonparametric tests (Nie et al. 1975, Hull and Nie 1981). The Spearman rank correlation procedure was used to examine relationships between activities and weather variables. Mann-Whitney U tests were used to investigate differences in activity between years and between breeding and nonbreeding nesting pairs during various nesting stages. Kruskal Wallis one-way analysis of variance and Tukey-type Multiple Comparisons (Zar 1984) were used to examine differences in activity patterns and among stages in the nesting cycle for both breeding and nonbreeding nesting pairs. Unless otherwise indicated, statistical significance was accepted at the $P = 0.05$ level.

RESULTS

In the two years of behavioral observations, 949 two-hour observation periods were completed on 31 territories. There were no significant differences for any

activity patterns between 1984 and 1985 for either breeding or nonbreeding hawks in any stage of the nesting cycle (Mann-Whitney U; $P > 0.05$). All subsequent analyses pooled data for both years. Data from 13 breeding pairs and 11 nonbreeding pairs were used for statistical analysis.

Obvious differences exist in how Red-tailed Hawks distribute their perching and flying activity over time (Fig. 5). Hawks spent most of their time perched ($> 80\%$ for all periods). More time was spent perching in the morning and evening periods than in the midday and afternoon periods. All three types of flight activity (display, agonistic, "other") were generally confined to the midday and afternoon periods. Flight outside of these periods was more common in the evening than in the early morning.

Flight activity was positively correlated with temperature and wind velocity, and inversely correlated with precipitation intensity (Table 8). Perched behavior was positively correlated with precipitation and inversely correlated with temperature and wind velocity. Cloud cover appeared to have little effect on behavior.

Generally, flight activity (display, agonistic, and "other") decreased over the nesting cycle, while perched activity increased for both breeding and nonbreeding pairs (Fig. 6). These changes were significant (Tukey-type

Figure 5. Percent time spent in various activities by Red-tailed Hawks for different periods of the day. See text for a description of activities and periods.

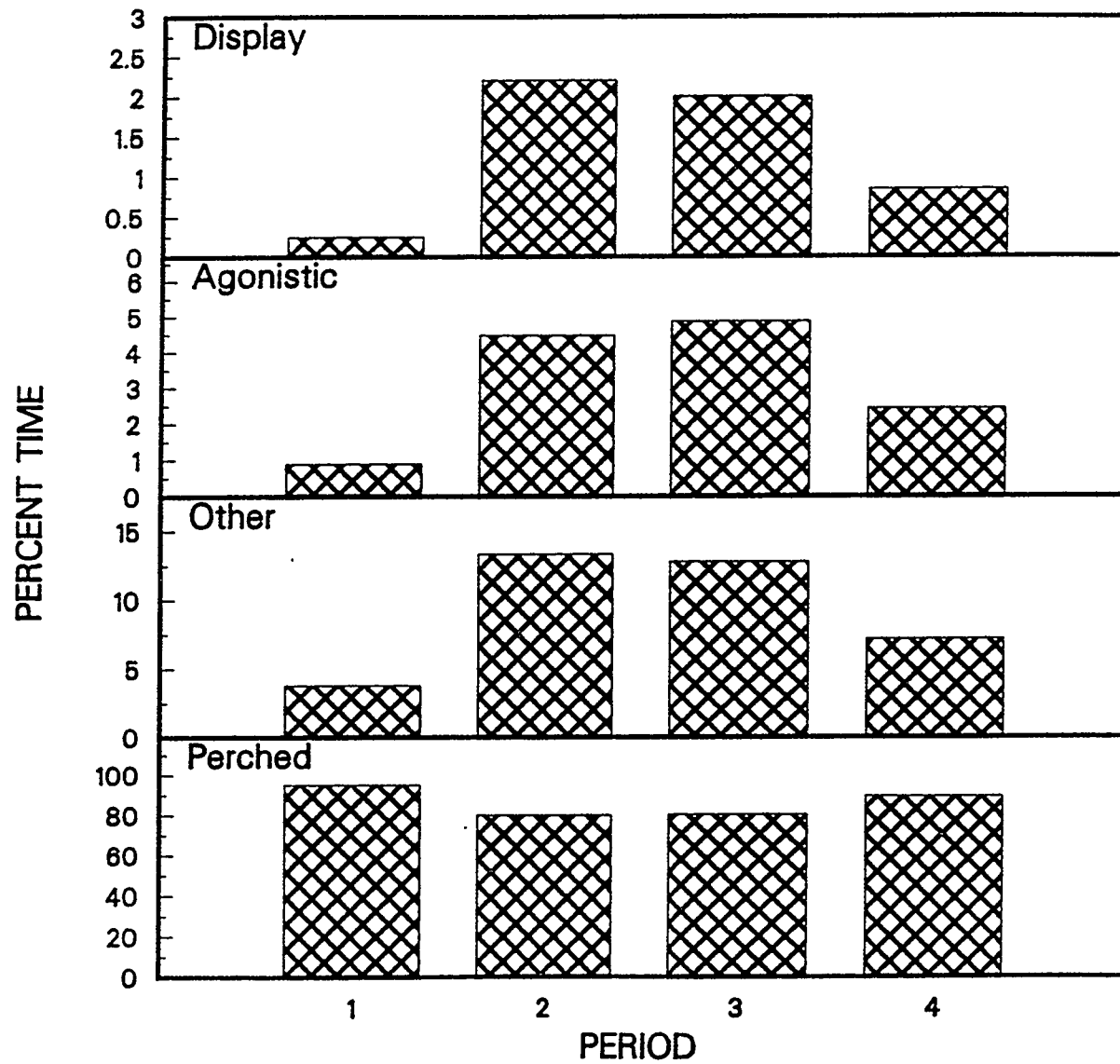
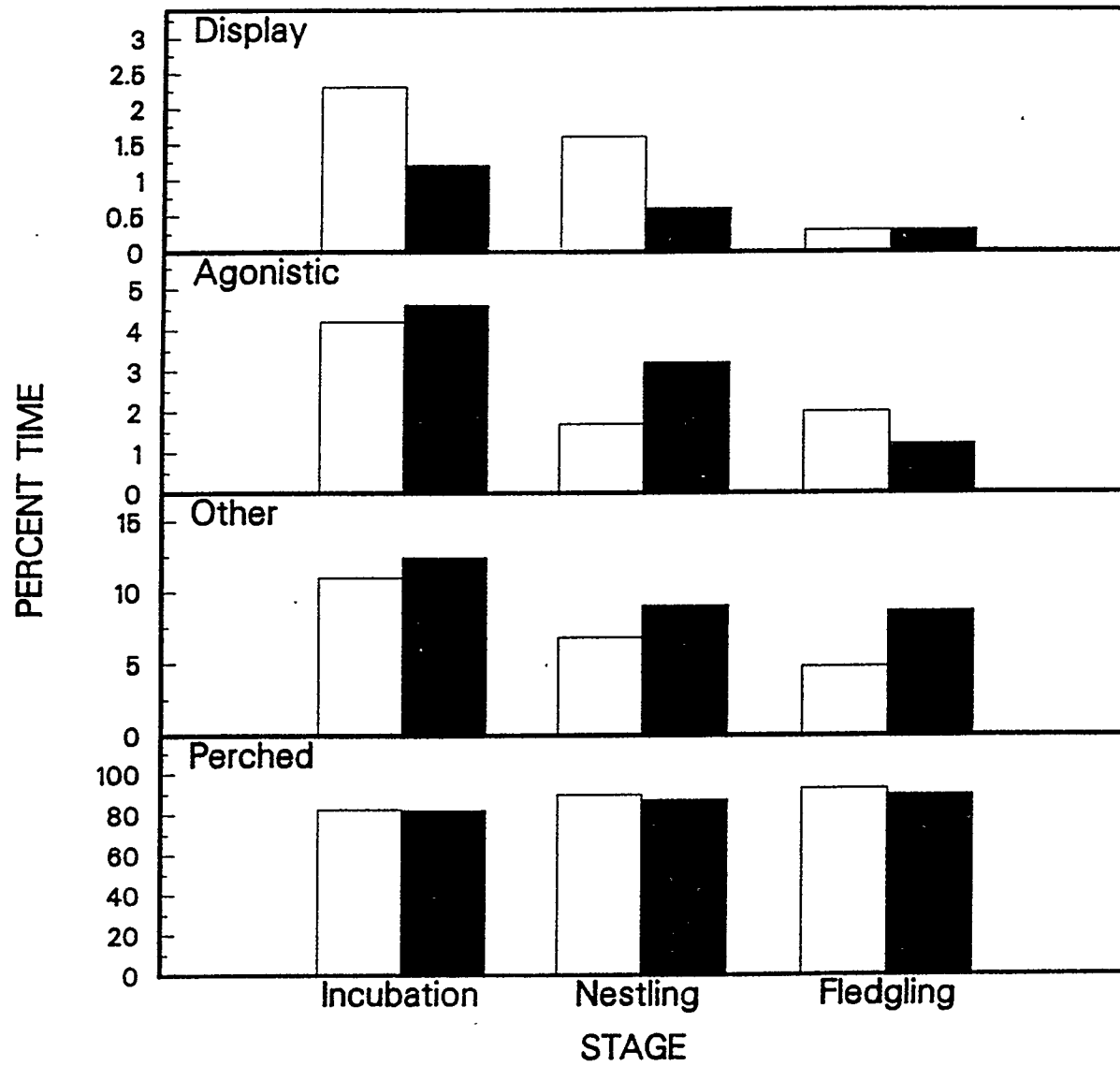


Table 8. Spearman rank correlations (ρ) between activities of Red-tailed Hawks and selected climatic variables.

	Category Of Activity			
	Agonistic	Display	"Other"	Perched
Mean temperature	0.09**	0.08*	0.19***	-0.18***
Mean wind velocity	0.20***	0.14***	0.20***	-0.25***
Precipitation	-0.11***	-0.06	-0.13***	0.13***
Cloud cover (begin)	0.03	-0.06	-0.05	0.07*
Cloud cover (end)	-0.01	-0.03	-0.01	0.02

* $p < 0.05$
 ** $p < 0.01$
 *** $p < 0.001$

Figure 6. Percent time spent in various activities by nonbreeding (open rectangle) and breeding (filled rectangle) Red-tailed Hawks in different stages of the breeding cycle. Data shown are seasonal means of pooled years (N=11 nonbreeding, 13 breeding).



multiple comparisons; all $P < 0.05$) between incubation and fledgling stages, but not between incubation and nestling stages or between nestling and fledgling stages (Tukey-type multiple comparisons; all $P > 0.05$). Exceptions to this pattern were that no significant differences were found between any stages for agonistic behavior among nonbreeding pairs (Kruskal-Wallis; $H = 5.68$, $P > 0.05$) or for "other" behavior among breeding pairs (Kruskal-Wallis; $H = 4.02$, $P > 0.05$).

There were few significant differences (Mann-Whitney U; all $P > 0.05$) in behavior between breeding and nonbreeding birds. During the nestling stage, breeding hawks exhibited significantly greater agonistic behavior than did nonbreeding hawks (Mann-Whitney U; $U = 102.0$, $P < 0.05$). Nonbreeding hawks showed significantly greater display behavior than breeding hawks during the incubation phase of the nesting cycle (Mann-Whitney; $U = 98.0$, $P < 0.05$). There were no significant differences in "other" or perched behavior between breeding and nonbreeding pairs.

DISCUSSION

The activity patterns exhibited by Red-tailed Hawks are typical of soaring birds of prey (Henty 1977). Flight activity is greatest near midday when thermal convective

currents are most favorable. Red-tailed Hawks in Puerto Rico also fly most frequently near midday (Santana C. and Temple 1988). Wakeley (1978a) found that Ferruginous Hawks (Buteo regalis) were involved in perching and low altitude flight in the morning and evening and that high altitude flight was limited to the hours between 0900 and 1800, and probably was related to the presence of suitable air currents. Similar changes in air currents probably affect Red-tailed Hawk flight behavior on the study area.

Temperature, wind velocity and precipitation intensity had significant effects on activity patterns while cloud cover had little effect. Ballam (1981) reported positive correlations between soaring activity and increases in ambient temperature, solar illumination, and wind velocity. Inverse correlations were found between soaring activity and increases in cloudiness and relative humidity. Preston (1981) reported similar results but failed to find a significant correlation between soaring activity and temperature. Both authors considered wind velocity to be the most important weather variable affecting soaring. Bildstein (1987) has found that Red-tailed Hawks fly more frequently in high winds than in low winds, and perch lower as wind speed increases.

Other aspects of Red-tail behavior are known to be affected by weather. Rate of prey delivery to nests

decreases with adverse weather conditions (Stinson 1980). Weather obviously affects the behavior of Red-tailed Hawks on the study area to some degree. It is probably a combination of weather influences, foraging behavior, and social interaction which account for the observed patterns.

