

**ECOLOGICAL CORRELATES OF HARRIS' HAWK
GROUPING IN SOUTHERN TEXAS**

A Dissertation

by

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**Submitted to the College of Graduate Studies
Texas A&M University-Kingsville
and
Texas A&M University
in partial fulfillment of the requirements for the degree of**

DOCTOR OF PHILOSOPHY

August 2002

Major Subject: Wildlife Science

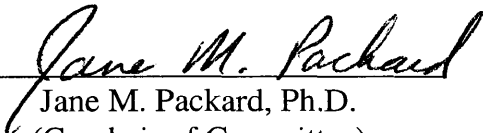
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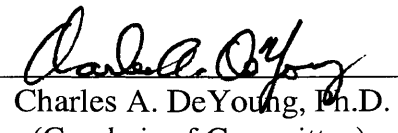
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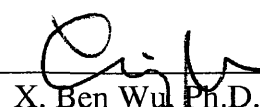
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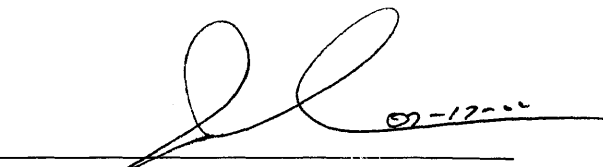

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ABSTRACT

Ecological Correlates of Harris' Hawk Grouping in Southern Texas

(August 2002)

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I surveyed Harris' hawk (*Parabuteo unicinctus*) grouping relative to rainfall and landscape patterns at eight southern Texas study sites during the fall non-breeding season. Objectives were to: 1) determine relationships among landscape use, grouping and abundance across sites, 2) characterize variation in grouping associated with rainfall patterns in the brushland and grassland ecoregions of the study area, and 3) explore which landscape measures best explained within site variation in grouping, considering 3 spatial scales (mesohabitat, territory, home range).

Although abundance was higher (17.1 ± 4.1 hawks/100km) than reported for more arid regions, observations of groups (>2 hawks) varied across sites (0.113 ± 0.037 groups/observation). Groups were not observed at 3 of 4 sites in the wetter, eastern grassland, where abundance was slightly lower than brushland. One grassland site with abundant hawks and groups was a drier, habitat fragment in a landscape devoid of woody vegetation. Abundance correlated with grouping but not with the landscape variables measured. However, hawks were typically found in areas with less fragmented woody

vegetation. Vegetation strata differed between random points and hawk locations at 5 sites, four of which had groups, but differences could not be generalized across sites.

Sightings of 3 hawks were more likely to be at brushland than grassland locations ($z = 2.34, p < 0.05$). Larger groups (4-5 hawks) and groups with young-of-the-year were sighted infrequently with no differences between ecoregions. Two indices of grouping were significantly negatively correlated with rainfall recorded near each site in the same year, but not with indices of rainfall during the previous year.

Only subtle differences in landscape vegetation were found between areas around grouped and non-grouped Harris' hawk locations. I compared vegetation patterns at three ecologically appropriate scales. The greatest differences were observed at the finest scale (simulating mesohabitat), leading to hypotheses related to prey availability for this group-hunting predator and distribution of scarce resources (e.g., water).

Results were interpreted relative to the Ecological Constraints Model predicting groups in harsh environments. To refine testable predictions from this model, I recommend using spatially explicit landscape measures to document distribution of resources relative to groups.

ACKNOWLEDGMENTS

This endeavor was financially supported by a fellowship from the Rob and Bessie Welder Wildlife Foundation and grants from the U.S. Fish and Wildlife Service, and the B.C. and Addie Brookshire Kleberg County Charitable Foundation. Texas A&M University-Kingsville provided a research assistantship during my first year. Without the support of these organizations, this project would never have been possible.