Stage in the nesting cycle should also influence behavior patterns. Behavior during the courtship stage of the nesting cycle was difficult to assess. Variation in arrival times and courtship periods made comparisons between nonbreeding and breeding birds impossible. A high incidence of both display and agonistic behavior was observed during this stage. Sample sizes did not allow statistical comparison with other stages. Differences in behavior between hawks that eventually laid eggs and those that did not were not noticeable.

Generally, all three types of flight decreased for both breeding and nonbreeding hawks over the incubation, nestling and fledgling stages of the nesting cycle. A concomitant increase in perching was also seen. The exceptions to this pattern were that agonistic behavior in nonbreeding pairs and "other" behavior in breeding pairs did not vary significantly between stages.

The seasonal decline in agonistic and display behavior might have been expected. Territorial defence is normally strongest at the start of the breeding season and decreases

later (Newton 1979). The firm establishment of territory boundaries and a corresponding decline in intrusions might be responsible for this. Increasing food provision duties for pairs with young on the nest would also decrease the time available for territorial behavior. Because Red-tailed Hawks forage primarily from perches (Janes 1984a), an increase in perching activity was expected as the nesting season progressed. Rates of agonistic and display behavior for the study area population are likely higher than other populations with lower densities, but no comparative data are available.

The lack of a significant decline in agonistic behavior in nonbreeding pairs over the nesting cycle is interesting. This type of behavior must be energetically demanding and involves risk of injury. It might be expected to cease when not required. These birds may be trying to disrupt the activities of breeding pairs or may be trying to enlarge their territories for future breeding seasons.

The lack of a significant decrease in "other" flight behavior over the nesting cycle by breeding birds is also noteworthy. Most "other" behavior consisted of soaring. If soaring serves partly a territorial defense function (Ballam 1984) the lack of a decrease might be due to the continued need to maintain the territory. Since soaring is

also used in foraging (Orde and Harrell 1977, Ballam 1984) the lack of a decrease might also be indicative of an increase in foraging activity. Thus the function of soaring may change seasonally.

The higher incidence of agonistic behavior in breeding birds than in nonbreeding birds in the nestling stage might have been expected. Breeding birds should have a greater need to maintain or even expand, territorial boundaries to ensure adequate food provisioning of young.

The higher incidence of display behavior among nonbreeding pairs than in breeding pairs in the incubation period is difficult to explain. It may be related to pair-bond maintenance, continued courtship behavior in the hope of laying eggs, or a technique (without risking injury) of territory maintenance. The maintenance of territorial boundaries may be important to successful breeding in the next year. In 1986, two pairs of birds were observed incubating in the area on the study area in July, suggesting that delayed breeding or replacement clutches may be possible with this population. This would lend support to the idea that nonbreeding birds were continuing display behavior in anticipation of breeding.

Since this study tried to evaluate the importance of food on the behavior of the population, it would have been advantageous if foraging birds could have been recognized.

The amount of time and effort spent on foraging could then be discerned. In the past, hawks in the "other" behavioral category have been assigned a foraging status (Soltz 1984). After observing birds for long periods in 1983, I did not feel confident that I could identify foraging birds. Red-tailed Hawks employ four different hunting techniques (Orde and Harrell 1977). They can strike from a perch, from direct flight, from soaring flight, or from a combination of direct and soaring flight. Further, Red-tailed Hawks do not display any unique indication of readiness to attack (Grier 1971). All of these factors point out the difficulty in directly assessing foraging behavior patterns with these birds.

Comparative data on Red-tailed Hawk activity patterns from other populations are sparse. Summer activity patterns of a population in Missouri showed that Red-tails were perched 95.4% of the time, were involved in flapping flight 1.3% of the time and soared 3.3% of the time (Diesel 1983). Equivalent values from this study were 86.1%, 2.1%, and 11.9% respectively. Juxtaposed, it appears that flight activity is more frequent in the study area population. This is true for both flight modes. Population densities were not available for the Missouri population but were likely lower than in the Calgary area (see Chapter 3).

The high population density of Red-tailed Hawks on the study area probably leads to much social interaction. This would involve more agonistic and display behavior. It would be interesting to compare the distribution of these behaviors with other populations.

CHAPTER FIVE

HOME RANGES AND UTILIZATION DISTRIBUTIONS

INTRODUCTION

During the breeding season, most raptors restrict their activities over a given period of time to a definite area known as the home range (Newton 1979). If all or part of the home range is defended against other individuals of the same species, the defended area is a territory (Odum and Kuenzler 1955). In hawks of the genus Buteo, a defended territory surrounding the nest is usually located within a larger home range (Craighead and Craighead 1956, Newton 1979). Nesting territories provide nest-sites, reduce or eliminate sexual disturbance and competition from hawks of the same species and may ensure an exclusive foraging area (Newton 1979). The undefended areas serve as additional feeding areas and may not be suitable as territories. Examination of the home ranges and territories of Red-tailed Hawks on the study area will provide further information on the role of food and space in determining breeding density.

The high density of Red-tailed Hawks on the study area may necessitate exclusive ranges. Home range areas are defined and measured without reference to other animals, or to any particular kinds of display or aggressive behaviors (Mace et al. 1984). However, they are strongly influenced by the manner in which individuals react to each other and are thought to reflect population features such as density and social structure (Braun 1985). The area actively defended will depend on intrusion pressure, because the amount of time available for the exclusion of intruders is limited. If birds obtain sufficient resources in a small area they often defend the entire area (Newton 1979). If adequate resources are found on the study area, the total area utilized by nesting pairs will be defended and mutually exclusive of areas used by other pairs. Overlap between territories will be minimal.

The space utilized by Red-tailed Hawks should be examined from a three-dimensional perspective. Smith and Murphy (1973) and Fitch et al. (1946) have noted that Red-tailed Hawk territories have three-dimensional structure. Territoriality was strongest at lower altitudes. The three-dimensional structure of the study area territories can be examined by calculating flight and perch location home range indices for each territory. Three-dimensional structure will be indicated if

significant differences are found between areas based on flight locations and areas associated with perched locations.

The breeding status of hawks on the study area should affect home range size and use. Smith and Murphy (1973) observed that breeding pairs of Red-tailed Hawks tended to range over larger areas than did nonbreeding hawks. The differences may have been related to differing food or habitat requirements, or may be associated with stronger territorial behavior in breeding birds. These differences should also be evident on the study area, resulting in breeding pairs having larger home ranges and territories than nonbreeding pairs.

Stage in the nesting cycle should also influence the home range size of breeding pairs and should have little influence on the size of nonbreeding pair home ranges. Generally, the home ranges of raptors change in size and shape during the nesting season, becoming larger towards the end (Newton 1979). Food requirements increase as the nesting season progresses, as growing nestlings place greater food demand on adults. If food resources are limited in the immediate area of the nest, adults may be forced to forage further away from the nest and an increase in home range size should result. Territorial interactions become fewer and less intensive as the nesting season

progresses (Smith and Murphy 1973) and this may allow for more foraging opportunity by breeding pairs. This study will attempt to determine how home ranges and use of space by Red-tailed Hawks on the study area vary with respect to overlap, three-dimensional structure, breeding status and stage in the nesting cycle.

This approach will necessitate the use of various techniques to determine home ranges and use of space. Home range studies have tended to focus on the size of home ranges. Home range size alone, may have limited ecological importance as it is probably determined by habitat composition, physiographic makeup, food distribution and many other factors (Sanderson 1966). These factors can be examined by determining how, when and why an animal uses the space available to it. The most common way of determining how an animal uses space is to determine utilization distributions (UDs).

Non-statistical home range methods calculate areas only. Several techniques are available because of the historical emphasis on calculating home range size. More recently, several statistical techniques have been developed to calculate utilization distributions and their associated indices of size. Both parametric and nonparametric statistical techniques are available.

A. ESTIMATION OF HOME RANGES

The most common non-statistical technique for calculating home range is the convex polygon method. Selected locations are connected by straight lines and the resulting polygon represents the home range. The ways in which locations are selected and the way in which the outermost points are joined are not precisely defined (Jenrich and Turner 1969). The minimum convex polygon (MCP) is the smallest convex polygon containing all the observed positions. The points are joined so that no inner angle is greater than 180 degrees (Schoener 1981). The area within the polygon is the estimated home range size. The MCP is equivalent to the maximum territory of Odum and Kuenzler (1955).

The convex polygon technique has been used extensively in the past and comparative values for many species are readily available. The values can be calculated by hand or through computer programs. There are several problems associated with the convex polygon technique. Convex polygon techniques are severely biased by small sample sizes and the shape is constrained to a convex polygon (Schoener 1981, Anderson 1982). They may also include space not actually utilized by the animal. The effects of large sample sizes are not clear. Schoener (1981) suggests

that with enough observations, convex polygon estimates should approximate true home ranges. Ford and Myers (1981) argue that very large sample sizes may result in overestimation of home range size.

B. ESTIMATION OF UTILIZATION DISTRIBUTIONS

The UD describes the relative intensity of an animal's use of areas within a defined space. It represents the probability of occurrence at each point in space (Van Winkle 1975). UDs can be calculated for individual animals or for populations (Ford and Krumme 1979). Statistical techniques for comparing the utilization distributions among individuals or populations are not available. The contours derived from UDs indicate the shape of the home range and can be visually compared. Boundaries can be determined by selecting a contour that encompasses a selected percentage of the total space used (Samuel et al. 1985). The area bounded by these contours indicates the size of the home range and can be statistically compared. The contour representing the area which accounts for some percentage of the space utilization is known as a minimum area versus probability (MAP) estimate. MAP (0.95) and MAP (0.50) are commonly determined (Ford and Krumme 1979, Anderson 1982).

Statistical techniques develop utilization distributions from which area measurements can be derived. Parametric techniques assume that the UD's conform to a known statistical distribution. Jenrich and Turner (1969) developed a technique in which locations were fitted to a bivariate (elliptical) normal distribution. The UD developed assumes that an animal's activity is concentrated in the central area of the home range and that the probability of occurring in a unit of area decreases with increasing distance from this center of activity. The indices calculated will be severely biased if the location data do not fit the assumed form of probability distribution. A test for bivariate normal distribution of animal locations is available (Samuel and Garton 1985). Calculation of bivariate normal UD's is also greatly influenced by extreme locations (Dixon and Chapman 1980). The shape of the UD's are constrained to ellipses and the analyses of shapes are limited when constraints such as normality must be assumed a priori.

If the form of the distribution is unknown, the home range and UD should be estimated from the data without making any distribution assumptions. Nonparametric statistical techniques are appropriate under these circumstances. Ford and Krumme (1979) developed a nonparametric technique which estimates the UD for a

population. Anderson (1982) developed another nonparametric technique using the Fourier transform. With this technique, a smoothing function is applied to a bivariate frequency distribution of location points from which the area under the resulting distribution can be calculated (Jaremovic and Croft 1987). No assumptions about distribution and shape are made with either nonparametric statistical technique.

Statistical techniques do have their disadvantages. The choice of appropriate boundaries can be difficult since extreme locations may have substantial effects on estimates of home range. It becomes difficult to estimate the tails of the UD and underestimation of home range sizes can result (Anderson 1982). Using a smaller MAP value (normally 0.50) helps to correct this bias. Ford and Krumme's (1979) method is restricted to a coarse grid size and requires extensive computational time (Anderson 1982).

Autocorrelation is thought to influence both nonstatistical and statistical estimates. This occurs when an animal's position at time $t + k$ is a function of its position at time t (Swihart and Slade 1985a). Independence of observations is not assumed in the MCP method, but autocorrelation can result in underestimates of home range. Highly autocorrelated data lead to redundancy and the actual sample size may be small (Swihart and Slade 1985a).

Autocorrelation is more of a problem in statistical techniques, which assume statistical independence between all successive relocations (Anderson 1982, Swihart and Slade 1985a, 1985b). The lack of independence will cause the effective sample to be smaller than the number of samples collected. This reduces the accuracy of the home range estimate. Tests of independence for data were first proposed by Schoener (1981) and are provided by Swihart and Slade (1985b).

Frequent monitoring of an animal's location jeopardizes the validity of the independence assumption but may be unavoidable. As Swihart and Slade (1985a) point out, short sampling intervals are essential in studying activity budgets, foraging ecology and temporal patterning of home range use. In these studies they recommend nonstatistical techniques. Statistical independence of animal locations seems impossible (Dunn and Gipson 1977). Any two successive sightings are almost certain to be in close proximity because of the natural physical limitations of an animal's mobility. Few, if any, pairs of relocations of individual animals may meet the criteria of independence (Laundré and Keller 1984). This is especially true for breeding territorial animals that center their activities around dens or nests. For Red-tailed Hawks, it may be even more difficult to have independent locations because they

restrict their perching activity to favored "territorial" perches (Fitch et al. 1946, Santana C. and Temple 1988).

METHODS

Observations of 31 hawk territories were made from mid-April to mid-August in both 1984 and 1985. Pairs of hawks were observed for two-hour periods. All territories were observed on a 2-day rotation, with observation times for each pair varied systematically to sample all times of the day. Observation periods began and ended according to a predetermined schedule which was not affected by the presence or absence of birds. Locations of birds were estimated visually every two minutes and plotted directly on a 1:10,785 aerial photograph mosaic map of the study area. Habitat details could be discerned on the maps allowing a high degree in accuracy in plotting locations. I believe that plotting was accurate to within 5 meters for most perched locations and 15 meters for most flight locations. Error in plotting flight locations increased as the altitude of hawks increased.