The Caesar Kleberg Wildlife Research Institute and its wonderful staff provided immeasurable logistical support. Becky, Yoli, Chris, Amy, Monica, Kailey, Linda, you all made things much easier for me. Thank you, ladies! Eric Redeker with his near limitless patience (and I tested it) provided invaluable GPS and GIS advice. Swarovski Optik provided drastically reduced prices on the optics used for this project. For this, my eyes are very thankful. For my poor color-blind eyes and my general mental well being, I thank Jim Sinclair for the many hours he spent working on classifying satellite imagery. His timely (and unpaid) intervention made finishing my degree on time possible. I also want to thank Dr. Dave Hewitt for all the time he spent working with me to be a better teacher, providing insight into research ideas, helping me search for a job, and just being a friend in general. Thank you also to Dr. Jamie Laurenz. I enjoyed our chats about science, teaching, and life in general. Thanks for your advice.

Thank you to Drs. Nestor Sherman and Mike Daniel at the TAMUK Department of Health and Kinesiology for providing access to their SPSS computer for doing my statistical analysis.

I also want to thank the members of my committee. Thank you to Dr. Ben Wu for agreeing to serve on my committee and providing ideas for landscape analyses. To my

co-advisor, Dr. Charlie DeYoung, thank you for helping to get me to Kingsville and for your willingness to work with me even before you knew what a Harris' hawk looked like. Although he was not a co-advisor on paper, Dr. Felipe Chavez-Ramirez was a co-advisor for all practical purposes. Despite working over long-distance, your advice was insightful and valuable, and your willingness to help me so much these last months was crucial. Thank you. My co-advisor, Jane Packard, accepted me as a student before she met me and worked as closely as possible with me given the 5-hour drive between us. She also was willing and able to deal with frantic phone calls and exasperating emails. She has been a solid mentor, a "caring coach" and a good friend. Thanks, Coach!

My friends helped me through some difficult times. Thank you, Alice, Amy, Catherine, Charity, Cody, David, Dawn, Diana, Elisa, Erika, Jan, Jennifer, Jenny, Larry, Mark, Melody, Rob, Roger, Shannon, Shari, Stephanie, Sue, Susan, and Wayne. There are many more people I want to thank individually, but this list would go on for quite a while. Thank you, friends!

Last and certainly not least, I want to thank my family. Mom, Dad, and Jennifer, you have always believed in me, even when I did not believe in myself. I never could have made it through the last four years without your love and support. I will never be able to write or say the words that can adequately express what you mean to me and how much I love you. Thank you!

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CHAPTER I

INTRODUCTION

PROBLEM STATEMENT

Little is known about Harris' hawks (*Parabuteo unicinctus*) in southern Texas. Although seemingly abundant in this region, their numbers appear to have diminished except in refuges and sanctuaries (Bednarz et al. 1988, Bednarz 1995). This trend has been attributed to changes in land use (Oberholser 1974, Bednarz 1995). Therefore, any information about this species in southern Texas will be useful for future management plans. Basic information is lacking for this region in regards to Harris' hawk behavior and abundance and how they relate to habitat, i.e., resources and conditions present in an area that produce occupancy-including survival and reproduction-by a given organism (Hall et al. 1997). In Arizona and New Mexico, Harris' hawks sometimes do and sometimes do not exhibit cooperative breeding and hunting behavior (Bednarz 1995), which involves > 2 individuals working together to hunt and raise offspring. However, no distinct relationships have been found between habitat characteristics and formation of Harris' hawk cooperative groups (i.e., > 2 individuals). Therefore, no clear model has been developed that provides clear predictions about how environmental factors might influence Harris' hawk group formation.

BACKGROUND

Animals form different kinds of groups for different reasons. They may form multi-species feeding assemblages (Diamond and Terborgh 1967, Master 1992,

Monkkonen et al. 1996, Hardie and Buchanan-Smith 1997) or same species aggregations (often herds or flocks) containing both related and unrelated members (Crook 1960; Jarman 1974, 1991). Most commonly, the advantages of grouping are associated with avoiding predation and obtaining food (Krebs and Davies 1993). As the number of individuals increases, the total amount of time spent scanning for predators often increases but the amount of time per individual decreases (Powell 1974, Bertram 1980) and the chance of escaping increases (Kenward 1978) except perhaps in primates (Treves 2000). Furthermore, more individuals present around a given individual decrease the chances that any given individual will be depredated (dilution effect, Calvert et al. 1979, Duncan and Vigne 1979). Individuals may move into the center of a group to place as many other individuals as possible between themselves and potential predators (selfish herd, Hamilton 1971, Viscido and Wetthey 2002). By observing other individuals in groups, an individual may increase their chances of locating food sources (Ward and Zahavi 1973, De Groot 1980). In some carnivore species, clumped and dispersed resources may prevent 1 or 2 individuals from defending them resulting in several individuals aggregated in the same area or even in a shared territory (Macdonald 1983, Kruuk and Macdonald 1985, Carr and Macdonald 1986, Woodroffe and Macdonald 1993).