An attempt was made to record the location of the hawk (usually the male) not associated with nest-duties (incubation, brooding, feeding, nest vigilance). The behavior of hawks was recorded for each location according

to predetermined categories (see Chapter 4). For the analyses in this chapter it was important to know only whether the locations were associated with flying (agonistic, nonagonistic) or perching. Occasionally, birds could not initially be located or were lost from view. Under these circumstances, an attempt would be made to locate or relocate the birds within the two-hour observation period.

To insure the independence of the home range indices being compared, no more than one year of location data were used from each nesting territory, unless breeding status changed between years. If breeding status changed, locations were included from both years (one year as breeding, one year as nonbreeding). This selection process resulted in the comparison of home range indices for 24 territories.

To compare the indices on a stage basis, a chronology for nonbreeding pairs had to be developed. Average laying, hatching and fledging dates calculated from breeding birds were used as the chronology for all nonbreeding nesting pairs for each year (see Chapter 3).

I used the minimum convex polygon method as a nonstatistical technique for determining home range size. The Fourier transform method (Anderson 1980) was used to provide two statistical estimates of home range sizes [MAP

(0.95), MAP (0.50)]. Sampling intervals were short (2 minutes) because they were designed to record activity budgets as well as location. Autocorrelation should not present a problem because birds were capable of crossing the longest dimension of the home range within the sampling interval. For Red-tailed Hawks, sampling designs consisting of autocorrelated bursts of relocations followed by long inter-burst periods may not bias home range estimates (Andersen and Rongstad 1989). In this study, bursts of relocations were separated by at least two days. The analyses of home range indices did not emphasize actual areas, but rather size differences associated with breeding status, stage in the nesting cycle, behavior, and habitat. With these types of comparisons, any underestimation or overestimation biases associated with autocorrelation should be equal among groups being compared. The actual areas are difficult to interpret without comparative data from other populations. The differences in areas associated with breeding status and stage in the nesting cycle will be the most important comparisons.

Location data were converted to Cartesian (x,y) coordinates using a CalComp 9000 digitizer, and entered into a computer for analysis. MCP areas and peripheral points were calculated using a Fortran program. The MCP and nest locations were then plotted at the same scale as

the aerial photo mosaic map using DISSPLA graphics software and a CalComp 1051 drum plotter. MAP (0.95) and MAP (0.50) indices and the UD were calculated using Anderson's (1982) Pascal program. Each UD was then plotted as a series of contours at the same scale as the aerial photo mosaic map using the Surface II graphics system (Sampson 1978) and the drum plotter. Transparent overlays of both MCP and UD plots were placed on the aerial photo mosaic map to examine habitat features associated with MCPs, nest locations and UDs.

Home range indices were compared using SPSS nonparametric tests (Hull and Nie 1981). Wilcoxon matched-pairs signed-ranks tests were utilized to compare home range indices based on agonistic versus nonagonistic flight locations as well as indices based on flight versus perched locations. Mann-Whitney U tests were used to determine differences associated with the year of study and with breeding status. Kruskal Wallis one-way analysis of variance and Tukey-type multiple comparisons (Zar 1984) were used to determine home range differences associated with stage in the nesting cycle. Unless otherwise stated, statistical significance was accepted at the $P = 0.05$ level.

RESULTS

MCPs were plotted for 15 territories in 1984 and 16 territories in 1985 (Fig. 7, 8). These MCPs were calculated from a total of 489 2-hour observation periods in 1984 and 460 periods in 1985. This represented a potential of 56,460 location records (one every two minutes). Hawks were visible for 40,047 location records or 70 percent of the time. Each MCP is representative of at least 500 location points. Little overlap of MCPs was seen on the study area in either year. Percent overlap was not calculated because not all contiguous territories were observed and plotted for any of the territories under observation.

In both 1984 and 1985, home range areas based on flight locations associated with agonistic behavior were significantly larger (Wilcoxon matched-pairs signed-ranks tests, all $P < 0.01$) than those based on nonagonistic flight locations for both breeding and nonbreeding pairs (Table 9). Areas based on flight locations were significantly larger (Wilcoxon matched-pairs signed-ranks tests, all $P < 0.01$) than those based on perch locations in both years (Table 10).

Red-tailed Hawks concentrate most of their activities in specific areas of the MCPs (Fig. 9, 10). The UD's shown

Figure 7. Plots of minimum convex polygons (MCPs) outlining home ranges of breeding (filled circles) and nonbreeding (open circles) territorial pairs on the study area in 1984.

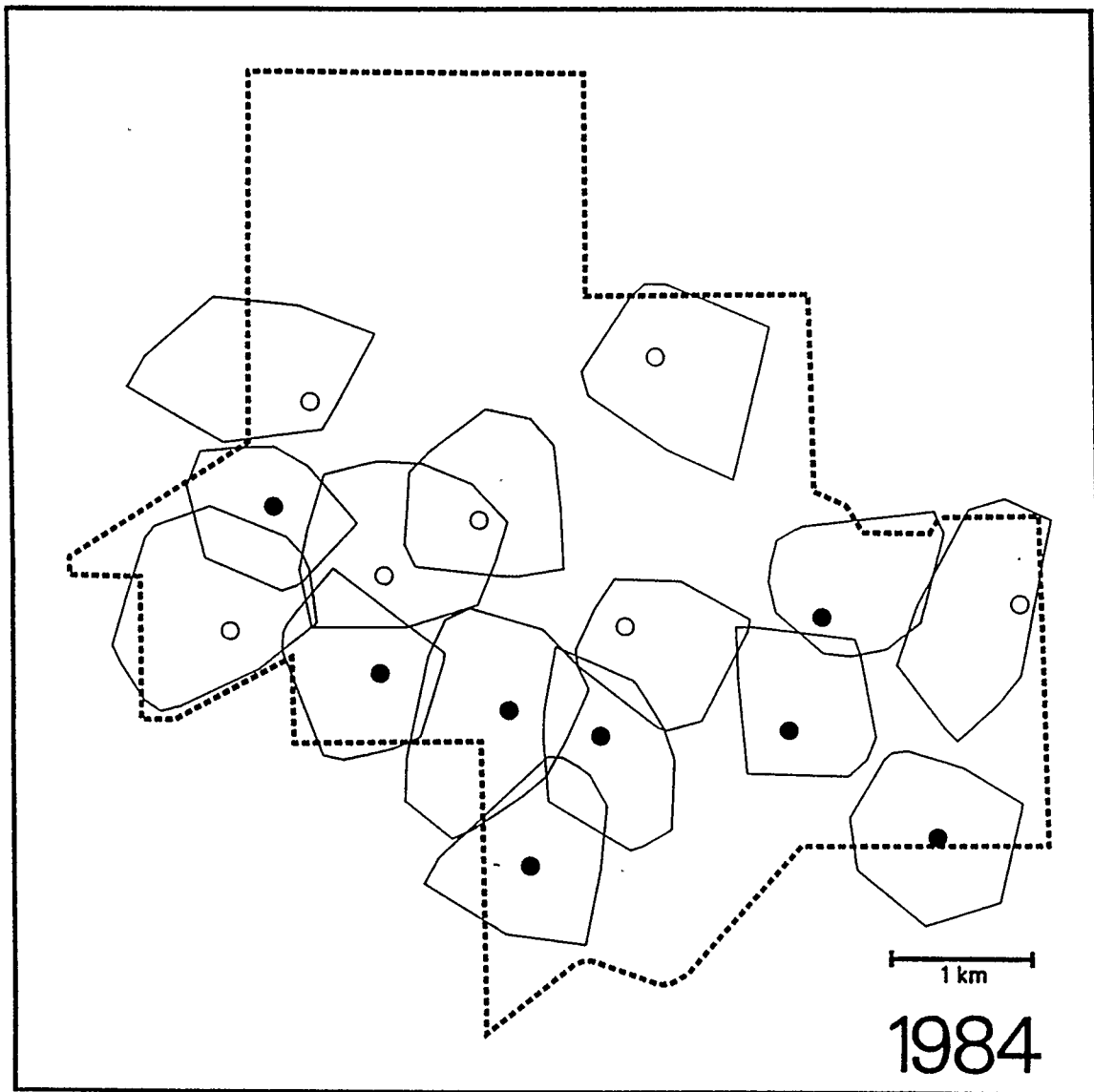


Figure 8. Plots of minimum convex polygons (MCPs) outlining home ranges of breeding (filled circles) and nonbreeding (open circles) territorial pairs on the study area in 1985.

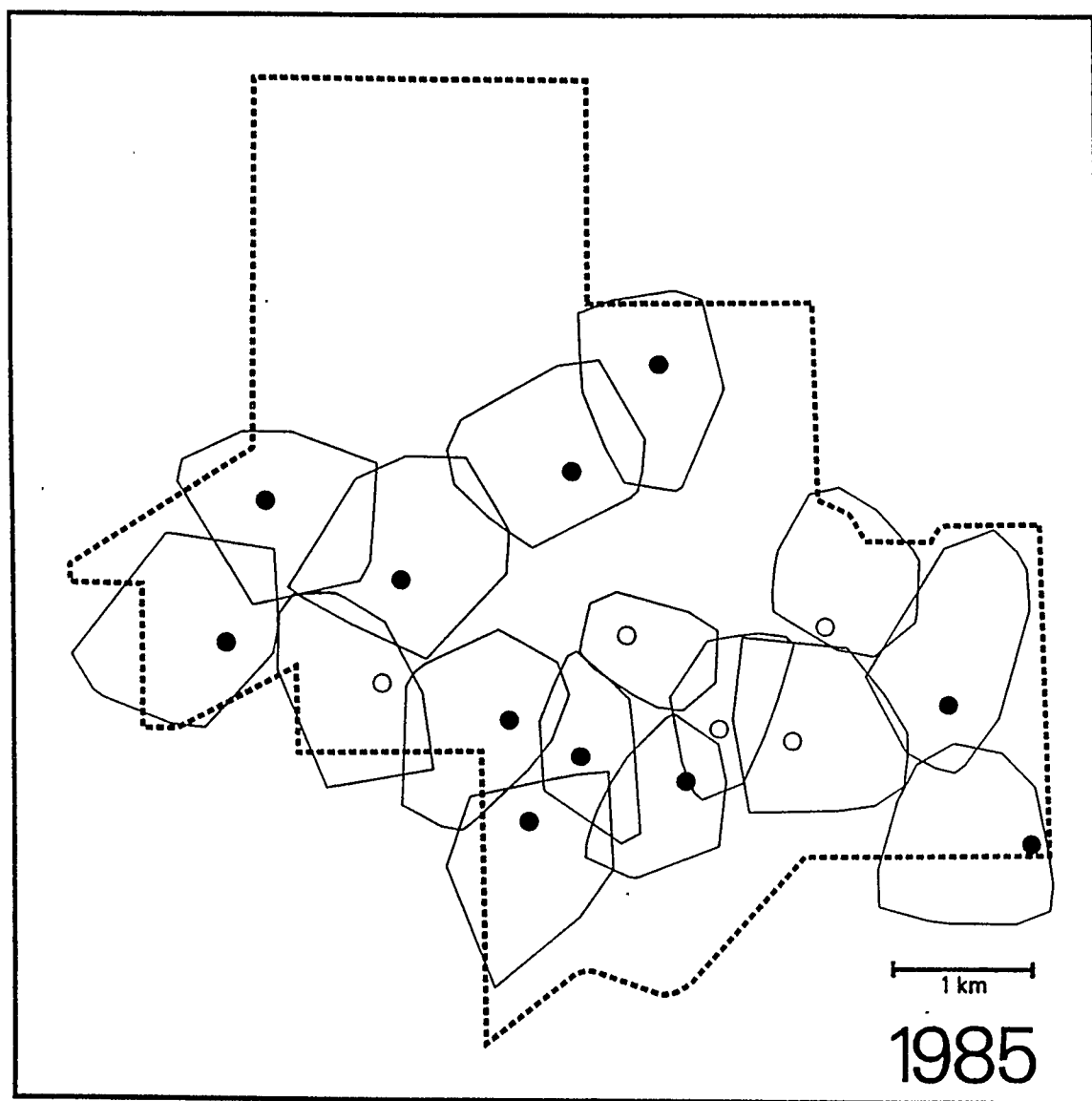


Table 9. Values of three home range indices based on agonistic flight locations and nonagonistic flight locations for both breeding and nonbreeding territorial pairs over the entire breeding season (N = 13 breeding, 11 nonbreeding).