Family groups include mated or closely related individuals that may work together to defend resources, raise offspring, obtain food, and avoid predation (Gaston 1978, Emlen and Vehrencamp 1983, Macdonald 1983, Rasa 1987, Packer et al. 1990, Mumme 1997, Hayes 2000, Brown 2001). Eusocial groups are highly specialized family groups and are primarily found in 3 insect orders (Krebs and Davies 1993) but appear to

occur in naked mole rats (*Heterocephalus glaber*; Jarvis 1981, Sherman et al. 1992).

Members of eusocial groups are highly related with individuals performing specialized tasks providing food and care for young and the few individuals that breed (Krebs and Davies 1993).

Much work in recent decades has focused on family groups (Stacey and Koenig 1990, Solomon and French 1997), particularly cooperatively breeding birds (Stacey and Koenig 1990) and the ecological influences on group formation and group size (Brown 1974, 1987; Gaston 1978; Koenig and Pitelka 1981; Emlen 1982*a,b*, 1984, 1995; Emlen and Vehrencamp 1983; Stacey and Ligon 1987, 1991; Koenig et al. 1992; Komdeur 1992, 1996; Cockburn 1998; Hatchwell and Komdeur 2000). In the last 20 years, work has focused on understanding 2 things: “why do young individuals delay dispersal and remain with their families?” and “why do individuals help?” (Emlen 1982*a,b*; Hatchwell and Komdeur 2000).

Work on the former question led to different models about the constraints of dispersal and the benefits of not dispersing. The Ecological Constraints Model (Emlen 1982*a*) suggests that some ecological constraint prevents young individuals from dispersing. It may be a lack of available territories (habitat saturation; Brown 1974, Ricklefs 1975, Gaston 1978) or due to variable or unpredictable conditions preventing some younger individuals from dispersing successfully regardless of territory area availability (Du Plessis 1995, Spinks et al. 2000). Other constraints may include shortage of breeding partners and probable breeding failure (Hatchwell and Komdeur 2000). The Benefits of Philopatry Model (Stacey and Ligon 1987, 1991) identifies intrinsic benefits of staying in natal areas. Benefits may include increased quality of an area based on

some localized resource or social benefits from having multiple individuals in the area (Koenig and Pitelka 1981, Emlen 1994, Brown 2001). Ten years ago, a more comprehensive model was proposed that incorporated both of these concepts into the Delayed Dispersal-Threshold Model (Koenig et al. 1992), which is analogous to the Polygyny Threshold Model (Verner and Willson 1966, Orians 1969).

The Delayed-Dispersal Threshold model (Koenig et al. 1992) highlights 5 parameters that determine the extent to which constraints and benefits influence delayed dispersal and group size:

1. *Relative density* – This is equivalent to habitat saturation. Greater density results in fewer available places of sufficient quality to disperse. It is unlikely to be sufficient by itself to result in delayed dispersal, but it likely influences the other parameters.
2. *Fitness differential between dispersing to breed and delaying dispersal* – As the difference in potential fitness decreases between individuals dispersing to breed or delaying dispersal, frequency of delayed dispersal will increase. This is particularly true if available areas are of lower quality than natal areas.
3. *Fitness of floaters (disperse but do not breed)* – Typically the fitness of floaters is lower than individuals that either disperse to breed or delay dispersal. However, in some cases, floaters may have better fitness at lowest quality areas or can occupy areas of sufficient quality to have higher fitness than delayed dispersers.
4. *Distribution of territory/habitat quality* – Depending upon the circumstances, variation in habitat quality and its distribution will influence the occurrence of grouping.

5. *Environmental variability* – High spatio-temporal variability in territory quality will result in grouping only if absolute quality of territories and potential territories fluctuates without changing the relative ranking of territories.