Breeding Status	Home Range Index	Area* (km ²)	
		Agonistic	Nonagonistic
Breeding	MCP	0.94 ± 0.25	0.80 ± 0.22
	MAP (0.95)	0.94 ± 0.25	0.65 ± 0.20
	MAP (0.50)	0.30 ± 0.08	0.20 ± 0.07
Nonbreeding	MCP	0.93 ± 0.24	0.75 ± 0.22
	MAP (0.95)	0.88 ± 0.23	0.62 ± 0.18
	MAP (0.50)	0.29 ± 0.09	0.19 ± 0.06

*mean ± SD

Table 10. Values of three home range indices based on flight and perched locations for both breeding and nonbreeding territorial pairs over the entire breeding season (N = 13 breeding, 11 nonbreeding).

Breeding Status	Home Range Index	Area* (km ²)	
		Flight	Perched
Breeding	MCP	1.08 ± 0.23	0.66 ± 0.22
	MAP (0.95)	0.84 ± 0.17	0.09 ± 0.04
	MAP (0.50)	0.26 ± 0.06	0.20 ± 0.01
Nonbreeding	MCP	1.04 ± 0.27	0.67 ± 0.23
	MAP (0.95)	0.85 ± 0.21	0.09 ± 0.08
	MAP (0.50)	0.26 ± 0.07	0.02 ± 0.01

*mean ± SD

Figure 9. Plot of utilization distribution (UD) contours, MCP (bold line) and nest location (filled circle) of a breeding nesting pair. Contours are indicative of the probability of occurrence at any point in space. This plot is for the pair occupying nest 0130 in 1984, and is representative of all breeding pairs.

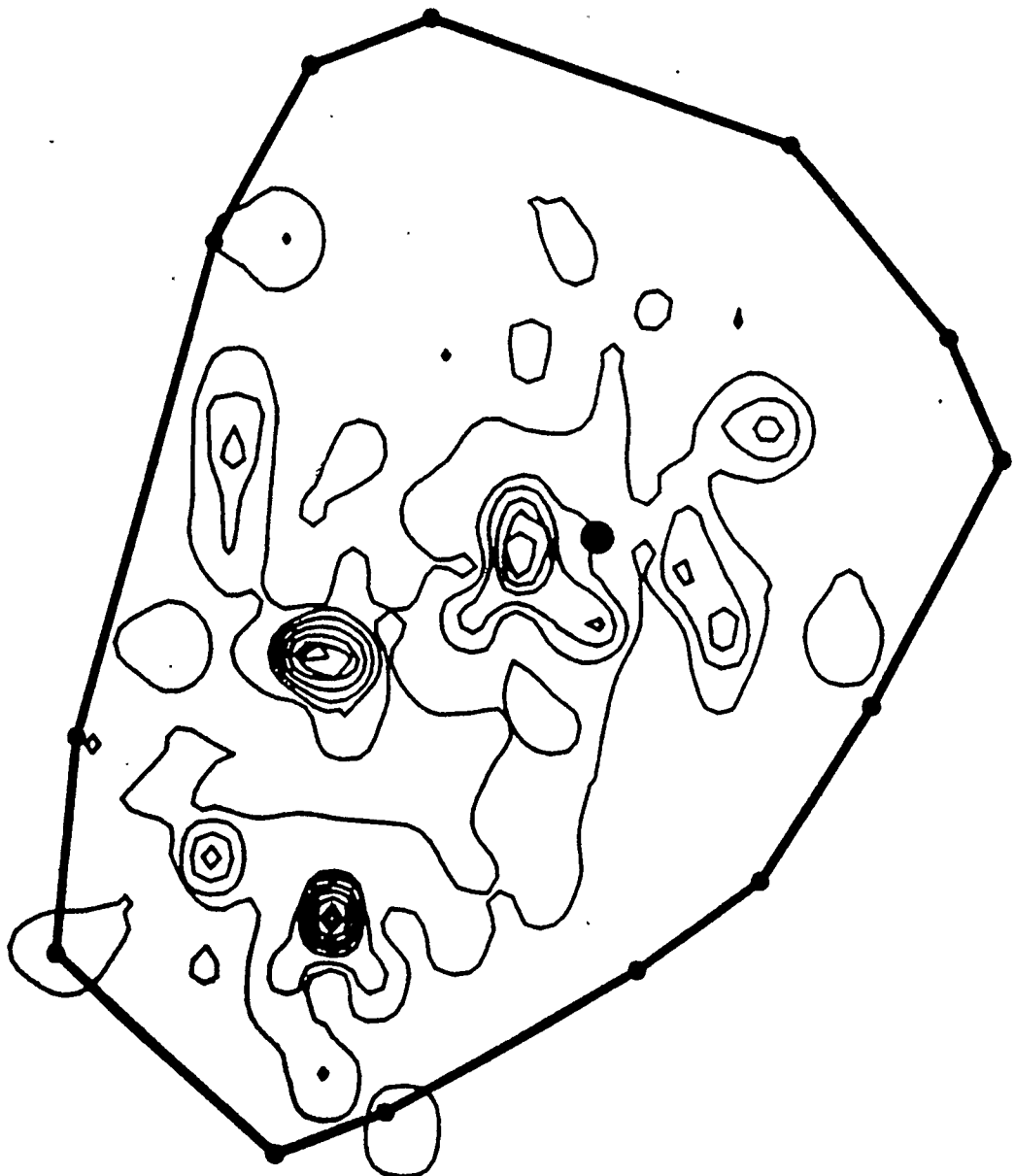
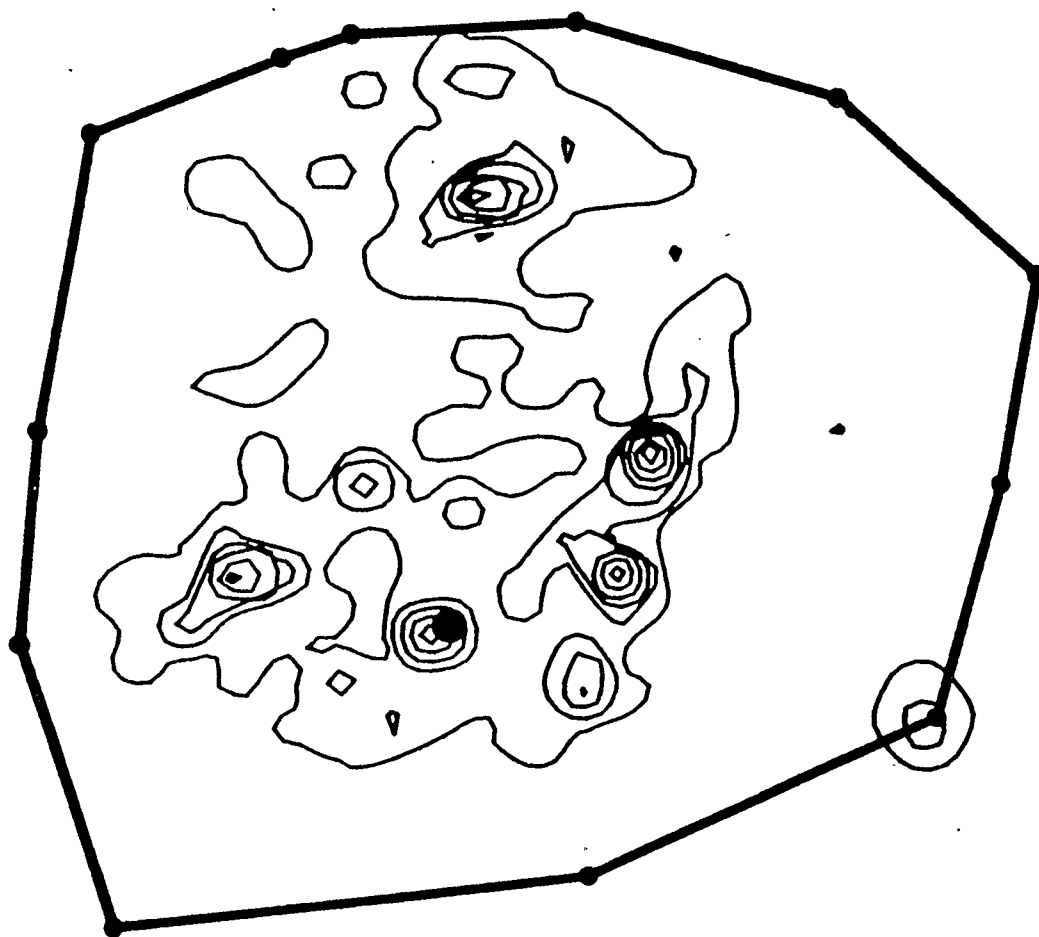


Figure 10. Plot of utilization distribution (UD) contours, MCP (bold line) and nest location (filled circle) of a nonbreeding nesting pair. Contours are indicative of the probability of occurrence at any point in space. This plot is for the pair occupying nest 0517 in 1984, and is representative of all nonbreeding pairs.



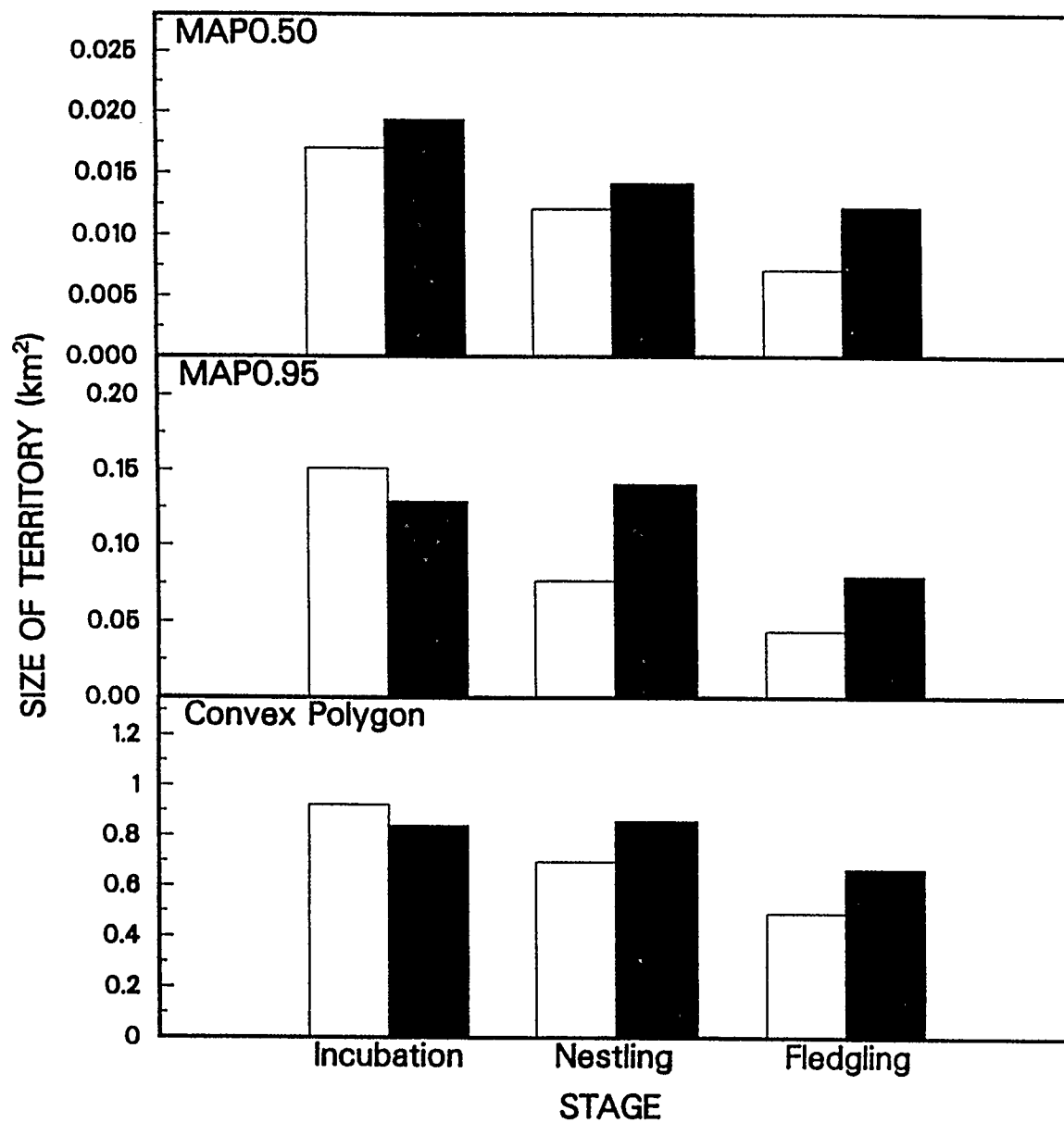
are typical of breeding and nonbreeding pairs. Most activity appears to occur centrally on the home range. Several peaks are normally present in each UD. When the UDs were overlain on the aerial photo mosaic map, the peaks corresponded to favorite perching locations (tree, fence or power pole). One peak is normally located in close proximity to the nest for both breeding and nonbreeding pairs. No discernible differences associated with breeding status were noticeable in the UDs. Variability in the UDs made any further comparison extremely difficult.

There were no significant differences in home range areas between 1984 and 1985 for either breeding or nonbreeding hawks in any stage of the nesting cycle (Mann-Whitney U; all $P > 0.05$). All subsequent analyses used pooled data for both years.

For the nestling stage of the nesting cycle, MAP (0.95) areas for breeding pairs were significantly larger (Mann-Whitney U = 28.0; $P < 0.02$) than those of nonbreeding pairs (Fig. 11). For all other indices, there were no significant differences between breeding and nonbreeding pairs (Mann-Whitney U; all $P > 0.05$) for any stage in the nesting cycle.

All three indices of home range in nonbreeding birds decreased over the course of the season. Only the differences between the incubation and fledgling stages

Figure 11. Home range areas based on all locations during various stages in the nesting cycle for both breeding (solid rectangle) and nonbreeding (open rectangle) pairs. Data shown are seasonal means of pooled years. $N = 13$ breeding, 11 nonbreeding pairs. Note that Y-axes differ for each index.



were significant (Tukey-type multiple comparisons; all $P < 0.05$). Decreases between the incubation and nestling stages, or between the nestling and fledgling stages, were not significant (Tukey-type multiple comparisons; all $P > 0.05$). For breeding birds, there were no significant differences in any home range estimates between any stages in the nesting cycle (Kruskal-Wallis; all $P > 0.05$).

DISCUSSION

Several lines of evidence suggest that Red-tailed Hawk pairs on the study area have exclusive use of their home ranges. First, there is little overlap between MCP plots of home ranges (Fig. 7, 8). Second, the use of space within these MCPs is greater towards the interior (Fig. 9 and 10), meaning that areas of overlap are seldom used. Third, home range indices based on locations where agonistic behavior was observed were significantly larger than those based on locations where nonagonistic flight behavior was observed. This suggests that defended areas encompass other utilized areas. Fourth, observations of intrusions suggested that agonistic behavior was intense at the periphery of the home range. Because all of the home range appears to be defended, home range and territory are synonymous for this population. Hereafter, the terms

territory and home range will be used interchangeably for the population on the study area.

The exclusive use of home ranges on the study area was expected. The study area has a very dense population and a high level of intraspecific competition would be expected. If food, space and any other resources are limited, exclusive use of space should be a necessity. Comparing a moderately dense population of Red-tailed Hawks in Michigan with a denser population in Montana, Craighead and Craighead (1956) found that home ranges and territories tended to overlap less in the western population. Sufficient food appears to be available within defended territories on the study area because no additional undefended feeding areas are present (Newton 1979).

Red-tailed Hawk territories on the study area seem to be three-dimensional. Indices based on flight locations were all significantly larger than indices based on perch locations. This suggests that hawks range over a larger area when flying. Observations seemed to indicate that intruders flying at very high altitudes evoked a less intense agonistic response than when intrusion occurred at lower altitudes. Vertical limits to Red-tail territories have been noted before in Utah (Smith and Murphy 1973). Fitch et al. (1946) and Petersen (1979) found that aggressive response to intruders was greatest at low

altitudes. To investigate the three-dimensional structure of territories on the study area any further, would require information on altitude for each flight location. Such information was not available.

The differential use of certain portions of territories was not surprising. The peaks in the UDs were associated with favorite perching areas. Perches in these areas offered good views of the nest and territory and did not seem to be associated with foraging activity. Few prey-capture attempts were initiated from these perches and many of them were located well away from suitable foraging habitat. The perches consisted of tall trees (usually the tallest in a group), fence posts, or power poles, and were often located on ridges or in other prominent locations. Intruders were often detected from perches and agonistic responses were initiated. Hawks may only be able to defend areas visible from these perches. Birds on these perches were conspicuous and perching on them may serve a territorial advertisement function. Some favorite perches did serve a "dual" purpose, offering excellent vantage points for both territorial vigilance and foraging opportunities. Fitch et al. (1946) and Santana C. and Temple (1986) have also noted preference for certain perches by Red-tailed Hawks.

Therefore, peaks in the UDs seemed to be associated with territoriality rather than foraging. This reinforces the suggestion that food may not be a limiting resource for the study area population. Janes (1984a) has suggested that perch sites might be a limiting resource for Red-tailed Hawks. However, perch sites on the study area seem to be very abundant. Perches that offer vantage points of territories, and that make hawks conspicuous, may be limiting but would be difficult to inventory.

Few significant differences in home range areas between breeding and nonbreeding pairs suggest that breeding pairs do not adjust to increased food demand by expanding their home ranges. Breeding pairs had slightly larger home ranges than nonbreeding pairs as measured by all three indices during all stages of the nesting cycle, but only one of these differences was significant. Breeding territorial pairs with nestlings have much higher food requirements than nonbreeding pairs and this might be expected to be reflected in larger home ranges. Petersen (1979) found that Red-tailed Hawks increase their home range size to provide food for newly hatched chicks. The lack of significant differences may mean that food is not limiting and that the original territory boundaries encompass sufficient food. It may also mean that all available space is occupied, and that no other space is

available without encountering the significant risk of injury and the energetic expenses associated with intrusions into other territories.

Decreases in home range indices of nonbreeding pairs over the season were expected. These birds have no additional food requirements associated with the nestling and fledgling stages of the nesting cycle. If the original territory boundaries were selected to provide enough resources to fledge young, a decrease in size after failing to lay eggs might be expected. Why did nonbreeding pairs remain on their territories and defend them throughout the breeding season? Maintenance of the territory has energetic costs and potential injury risks. These disadvantages must be outweighed by some advantages. Benefits could include access to exclusive foraging areas in a familiar setting for the remainder of the breeding season. By discouraging encroachment by neighboring or new pairs they may be able to ensure reoccupancy in the following year. Upon arrival in the next spring, territory boundaries may be easier to establish than if they were not defended in the previous season.

Clearly, there were no significant increases in territory sizes of breeding pairs as the nesting season advanced. If food were limiting on the study area and territoriality functions primarily to preserve a food

supply, territory size might have been expected to increase during the nestling stage due to increased food demand. If food is superabundant and territoriality functions to secure a minimal space for breeding and nesting, territory size should have remained relatively stable for breeding birds. Raptors often change their hunting areas during the breeding cycle, presumably in response to seasonal changes in prey-distribution, prey needs and nesting duties (Newton 1979). This results in home ranges increasing in size towards the end of the breeding season. The lack of increases in territory size in successful breeding pairs on the study area suggests that either food is superabundant or that original boundaries contained sufficient food.

CHAPTER SIX

FEEDING ECOLOGY

INTRODUCTION

In this study, feeding ecology was investigated with the goal of determining the importance of food and foraging to the population of Red-tailed Hawks on the study area. This required the identification of the major prey species and how, when and where these prey are acquired. The information gained will be used in Chapter 7 to determine if habitat selection is related to prey abundance within habitats.

General prey preference factors and pre-attack postures of Red-tailed Hawks have been determined (Grier 1971, Snyder 1975, Steenhof and Kochert 1988), but more specific information on food habits should be dependent on locality. The food habits of hawks can be determined by examining stomach contents, food pellet composition, prey remains found at nests, or by direct observation of prey captures. There are advantages and disadvantages associated with each technique.

Stomach content analysis involves sacrificing birds and was inappropriate for this study because adults were under behavioral study for the entire breeding season. Food pellets containing food remains (mostly hair, feathers, and bone) are cast periodically and can be indicative of diet. Pellet analysis is useful for owls but is less reliable for hawks (Johnson 1981). More corrosive gastric juice and longer digestion periods in hawks results in remains that are difficult to identify. Pellets would also be difficult to obtain for the free-ranging adult birds in this study.

Prey remains found at nests can be a useful method of determining food habits (Marti 1987). Remains are usually easy to identify and quantify. Disadvantages with this technique include disturbance of nesting pairs and biases towards larger prey items that are not swallowed whole.

Direct observation of prey captures is the most reliable means of estimating food habits and has the fewest biases (Collopy 1983). Intense observation over long periods is necessary to ascertain food habits with this technique. By making direct observations, the time, method and location of the attempt to capture prey can also be determined. This study will use a combination of direct observation and examination of prey remains found at nests to determine what prey are utilized, when they are

captured, how they are captured and where they are captured.

Direct observation of prey-captures will also allow the measurement of hunting success. Hunting success is the ratio of successful prey-capture attempts to the total number of prey-capture attempts (Wakeley 1974, Toland 1986). Many factors may influence the hunting success of raptors (see Toland 1986), but the prey and method selected should maximize energetic gain and minimize energetic expenditures (Village 1983b). In Red-tailed Hawks, hunting success is closely related to method of hunting (Orde and Harrell 1977, Ballam 1981, Diesel 1983, Toland 1986). Hunting success in this study, will be examined according to prey species, time of day, method and location.

METHODS

Any identifiable prey remains found during nest visits in 1983, 1984, and 1985 were recorded. The results were pooled because sample sizes were low. Each piece was identified taxonomically to species if possible and the proportion of the prey remaining was estimated.

All attempts to capture prey occurring during observation periods in 1984 and 1985 were noted and the results pooled for all years because of low sample sizes.

All observations were made with either binoculars or a 15-45x telescope. Time of the prey capture was recorded and period determined (see Chapter 4). All attempts were classified as either successful, unsuccessful, or having unknown success.

If possible, the prey species at which the capture attempt was directed at was recorded. If the attempt was successful, it was often possible to observe the prey directly as the bird flew away or fed. If unsuccessful, it was difficult to ascertain the prey species. Familiarity with habitat and prey availability within habitats assisted identification. Vegetation and low topography sometimes obscured vision and made identification of the prey species impossible.

Classification of the method of hunting was based on a variation of Wakeley's (1978a) system. Four methods of hunting were recognized according to location of the bird prior to the attempt to capture prey. Strikes originated from: (1) ground; (2) perches; (3) low flight (below 100m); or (4) from high flight (above 100m). Habitat in which the prey-capture attempt was made was also recorded, using the major habitat categories described in Chapter 2.

Hunting success was calculated by dividing the number of successful captures by the total number of attempts with known outcomes. Hunting success was determined according

to prey species, hunting method, time period, and habitat type and was analyzed using contingency table analysis (Zar 1984). Statistical significance was accepted at the $P = 0.05$ level.

RESULTS

Richardson's ground squirrels were the predominant prey item found during nest visits (Table 11). Northern pocket gophers were less numerous and were the next most frequent item. Very few meadow voles (Microtus pennsylvanicus) and no deer mice (Peromyscus maniculatus) were found.

Most attempts to capture prey (81.2% of attempts on known prey), were directed at Richardson's ground squirrels (Table 12). Small mammals (meadow voles and deer mice), passerines, and northern pocket gophers accounted for a relatively small proportion of attempts on known prey (11.0%, 4.1%, 3.7% respectively). Prey species could not be determined in a large number of prey capture attempts.

Hunting success differed significantly between prey species ($\chi^2 = 22.98$, $P < 0.0001$). However, when the unknown category was removed from the analysis, there were no significant differences in success between prey species ($\chi^2 = 2.39$, $P > 0.50$).

Table 11. Prey remains found at nests 1983-1985. Items found are from 39 nest visits in which prey remains were found.

Species	Number Of Individuals	% Total
Richardson's ground squirrel (<u>Spermophilus richardsonii</u>)	45	80.3
Northern pocket gopher (<u>Thomomys talpoides</u>)	5	8.9
Meadow vole (<u>Microtus pennsylvanicus</u>)	2	3.6
Long-tailed weasel (<u>Mustela frenata</u>)	2	3.6
Black-billed Magpie (<u>Pica pica</u>)	1	1.8
Garter snake (<u>Thamnophis</u> spp.)	1	1.8
Total	56	100.0

Table 12. Prey capture attempts for various prey taxa and their rates of success.

Prey Type	Number Of Attempts	Number Successful	% Successful
Richardson's ground squirrel (<u>Spermophilus richardsonii</u>)	177	104	58.8
Small mammal (<u>Peromyscus</u> or <u>Microtus</u>)	24	20	83.3
Passerines	9	4	44.4
Northern pocket gopher (<u>Thomomys talpoides</u>)	8	8	100.0
Unknown	121	26	21.5
Total	339	162	47.8

Most prey-capture attempts were initiated from perches or from low soaring flight (Table 13). Few prey-capture attempts were attempted from high soaring flight. There was no significant difference in hunting success between methods ($\chi^2 = 3.21$, $P > 0.36$).

While hunting from perches, hawks would detect a prey item, leave their perches and alternate between flapping and gliding flight in a straight-line gradual descent before attempting to strike the prey with their feet. If successful, hawks would usually either consume the prey near the point of capture or deliver the prey to the nest. If the attempt was unsuccessful the hawk usually flew to a nearby perch and would often try again. Occasionally after an unsuccessful strike on a ground squirrel, the birds would land on the ground and focus their attention on a burrow entrance. If prey surfaced, they would lunge at it.

Birds hunting from low flight would partially fold their wings and dive at prey. Just before impact, hawks would "back-pedal" (Orde and Harrell 1977) to slow down and adjust their location with their wings spread and feet forward. Dives were sometimes preceded by hovering. Hawks were sometimes able to use strong head winds to maintain a steady position over the ground while searching for prey. Strikes attempted from flight could result in

Table 13. Prey capture attempts with different hunting methods and their rates of success.