Harris' hawks facultatively form cooperative family groups (> 2 birds) resulting primarily from delayed dispersal (Bednarz 1987, Dawson and Mannan 1991*a*, Bednarz 1995). They are widely distributed from the southern U.S.A. (primarily Arizona, New Mexico, and Texas) to southern South America (central Chile), but have primarily been studied only at the extreme northern and southern extents of their range (Jiménez and Jaksić 1993, del Hoyo et al. 1994, Bednarz 1995). Harris' hawks exhibit substantial geographic variation in their tendencies to form groups. Observations of groups have varied from 84% in Arizona (Dawson and Mannan 1991*a*) to 51% in New Mexico (Bednarz 1987) to 5-13% in Texas (Griffin 1976, Brannon 1980) to none in central Chile (Jiménez and Jaksić 1993). The spatial scale of previous studies have been relatively limited by necessity to adequately collect various data on pairs and groups, group sizes, contributions of non-dispersing young, territoriality, and habitat characteristics (Bednarz 1987; Bednarz and Ligon 1988; Dawson and Mannan 1991*a,b*). Attempts to ascertain differences in various habitat characteristics, mostly vegetation composition and prey abundance at fine spatial scales (Bednarz and Ligon 1988), between group and non-group nest sites have not yielded much information on the proximate environmental factors influencing why Harris' hawks facultatively form groups.

Harris' hawks occupy their territories throughout the year, forming groups outside of a breeding context (Bednarz 1988, Faaborg and Bednarz 1990, Dawson and Mannan 1991*b*). As in the breeding season, they will often cooperatively hunt for large prey like

cottontail rabbits (*Sylvilagus* spp.) and jackrabbits (*Lepus* spp.; Bednarz 1988, Faaborg and Bednarz 1990, Dawson 1988, Dawson and Mannan 1991*b*). Because success at capturing large prey is positively correlated with group size (Bednarz 1988, 1995; Dawson 1988), and because they form groups during the non-breeding season (Bednarz 1988, Faaborg and Bednarz 1990, Dawson and Mannan 1991*b*), cooperative hunting is believed to be a primary factor influencing group formation in this species (Bednarz and Ligon 1988, Dawson and Mannan 1991*b*).

Other factors have been suggested to influence grouping in this species. Habitat saturation has also been suggested for populations in Arizona (Dawson and Mannan 1991*b*), but I suspect a better interpretation might be based on the Marginal Habitat Hypotheses (Koenig and Pitelka 1981), which has also been incorporated into the Delayed-Dispersal Threshold Model (Koenig et al. 1992). The Marginal Habitat Hypothesis predicts groups will form in areas where territories are of similar and high quality but little marginal habitat exists into which young can disperse. Dawson and Mannan's (1991*b*) description of their study area, which has the highest grouping rates reported, relative to that of Bednarz and Ligon's (1988) matches the predictions of the Marginal Habitat Hypothesis. Water may be a possible localized resource that increases habitat quality (Bednarz et al. 1988, Dawson and Mannan 1991*b*, Bednarz 1995) and therefore the likelihood of delayed dispersal. However, no clear or consistent explanation exists for why Harris' hawks facultatively form groups and why they exhibit geographic variation in their behavior.

Little is known about Harris' hawks in Texas, yet southern Texas presents a unique opportunity to examine Harris' hawk grouping behavior under different environmental

conditions. This is primarily due to the presence of at least 2 distinct ecoregions in the area (Diamond et al. 1987, Olson et al. 2001) resulting from a strong east-west rainfall gradient (Le Houerou and Norwine 1987, Norwine 1995). Therefore, southern Texas has areas with diverse climate and landscape patterns, and Harris' hawks occupy these different areas (Appelt, personal observation). Thus, in a small geographic area, Harris' hawk grouping patterns can be compared in relation to diverse environmental variables.

PROJECT OBJECTIVES AND PREFACE TO THE DISSERTATION

This project focused on three objectives directed toward Harris' hawks in southern Texas. These 3 objectives are related to the first, fourth, and fifth parameters of the Delayed-Dispersal Threshold Model listed previously.