Hunting method	Number Of Attempts	Number Successful	% Successful
Perch	263	127	48.3
Low flight	58	26	44.8
Ground	13	9	69.2
High flight	5	0	0.0
Total	339	162	47.8

"half-strikes" (Tarboton 1978) in which the dive was interrupted well before nearing the ground.

Observations were distributed equally over all time periods and suggest that more prey-capture attempts occurred in the morning periods than in the afternoon or evening periods (Table 14). There was no significant difference in hunting success between time periods ($\chi^2 = 4.62$, $P > 0.20$). Hunting success declined as the day progressed.

Most prey captures were initiated in grazed pasture (65.2%) and hayfield (19.8%) habitats (Table 15). Few prey captures were attempted in any other habitats. Hunting success did not differ significantly according to habitat type ($\chi^2 = 5.52$, $P > 0.36$).

DISCUSSION

From observed prey-capture attempts and from prey items at nests, it is clear that Red-tailed Hawks on the study area depend on Richardson's ground squirrels as the major source of food. The numerical dominance of ground squirrels underestimates the biomass dominance because of their relatively large size. Small mammals other than Richardson's ground squirrels seem to have a secondary role in Red-tailed Hawk diets. The importance of Richardson's ground squirrels to the study site population was expected.

Table 14. Prey capture attempts in different time periods and their rates of success.

Time Period	Number Of Attempts	Number Successful	% Successful
Before 10:30 h	98	59	60.2
10:30-14:30 h	104	52	50.0
14:31-18:30 h	64	26	40.6
After 18:30 h	73	25	34.3
Total	339	162	47.8

Table 15. Prey capture attempts in different habitats and their rates of success.

Habitat	Number Of Attempts	Number Successful	% Successful
Pasture	221	116	52.5
Hayfield	67	27	40.3
Cropland	31	7	22.6
Fallow	13	7	53.8
Wooded	3	3	100.0
Other	4	2	50.0
Total	339	162	47.8

Rothfels (1981) found ground squirrels to be the most common food item left at nests in the study site area. Richardson's ground squirrels are an important prey species for other populations of Red-tailed Hawks in Alberta (Schmutz et al. 1980, McInvaille and Keith 1974).

Hawks on the study site seem to be successful (58.8%) in hunting ground squirrels. The low success rate for unknown prey species is biased because the identification of prey category was often dependent on the observation of a successful attempt. When attacks on unknown prey were removed from analysis, there was no significant difference in success rates among prey species.

Red-tailed Hawks on the study area forage mainly from perches. This is common method of foraging in other Red-tail populations (Janes 1984a, 1985). Foraging from low flight and high flight was less common than foraging from perches. This suggests that soaring flight in this population serves purposes other than foraging. It likely serves a territorial function as suggested by Ballam (1981).

Success rates did not differ significantly according to hunting method. The highest success rate was seen in the few attempts made from the ground. These attempts were often initiated after failed attempts from perches. Success rates while foraging from perches were similar to

those while foraging from low flight. Red-tailed Hawks were unsuccessful in the few attempts made from high flight.

Hunting success according to method has been determined in other studies of Red-tailed Hawks. However, comparison with other populations is difficult because of inconsistency in the classification of prey-capture methods. Hunting success can be compared without regard to method. Hawks on the study area had an overall success rate of 47.8%. Comparative rates are 78.8% in South Dakota (Orde and Harrell 1974), 16.8% in Arkansas (Ballam 1981) and 33.3% in Missouri (Diesel 1983). The variability seen in overall hunting success in different populations may reflect differences in prey species and availability, habitat differences or sampling differences. The studies of other populations did not provide enough information regarding these differences to allow a proper comparison.

The diurnal distribution of prey captures showed that Red-tails make more attempts to capture prey in the morning and midday periods than in afternoon and evening periods. This may partly reflect the activity and availability of prey (especially ground squirrels). In spring and autumn, the activity of Richardson's ground squirrels above ground occurs between 0800 and 1800, while in midsummer activity is bimodal with peaks at 0600 to 1000 and at 1400 to 1900

(Michener and Koeppel 1985). An increase in afternoon and evening prey-capture attempts should have been expected if the distribution was solely related to ground squirrel activity patterns. However, the vulnerability of prey may also play a role. Richardson's ground squirrels often appeared sluggish when they first emerged in the morning and this may have increased their vulnerability to predation. Ground squirrels were also observed to enter burrows in hot afternoon conditions making them invulnerable to predation by hawks.

The temporal distribution of prey captures may also reflect hunger in adults or nestlings. Red-tails probably do not hunt or feed at night, and hunger and nestling food demand should be greatest in the morning periods. A corresponding increase in attempts to capture prey would then be expected.

Although there were no significant differences in hunting success according to time period, success rates did decline over the course of the day. Again, this may reflect decreased activity and vulnerability to predation by ground squirrels. Low success in the later periods may prevent some hawks from trying to capture prey.

Most prey-capture attempts occurred in pasture and hayfield habitats. This probably reflects both habitat availability and prey availability. Habitat availability

and utilization as it relates to prey abundance will be examined in Chapter 7.

Although success does not differ significantly with habitat, rates in wooded habitats and cropland appear to stand out. The importance of the high success in woods cannot be determined because of the low sample size. Low success in cropland seems to be evident and may be due to low prey vulnerability in this habitat type. Prey may be able to escape more easily in cropland cover than in other habitat types. Vegetative cover has been thought to affect the vulnerability of prey for several Buteo species (Wakeley 1978b, Baker and Brooks 1981, Bechard 1982).

CHAPTER SEVEN

HABITAT SELECTION

INTRODUCTION

The importance of food to Red-tailed Hawks on the study area should be revealed by habitat selection. Chapter 6 suggested that Richardson's ground squirrels are the major prey item on the study area and that foraging usually occurs in pasture habitats. If hawks spend much of their time foraging, analyses of locations should reveal that pasture habitats are preferred. When preferences are compared with food availability within habitats, the importance of food to the population can be determined.

Time spent in various habitats should be indicative of habitat preference. Optimal foraging theory predicts that animals should concentrate their activity in subregions of the home range according to resource density (Ford 1983). This should result in more time being spent in patches yielding the greatest net gain of energy (Royama 1970). Red-tailed Hawks on the study area should spend more time in habitats having the highest profitability of prey.

Habitat features which affect the accessibility of food may also be important in influencing habitat selection (Janes 1985). Vegetative cover has been thought to limit accessibility to prey for several Buteo species (Wakeley 1978b, Baker and Brooks 1981, Bechard 1982). Conversely, Janes (1985) found no consistent relationships between vegetation structure and the distribution of foraging behavior of Red-tailed Hawks.

Other factors such as topography (especially cliffs and outcrops), perch availability and distribution may influence habitat selection in Red-tailed Hawks (Janes 1984a). The location of nesting sites, predators, competitors and physiological factors can also play a role (Janes 1985).

To understand the role of food on habitat selection, it will be necessary to determine relative prey abundance for each habitat type. Analyses of prey captures and prey items found at nests in Chapter 6 suggest that Richardson's ground squirrels and northern pocket gophers are the most important prey species. Counts of ground squirrel burrows and pocket gopher mounds will be used as indices of prey abundance for different habitats (Reid et al. 1966, Schmutz et al. 1980, Rothfels 1981). Pasture habitats should have the greatest abundance of burrows (Rothfels 1981).

Most prey-capture attempts occurred in pasture and hayfield habitats (see Chapter 6). To help determine if hawks are selective in the types of habitat they forage in, the number of actual prey captures in habitats will be compared to the the expected number based on habitat availability. If prey captures within habitats are not in proportion to availability, selection can be inferred.

Raptor habitat selection for suitable prey habitats can also be detected by the inclusion of a relatively constant amount of prey-producing habitat within home ranges (Janes 1984a). Brown's (1964) principle of economic defendability predicts that smaller territories should contain more resources per unit area than larger ones. Territory size on the study area should be adjusted so that total prey availability will be similar for all territories. Because Richardson's ground squirrels seem to be the most common prey of Red-tailed Hawks on the study area, and these animals are most common in pasture habitats (Rothfels 1981), territory size should be negatively correlated with the proportion of pasture.

If prey abundance is a major factor affecting the dispersion and density of Red-tailed Hawks on the study area, then hawks should be selective in the areas they search for prey. A direct assessment of foraging habitat preferences based on hawk locations was not possible

because Red-tailed Hawks do not show signs of active foraging (see Chapter 4). Selection should still be evident in the time spent in different habitats, if foraging is a primary activity. A breakdown of time spent in different habitats according to all locations, perched locations or locations associated with low soaring and perched activity will be necessary. This should cover all locations where prey-capture attempts occurred. Red-tails should spend more time in habitats with the highest abundance of prey. Selection for habitats based on prey-capture attempts should coincide with selection based on time spent in various habitats. If they do not coincide, hawks are probably spending much of their time in various habitats for purposes other than foraging.

A. DETERMINING SELECTION AND PREFERENCE

Most available methods for determining habitat selection and preference involve measuring the usage of habitats as well as their availability. Critical to understanding these procedures is a definition of all terms (Mosher et al. 1987). Johnson (1980) has provided suitable definitions. Usage refers to a measure of the quantity of the component used by the consumer in a fixed period of time. Availability is the accessibility of the component

to the consumer. Selection involves the consumer actually choosing the habitat component. Usage is selective if components are used disproportionately to their availability. Preference for a habitat component reflects the likelihood of a component being chosen if offered on an equal availability with other components.

Four orders of selection are identified by Johnson (1980). First-order selection reflects the selection of the physical or geographical range of a species. Selection of the home range within the geographical range is second-order selection. The use of habitat components within the home range reflects third-order selection. Fourth-order selection involves procurement of food items from within the home range. This chapter examined selection at the third level (within the home range).

Various methods are available for determining habitat selection (see Alldredge and Ratti, 1986). Johnson's (1980) technique utilizes a rank-order procedure in which the relative ranks of utilized and available habitat components are compared for each individual. Differences between selection rank and availability rank for each habitat are averaged among individuals to obtain estimates of the relative selection of any given habitat. The magnitude of the average differences is used to order the habitats according to preference. The technique tests the

null hypothesis that all habitat components are equally preferred and compares components using the the multiple comparison technique of Waller and Duncan (1969). A critical significant difference is computed for each pair of habitats compared.

There is no clear "best" method of determining habitat selection and preference. The technique of Johnson (1980) was considered acceptable by Alldredge and Ratti (1986). Delineation of study area boundaries can affect second-order selection analysis using Johnson's (1980) technique (Porter and Church 1987). Since only third-order selection is examined in this study, analyses should not be affected by this problem. Johnson's method is becoming increasingly more popular and was therefore chosen for this analysis.

METHODS

Habitat types were delineated as outlined in Chapter 2. Availability of habitats within home ranges for each pair was determined by calculating the area of each habitat type within the MCP for each home range (see Chapter 5) using a CalComp 9000 digitizer tablet.

Indices of prey abundance in each habitat type were obtained by counting active Richardson's ground squirrel

burrows and "fresh" northern pocket gopher mounds (Reid et al. 1966) along transects 100 m long and 2 m wide in July of 1984. Active ground squirrel burrows had either signs of recent digging, feces, or clipped vegetation at their entrances. "Fresh" pocket gopher mounds consisted of black earth with little vegetation growth. Transects began at randomly-placed points within habitats and ran in randomly-selected directions. The sites where transect sampling occurred were randomly chosen throughout the study area. One hundred transect samples were obtained in each of pasture, hayfield, cropland, and fallow habitats. No transects were attempted in wooded habitats because extensive searching revealed that both ground squirrels and pocket gophers were very uncommon in this habitat type. The "other" habitat category was a composite of various habitats and was also not sampled. Differences in burrow and mound counts among habitats were examined using Kruskal-Wallis one-way analysis of variance and Tukey-type multiple comparison procedures (Zar 1984).

To determine if prey captures within habitats occurred in proportion to the availability of habitats within home ranges, observed and expected distributions of prey captures were calculated. Data from 1984 and 1985 were pooled because of low sample sizes. For all territories in both years, 339 prey-capture attempts made for which the

outcome was known (see Chapter 6). These formed the basis for the observed distribution of prey capture attempts. An expected distribution of prey captures was calculated from the average percent availability of habitats within home ranges. Expected distributions and actual distributions were then compared using contingency table analysis (Zar 1984). Individual habitats were compared by subdividing the contingency tables (Zar 1984).

Sizes of territories and the amount of pasture within territories were compared with simple linear regression. MCP estimates of home range were used (see Chapter 5). Breeding and nonbreeding pairs were considered separately. To insure the independence of the samples being compared, no more than one year of data were used from each nesting territory, unless breeding status changed between years. If breeding status changed, sizes from both years (one year as breeding, one year as nonbreeding) were used. This selection process resulted in the comparison of sizes for 24 territories (13 breeding, 11 nonbreeding).