- 1) Determine relationships among landscape use, grouping and abundance
- 2) Characterize variation in grouping associated with rainfall patterns in the brushland and grassland ecoregions of the study area
- 3) Explore which landscape measures best explain within site variation in grouping considering 3 ecologically appropriate spatial scales.

This dissertation consists of 5 chapters. This introduction constitutes the first chapter, and is written in the format of *The Journal of Wildlife Management*. Chapter Two will be submitted to the *The Wilson Bulletin*. It is written in the format required by that journal and addresses the first objective. Chapter Three is formatted for submission to *Behavioral Ecology and Sociobiology* and addresses the second objective. Chapter Four is formatted for submission to *Oikos* and addresses the third objective. Chapter Five is formatted as a commentary for *Animal Behaviour* and represents a summary of the

previous chapters and culminates in an integrative conceptual model explaining the facultative nature of Harris' hawk grouping behavior from which hypotheses and predictions can be generated with suggestions for future work. This dissertation also includes 8 Appendices that provide supporting data for the preceding chapters.

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CHAPTER II

HARRIS' HAWK ABUNDANCE, GROUPING AND LANDSCAPE USE IN A NON-BREEDING CONTEXT IN SOUTHERN TEXAS

Harris' hawks (*Parabuteo unicinctus*) are widely distributed from southern North America through Central America and much of South America (del Hoyo et al. 1994, Bednarz 1995). Throughout their broad latitudinal range, they occupy areas containing various types of vegetation and prey (Bednarz et al. 1988, Jiménez and Jaksić 1989, 1993, Bednarz 1995). Furthermore, they demonstrate different tendencies to form cooperative groups in different geographic regions (Griffin 1976, Brannon 1980, Bednarz and Ligon 1988, Dawson and Mannan 1991a, Jiménez and Jaksić 1993). Despite differences in vegetation, prey, and behavior, Harris' hawks likely use areas with similar general characteristics (Bednarz et al. 1988, Bednarz 1995): suitable nesting sites (Janes 1985), perches for hunting (Janes 1985, Widén et al. 1994, Malan and Crowe 1997, Wolff et al. 1999), cover and forage for prey (Janes 1985, Marzluff et al. 1997, Malan 2001), adequate openings in cover (i.e., bare ground) for detecting and capturing prey (Janes 1985 and references therein, Malan and Crowe 1997), and water (Dawson and Mannan 1991b, del Hoyo et al. 1994). Common structural components exist in different areas (e.g., semi-open shrub/grassland with trees for nesting and perch hunting) with different species compositions (see habitat descriptions in Bednarz et al. 1988 and Bednarz 1995). Data from New Mexico (Bednarz 1988a, Bednarz and Ligon 1988) and central Chile (Jiménez and Jaksić 1989, 1993) reveal similar percent shrub and herbaceous vegetation cover.

Landscape structure, or spatial relationships between distinctive elements in an area in relation to their composition and configuration (Forman and Godron 1986, McGarigal and McComb 1995), likely influences whether an area is occupied by Harris' hawks (Cody 1985). Landscape structure can influence patterns of species richness (Wiens 1976, Turner 1989) correlating with abundance and population dynamics (McGarigal and McComb 1995, Collins and Barrett 1997, Bowers and Dooley 1999). Sometimes, fragmentation and heterogeneity are positively correlated with abundance in particular species of birds and mammals (Cody 1985, McGarigal and McComb 1995, Collins and Barrett 1997, Bowers and Dooley 1999). However, relationships are not always observed, or they may be complex and difficult to assess due to the variety of ways to express landscape structure and the variety of available analytical approaches (i.e., no one correct way to analyze relationships between landscape and abundance, McGarigal and McComb 1995, Bajema and Lima 2001, Bowman et al. 2001).

Harris' hawk abundance and grouping might be related to landscape structure. Characteristics like diversity of elements (classes), amount of coverage provided by particular classes (e.g., woody vegetation), size and shape of patches, patch distribution, amount of edge, and distance between patches can influence where particular prey species will be located, their abundance, and their availability (Wiens 1976, Knick and Dyer 1997, Malan and Crowe 1997, Malan 2001). Black-tailed jackrabbits (*Lepus californicus*) in Idaho used areas with higher heterogeneity, more shrub cover, and larger, more variable shrub patches than expected (Knick and Dyer 1997). Cottontail rabbits (*Sylvilagus* spp.) use areas with dense brush adjacent to open areas with herbaceous vegetation for foraging (Davis and Schmidly 1994). Woodrats (*Neotoma* spp.) also

occupy woody cover (Box 1959, Davis and Schmidly 1994), and cotton rats (*Sigmodon hispidus*) are associated with herbaceous cover (Kincaid et al. 1983, Davis and Schmidly 1994), but both are Harris' hawk prey species (Bednarz 1995). Harris' hawks tend to hunt cooperatively for larger prey species like cottontail rabbits and jackrabbits (Bednarz 1988b). Therefore, whether Harris' hawks form groups might be influenced by whether structure enhances abundance and availability of lagomorphs or smaller prey. Landscape structure might influence coordination of cooperative hunting directly. Large contiguous stands of dense tree and shrub cover might prevent several individuals from coordinating their activity (Gittleman 1989). Landscape structure might result in localization of some resource (e.g., prey, perches, water) resulting in grouping in the vicinity of the resource (Koenig and Pitelka 1981).

Only two studies provide extensive quantitative data describing areas used by Harris' hawks (Bednarz 1988a, Bednarz and Ligon 1988). Both examined 21 characteristics in a relatively small area (75 m radius) around nest sites in New Mexico. Only Bednarz and Ligon (1988) have compared occupied and unoccupied areas. Analyses of composition, but not configuration, revealed percent forb cover, tree density, tree trunk diameter, and importance of sage (*Artemisia filifolia*) and mesquite (*Prosopis glandulosa*) were greater in areas occupied by hawks. Importance was based on the product of height and density. Percent litter was less in occupied areas. None of these variables were spatially explicit or differed between group and pair nest sites.

Very little is known about abundance and grouping of Harris' hawks in Texas. The only data published on Texas Harris' hawk abundance is based on Christmas Bird Count (CBC) data (Bednarz et al. 1988, Root 1988, but see Kim 2001). Grouping in

Texas, which is less common than in Arizona and New Mexico (Bednarz 1995), has been observed in the contexts of cooperative breeding (Griffin 1976, Brannon 1980) and cooperative hunting (Coulson and Coulson 1995). Brannon's (1980) unpublished thesis research conducted in Uvalde County and Coulson and Coulson's (1995) recollections of group hunting in Webb County in the early 1980s represent the only southern Texas Harris' hawk grouping data.

This study had three primary objectives: 1) determine whether relative abundance of Harris's hawks varies throughout the southern Texas region, and if so, whether differences relate to landscape structure, 2) determine whether Harris' hawks are located in areas with specific structural characteristics that differ from what is present in the larger landscape, and 3) determine the degree and range of Harris' hawk grouping throughout the region and whether it is correlated with landscape structure. The results were used to generate hypotheses for future study.

STUDY AREAS AND METHODS

Study areas—This study included sites throughout the southern Texas region ranging from the Gulf of Mexico in the east to the Rio Grande Valley in the west and south (Fig. 1). Study sites (36.5 km² – 210.5 km²) included ranches and wildlife management areas inhabited by Harris' hawks. These sites provided diverse habitat characteristics both within and among sites primarily due to an east-west rainfall gradient from approximately 700 mm in the east and 560 mm in the west (Le Houerou and Norwine 1987, Norwine 1995, National Oceanic and Atmospheric Administration 1999). Selected ranch sites included three locations (Rincon, Don Ricardo, North Santa Gertrudis) on the King Ranch (Kleberg County), which encompasses a large area

relatively close to the coast, and the Calcasieu (Duval County), Killam (Webb) and Faith (Dimmitt, Webb and Maverick Counties) ranches in the drier central and western portions of the region. Wildlife management areas in this study included Laguna Atascosa National Wildlife Refuge (Cameron County) near the coast and Chaparral Wildlife Management Area (Dimmitt and LaSalle Counties) in the drier west. Sites were assigned codes based on their name and east (E) or west (W) location: Calcasieu (CU-W), Chaparral (CH-W), Faith (FR-W), Killam (KM-W), Don Ricardo (DR-E), Laguna Atascosa (LA-E), North Santa Gertrudis (NSG-E), and Rincon (RN-E).