Habitat selection and preference were determined using a Fortran program supplied by Johnson (1980). Usage of habitats was determined by summing the number of hawk locations within each habitat type. If a location fell on the border between two habitat types, each habitat was assigned "half" a location. The habitat of all hawk

locations was determined by comparing location on the aerial photo mosaic with an aerial photo mosaic on which habitats had been marked. Locations and behavior records of hawks were available for two-minute intervals during two-hour observation periods (see Chapters 4 and 5). The program calculated selection based on all locations, perched locations, and perched and soaring locations (see Chapter 4). Only "other" soaring locations were utilized (see Chapter 4). The program ranked habitats in terms of preference and identified those differences in mean ranks which were significant according to Waller-Duncan multiple comparison procedures (Waller and Duncan 1969).

RESULTS

Counts of Richardson's ground squirrel burrows differed significantly (Kruskal-Wallis, $H = 131.84$, $P < 0.0001$) among habitats (Table 16). Pasture had significantly greater counts than any other habitat (Tukey-type multiple comparisons, all $P < 0.0001$). Burrow counts were significantly greater in fallow than in cropland or hayfield (Tukey-type multiple comparisons, all $P < 0.005$). There was no significant difference in burrow counts between cropland and hayfield (Tukey-type multiple comparisons, $Q = 1.39$, $P > 0.05$).

Table 16. Counts of Richardson's ground squirrel (RGS) burrows, and northern pocket gopher (NPG) mounds, along transects in different habitats. N = 100 transects for each habitat type.

Habitat	RGS		NPG	
	Mean	SD	Mean	SD
Pasture	6.34	5.03	1.16	2.10
Hayfield	1.16	2.72	7.14	6.71
Cropland	0.95	1.73	0.32	0.68
Fallow	1.57	1.82	0.18	0.61

Northern pocket gopher counts also differed significantly among habitats (Kruskal-Wallis, $H = 146.00$, $P < 0.0001$). Hayfields had significantly more mounds than any other habitat (Tukey-type multiple comparison, all $P < 0.0001$). Mound counts were significantly greater in pasture than in fallow (Tukey-type multiple comparisons, $Q = 3.72$, $P < 0.002$). There were no significant differences in mound counts between pasture and fallow habitats or between pasture and cropland habitats (Kruskal-Wallis, all $P > 0.05$).

The observed distribution of prey-capture attempts among different habitat types differed significantly ($\chi^2 = 147.76$, $P < 0.0001$) from the expected distribution (Figure 12). Significantly more prey captures than expected were attempted in pasture and hayfield habitat types (χ^2 , all $P < 0.001$). Significantly fewer than expected attempts were made in wooded habitats ($\chi^2 = 125.69$, $P < 0.001$).

As the size of territory increased, so did the area of pasture for both breeding and nonbreeding pairs (Fig. 13 and 14). The regression of area of pasture on size of territory was significant for both breeding ($F = 5.44$, $P < 0.04$) and nonbreeding birds ($F = 16.40$, $P < 0.003$).

Average habitat availability was similar for both breeding and nonbreeding pairs (Table 17). Wooded and pasture habitats were the most abundant and seemed to

Figure 12. Observed (solid rectangle) and expected (open rectangle) numbers of prey capture attempts in different habitat types. Data from 1984 and 1985 were pooled ($N = 339$ attempts).

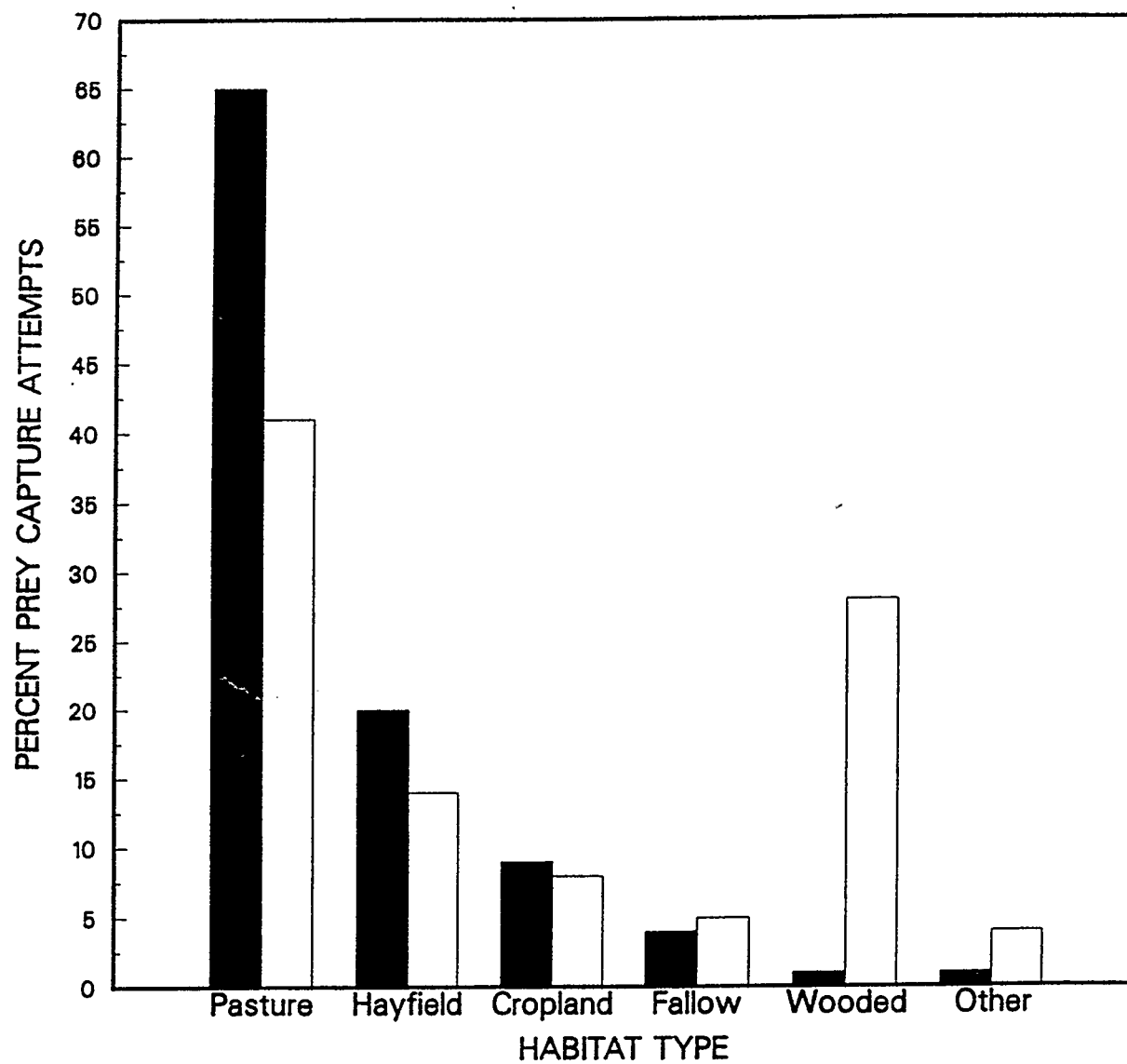


Figure 13. Regression of area of pasture habitat within territories on territory size for breeding pairs. The fitted linear regression line is shown ($Y = 0.99x + 0.67$). $N = 13$ territories.

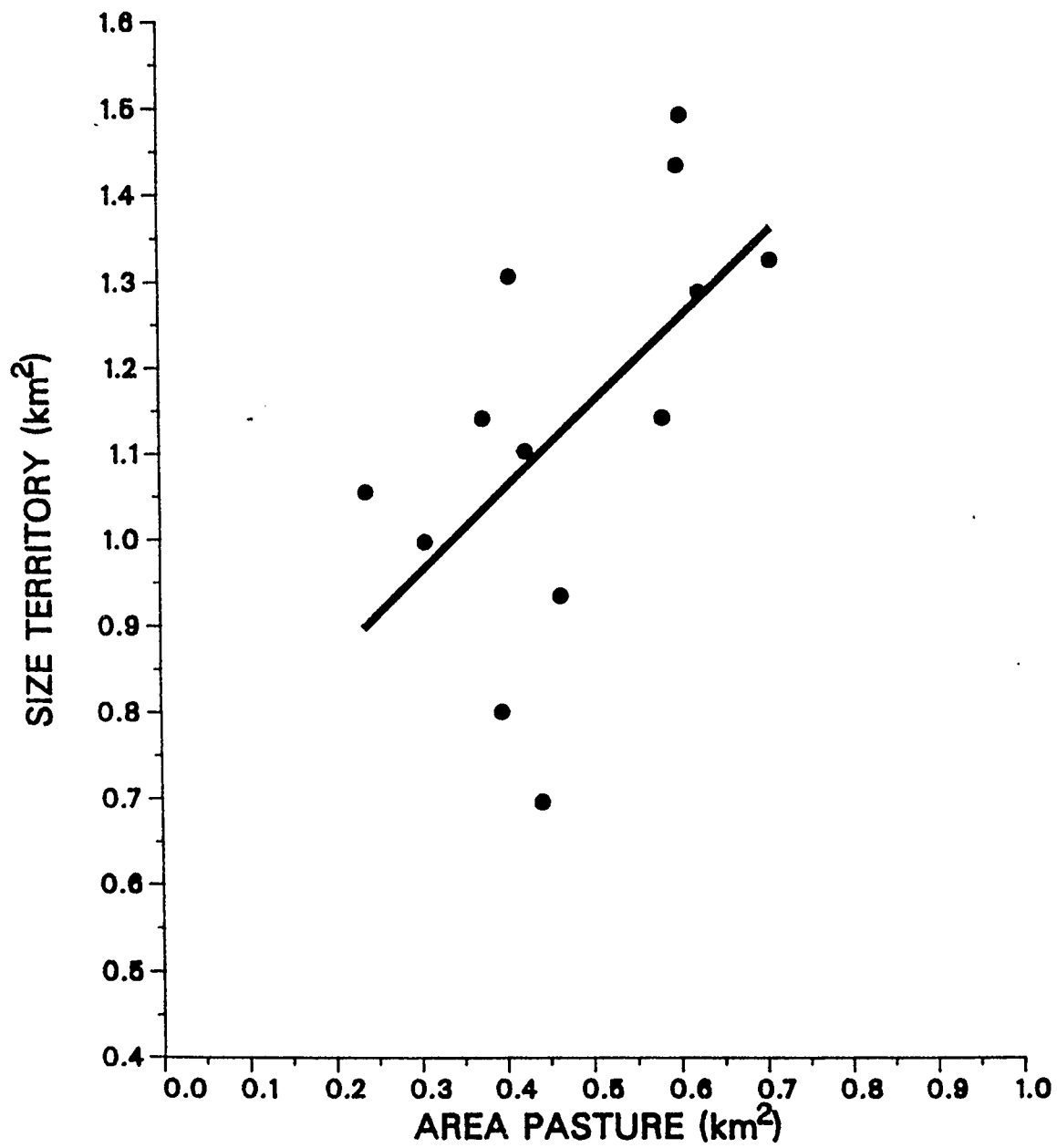


Figure 14. Regression of area of pasture habitat within territories on territory size for nonbreeding pairs. The fitted linear regression line is shown ($Y = 1.55 x + 0.46$). $N = 11$ territories.