Hawk Data Collection.-Between 25 September and 15 November 2000, I conducted road transect surveys (Andersen et al. 1985; Fuller and Mosher 1987) at each study site. Data collected from these surveys were used to estimate relative abundance and the degree to which grouping was occurring at each site. Although vegetation structure can affect visibility, the types of vegetation and variability along roads at study sites were generally similar. Because detectability estimates were not available, survey methods were standardized and relative abundance was estimated rather than density (Fuller and Mosher 1987). I visited six sites twice (15-34 days between visits, mean = 25 days) and performed surveys in the morning (0.5-4 h after sunrise) and late afternoon (4-0.5 h before sunset) each of two days per visit (0-2 days between consecutive survey days). At DR-E and NSG-E, heavy rains in early November made a second visit impossible. Thus, eight surveys were conducted at six sites and four surveys on two sites.

Transect lengths were 38.54-57.56 km (mean = 48.24 km) depending on each site's size, shape, and road availability. A road was defined as a path on which a truck

could travel in approximately a straight line. Transects incorporated paved roads, gravel or dirt roads of varying size and maintenance, fence lines, and petroleum pipeline/power line/telephone line rights-of-way. Survey routes were selected to systematically cover the area of each site. Potential roads were identified using digitized aerial photography (digital orthophoto quarterquadrangles, DOQQs; EROS Data Center, Sioux Falls, SD, USA) and traced to a geographic information system (GIS). Using only the traced roads as reference, a systematic survey route was selected based on the following criteria: 1) approximately 40-60 km in length, 2) within 3 km of any terrestrial point within a study site, 3) minimal number of turns >90 degrees, and 4) as few points on a route as possible within 600 m of each other. By selecting routes from traced roads and not from aerial photos, the routes were not biased toward areas containing particular features. However, in most cases, when I visited a site to familiarize myself with a route, I made some alterations to accommodate changes at sites since the photographs were taken. All adjustments were made based upon the above criteria.

I conducted all surveys by truck at 25 kph as driver and sole observer noting all observations of Harris' hawks. I calculated the number of Harris' hawks per 100 km traveled for each survey at a site and used the mean of all surveys ($n = 4$ or 8) to estimate relative abundance at that site. Each observation was classified as either a group (more than two birds) or non-group (pair or individual). Groups consisted of individuals located within ~ 300 m of one another. I chose 300 m because Harris' hawks frequently distribute themselves along a series of up to four telephone/power poles (~ 100 m apart). As an index of grouping for a site, I calculated the proportion of observations consisting of groups (i.e., # of group observations/total # of observations) for each survey and

calculated the mean of all surveys at the site. I recorded the location of each Harris' hawk using a global positioning system (GPS) unit (Pathfinder, Trimble Navigation, Sunnyvale, CA, USA) with sub-meter accuracy. Each location was recorded one of 3 ways: 1) physically placing the GPS unit at a hawk's location, 2) using a pole-mounted laser rangefinder/compass interfacing directly to the GPS unit, or 3) manually entering the bearing from a compass and distance from a hand-held laser rangefinder into the GPS datalogger with the GPS antenna mounted to the vehicle.

Vegetative Strata Data Collection and Analysis.-To compare the three-dimensional structure present at a study site to locations used by hawks, I visually estimated the percent cover provided by vegetation at different strata at each hawk location and at random points along transects. I used ArcView GIS software to randomly distribute 30 points along each transect's length. All random points were <300 m from the transect and >600 m from other random points. I navigated to each random point using a GPS unit to make strata estimates. When I was physically unable to reach a point, I made the estimate as close to the point as possible perpendicular to the transect. When a point was located in water, I made the estimate from a point 50 m toward and perpendicular to the transect from the water's edge. Strata cover within 50 m of a point or hawk location was estimated for percent exposed bare ground and percent short herbaceous cover (<15 cm), tall herbaceous cover (>15 cm), brush cover (woody/cacti <3 m high), and tree cover (woody >3 m high) based on the following intervals: 0-5%, 6-25%, 26-50%, 51-75%, 76-95%, > 95%. I used Chi-square tests to compare strata cover at random points and hawk locations. When tests were significant, I used the Freeman-

Tukey Deviate test to determine which cells contributed to Chi-square significance (Bishop et al. 1975).