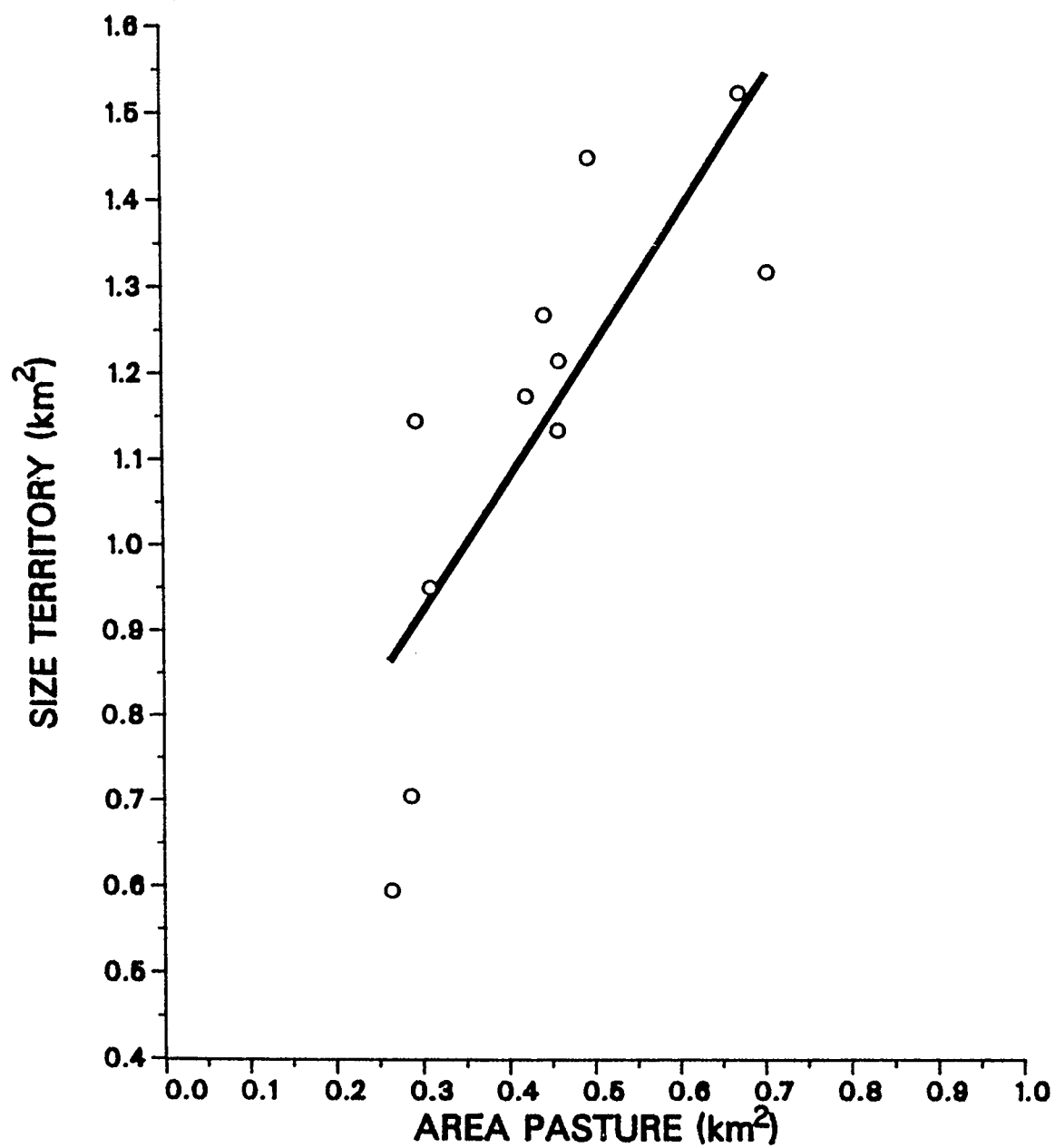


Table 17. Percent habitat availability, and percent use based on all, perched, perched or soaring locations, for both breeding (B) and nonbreeding (NB) pairs.

Habitat	% Available		% Use					
			All		Perched		Perched Or Soaring	
	B	NB	B	NB	B	NB	B	NB
Pasture	42.5	38.9	41.9	42.6	40.1	40.9	40.9	41.7
Wooded	23.0	32.7	38.9	46.0	41.6	49.0	40.3	47.8
Hayfield	16.8	11.5	12.0	6.6	11.9	6.2	12.0	6.3
Cropland	9.7	7.1	5.2	1.9	4.7	1.6	5.0	1.8
Fallow	4.4	6.2	0.3	1.8	0.1	1.5	0.2	1.6
Other	3.5	3.5	1.7	1.2	1.6	0.9	1.6	0.9

receive the highest use. Usage was similar for both breeding and nonbreeding pairs, regardless of the type of location.

The rank ordering of habitat means according to selection reveals only one consistent pattern. Wooded and "other" habitat types appear to be the most preferred habitats in all comparisons (Fig. 15). The only comparison where all habitats were not used with equal intensity was for perched locations of breeding pairs (Hotellings's T , $F = 4.25$, $P < 0.05$). In this comparison, selection for wooded habitats was significantly greater than selection for any other habitat (Waller-Duncan, all $K = 100$). For all other comparisons the rank ordering of habitats according to selection was not significantly different from the rank ordering of the availability of habitats (Hotelling's T , all $P > 0.05$).

DISCUSSION

The Richardson's ground squirrel burrow counts clearly identify pasture as the important source of potential prey for Red-tailed Hawks on the study area. Hayfields appear to have the greatest abundance of northern pocket gophers. Since ground squirrels and pocket gophers form the bulk of

Figure 15. Habitat preference by breeding and nonbreeding pairs based on all, perched, and perched or soaring locations. Habitats are rank ordered from most preferred to least preferred (left to right). Habitat types underscored by solid lines are not significantly different according to the Waller Duncan procedure. Those underscored by an outlined line differ significantly from the habitat type which is not underscored. Habitats types are abbreviated: W (wooded), O (other), C (cropland), H (hayfield), P (pasture), F (fallow). N = 13 breeding, 11 nonbreeding pairs.

BREEDING

LOCATIONS

NONBREEDING



ALL

PERCHED

PERCHED
OR
SOARING

W O C H P F

W O C H P F

W O C P F H

W O H F P C

W O H P F C

W O H F P C

Red-tail diets on the study area (see Chapter 6), hawks should be expected to forage in these habitats.

Contingency table analysis of the distribution of prey-capture attempts in different habitats showed that significantly more prey-capture attempts were made in pasture and hayfield habitats than expected. It appears that prey-capture attempts are occurring where prey are most abundant. Fewer prey-capture attempts than expected were made in wooded habitats. Wooded habitats were relatively void of either major prey species. Thus, the distribution of prey-capture attempts in habitats coincides well with the distribution of prey within those habitats.

Analysis of time spent in different habitats showed a different pattern. Prey abundance within habitats seemed to have little effect on time spent within habitats. Red-tailed Hawks on the study area showed few habitat preferences regardless of whether all locations, perched locations, or perched and soaring locations were used. Pasture had the greatest abundance of ground squirrel burrows and the most prey capture attempts, yet there was no significant preference for this habitat type. Similarly, hayfield habitats had the highest abundance of pocket gopher mounds but there was no significant preference for this habitat type. Wooded habitat was consistently the most utilized and the most preferred, but

few prey capture attempts were here. Further, both ground squirrels and pocket gophers were rarely found in wooded habitats.

Habitat features such as perch availability and the amount and distribution of vegetative cover may account for the above preferences (Baker and Brooks 1980, Bechard 1982, Janes 1984, 1985). I feel, however, that the observed preference patterns are the result of territorial behavior and a superabundant prey supply within territories. Red-tailed Hawks on the study area spent a large amount of time on conspicuous perches, especially in wooded habitat (see also Chapters 4 and 5). This probably serves a territorial advertisement function as well as allowing nest vigilance. Hawks did not appear to be foraging from these perches. I believe that this means that the hawks do not spend a great deal of time foraging and that food is not a limiting resource. When food is required, I believe that hawks hunt in spurts, usually until successful, in favorite hunting areas. Observations of hawks indicated that hunting in spurts was common. The areas in which intensive hunting occurred were small in comparison to the size of the territory. Wakeley (1978b) has also observed that hunting strikes in Ferruginous Hawks tend to be concentrated in relatively small areas. The behavior of Red-tailed Hawks on the study area seems to indicate that,

in terms of time spent in various activities, foraging is secondary to territory defence and nest vigilance.

This idea is further supported by the relationship between territory size and the amount of pasture within territories. Red-tails on the study area do not seem to adjust their territory size to the amount of food. Regressions of size and amount of pasture for both breeding and nonbreeding hawks seem to indicate that as territory size increases so does the amount of pasture habitat. A relatively constant amount of prey-producing habitat was not found among Red-tail territories, suggesting that territorial boundaries are not solely chosen to include foraging areas (Janes 1985).

Why some territories are larger than others is unknown. Presumably larger territories would have greater defence costs. Other unknown habitat features may account for the size differences. The amount and distribution of territorial perches may play a role.

CHAPTER EIGHT

GENERAL DISCUSSION

A. THE IMPORTANCE OF FOOD

This study has demonstrated that the density of nesting pairs of Red-tailed Hawks on the study area is apparently not limited by food. The abundance of nests, alternate nests, and potential nest-sites on the study area suggests that nest-sites are also not limiting. This makes the population unusual in that food or nest-site availability normally limit breeding densities of raptors (Newton 1976, 1979). Space itself, or an unidentified resource, may be limiting densities on the study area.

The density of Red-tailed Hawks on the study area is the highest recorded in North America. The high rates of nonbreeding were unexpected but facilitated the comparison of activity patterns, home range and habitat selection for two segments of the population (breeding versus nonbreeding) with very different food demands. Nestlings would place higher food demand on breeding pairs. In addition, food demand for breeding pairs should increase as the nesting season progresses because of chick growth and activity. A comparison of activity patterns, home range,

and habitat use between breeding and nonbreeding pairs should have revealed differences associated with differing food requirements as the nesting cycle progressed.

Few differences in time spent per activity were found between breeding and nonbreeding hawks. This indicates that hawks do not alter their activity patterns in response to food demand imposed by nestlings. Perching occupied most of the time budget of Red-tailed Hawks and increased as the nesting cycle progressed in both breeding and nonbreeding birds. The increased amount of time spent perching as the nesting season progressed may reflect increased foraging. If this were true, however, differences should have been evident between breeding and nonbreeding birds.

I believe that the amount of time spent perched is related to territorial activity and resting. Territorial hawks (both breeding and nonbreeding) can make themselves conspicuous and obtain good views of their territories by perching on tall perches. While perched, birds may be able to advertise territorial status without initiating agonistic interactions. Intruders and predators can be detected from these perches. Boundaries of territories may, in part, be determined by various topographic features which limit visibility. Hawks may only be able to defend the area that is visible from such territorial perches.

Perching also provides the opportunity to rest. As the nesting season progresses, agonistic behavior and intrusion pressure declines. This may afford hawks more time to rest.

Red-tails on the study area maintained exclusive home ranges (territories). This is typical of most species of Buteo (Craighead and Craighead 1956, Newton 1976, 1979). Exclusive home ranges suggests that all resources found within territories are defended and is characteristic of species relying on large vertebrate prey (Newton 1975). Intruders should be completely excluded when the benefits of territory defense increase faster than the costs as degree of exclusion increases (Wittenberger 1981). The study area population appeared to exhibit a high degree of territoriality, suggesting that pairs must be incurring benefits which outweighed the costs of defense. Sufficient food is an obvious benefit, but does not appear to be the sole cause of territoriality in the study area population.

High food demand associated with breeding and later stages in the nesting cycle did not appear to result in territory size increases. Rather, territory size appeared to decrease as the nesting season progressed for both breeding and nonbreeding pairs. This seems to indicate that food is superabundant or that initial boundaries contain sufficient food for the entire nesting season.

Because hawks tend to restrict their activity to small regions of the home range and to forage in restricted areas, it appears that territorial boundaries are not established solely to provide sufficient food.

This is further supported by the observation that Red-tailed Hawk territories on the study area did not seem to include a constant amount of food-producing habitat. If food was the predominant defended resource, territory size should have been negatively correlated with food abundance (Brown 1964, Janes 1984a). Pasture habitat contained the most potential prey. However, the amount of pasture habitat was positively correlated with territory size.

Richardson's ground squirrels were clearly the major prey species of Red-tailed Hawks on the study area. Most prey-capture attempts occurred in pasture. This suggests that if food and foraging are important to the study area population, hawks should spend much of their activity in pasture habitats. This clearly was not the case, as hawks showed no preference for this habitat type. Instead, hawks were found most often in wooded habitats. This likely reflects territory advertisement, nest vigilance, and resting by birds. The amount of time spent in habitats on the study area does not appear to be related to foraging activity.

If food is not the limiting resource, presumably another resource or other resources may be limiting and require defense. These resources must be economically defensible, meaning that the benefits associated with acquisition of the resource outweigh the costs of defending the resource (Brown 1964). Space to perform breeding activities may be limiting (Schmutz 1977, Rothfels and Lein 1983). Collectively the resources necessary for survival and for successful reproduction are probably numerous and territoriality may serve to acquire all of these requisites. Competition for all of these resources (including food) contained in a minimum fixed amount of space may be limiting the breeding density of the population. This competition is manifested in the form of territorial behavior.

B. FUTURE RESEARCH

A comparison of various features of this population with another less dense population would be useful. This would help to determine if the observed activity patterns, home ranges and habitat use are characteristic of the study area only. Further inferences on the limitation of breeding density could then be made.

The stability of the breeding population on the study area should be assessed. It would be useful to know if hawks return to the same territory each year. It would also be interesting to know the age of birds on territories, turnover rates, and whether local offspring eventually return to breed. Do boundaries change significantly with new owners? What role do conspecifics (especially Swainson's Hawks) play in determining breeding density and territory boundaries on the study area?

The high rates of nonbreeding on the study area should be the object of further investigation. This study points out the need for all future investigations to assess thoroughly the nonbreeding component of breeding populations. It would be interesting to know if nonbreeding is a regular occurrence on the study area or whether it was confined only to the years of investigation. The cause of failure to lay eggs would also be helpful but difficult to assess. The significance and abundance of floaters in surrounding areas should also be determined.

A more thorough investigation of the feeding ecology of the study area population of Red-tails might prove useful. If prey abundance could be determined in areas within habitats, it might explain, in part, why certain portions of the home range receive high use. Predator-prey interactions should be further investigated. How stable is

the ground squirrel population and how is it affected by Red-tailed Hawks? Or conversely, how is the hawk population affected by ground squirrel population dynamics?

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