Landscape Structure At Study Sites.-I obtained 20-m resolution multi-spectral satellite imagery (SPOT Image, Reston, VA, USA) for each study site. All imagery was taken 0-3 months before the initial surveys. The imagery was geo-referenced using the DOQQs, and the imagery was divided into 100 classes based on the spectral similarity of each pixel using ERDAS Imagine software (ERDAS 1997, Wu et al. 2000). Based upon the primary component of each class determined from the DOQQs and familiarity with each study site, the resulting 100 classes were then grouped into four classes: woody, herbaceous, bare ground, and water. Using Spatial Analyst and Patch Analyst ArcView extensions, spatial and non-spatial metrics (Gustafson 1998) were calculated based on FRAGSTATS software (McGarigal and Marks 1995) for each site at the landscape and class level. These metrics (see Table 1 for names, abbreviations, and descriptions) provide information about the composition and configuration of the landscape: relative abundance of a class type, fragmentation, patch shape complexity, amount of edge, interspersions of each patch type relative to one another, and patch type diversity. To determine whether correlations existed between a site's composition and configuration and Harris' hawk relative abundance and grouping, I compared metrics for each site to Harris' hawk abundance and index of grouping using Kendall's non-parametric rank correlation.

To quantify spatial heterogeneity of each landscape class at a number of spatial scales, I calculated lacunarity with ArcView Spatial Analyst using a gliding window algorithm (Plotnick et al. 1993, Wu and Sui 2001). For this method, a box ($r \times r$ pixels)

is moved from the upper left hand corner of a landscape to the bottom right hand corner at intervals of one pixel to the right per step. The number of occupied pixels within the box (box mass) is determined at each interval, and lacunarity is calculated based on the variance and mean of the box masses (Table 1). Box size can be changed to examine lacunarity at a number of different scales (grain size, Withers and Meentemeyer 1999). A lacunarity curve (log-log plot of lacunarity against box size) can be used to quantify spatial heterogeneity at different spatial scales within a site (Plotnick et al. 1993, 1996; Wu et al. 2000). For this study, I used the following box sizes $r = 1, 2, 4, 8, 16, 32, 64, 128, \text{ and } 256$ pixels. At $r = 1$, lacunarity is simply the inverse of the proportion of a class in the landscape (Plotnick 1996). To determine whether Harris' hawk relative abundance and grouping correlate with site heterogeneity, I used lacunarity values calculated at $r = 32$ and $r = 64$ because they are closest in scale to other analyses conducted in this study (see below). Lacunarity can only be calculated for one variable at a time (Plotnick et al. 1996). I performed binary comparisons (Plotnick et al. 1996) for each class (woody, herbaceous, bare ground, water), in which a given class was compared spatially with all other classes combined.

Landscape Structure At Areas With and Without Hawks.-The location of each hawk was imported into a GIS, and individuals in a group or pair were merged as a single unit of observation. Next, a circle (500 m radius) was created around each observation. I used 500 m for three reasons. First, it is similar to the distance within which Harris' hawks are typically located from nesting locations in their territory during non-breeding periods (600 m; Dawson and Mannan 1991b). Second, 500 m is the approximate distance they will chase conspecifics from old nests (500 m; Dawson and Mannan

1991b). Third, 500 m is the minimum distance between nests of different breeding groups in New Mexico (Bednarz 1987, 1995). This distance is based on studies outside of Texas, but no comparable data for territory size exist for Texas at this time. Therefore, 500 m was assumed to be an appropriate dimension for this study.

In many cases, the circles around separate observations overlapped. Therefore, I merged overlapping circles for group observations. I repeated the process for all non-group observations, but I excluded any non-group observations for which their circles overlapped with those of groups (see Chapter 4). This maximized the number of independent areas used by hawks for analysis. I also created 500 m circles around each of the 30 random points at each study site, similarly merging overlapping circles and excluding points whose circles overlapped with those of Harris' hawks. At five sites, 1-10 non-random 500 m circles were placed at locations along transects (centers within 300 m of transects) where no Harris' hawks had been observed and no random points were present. The result was spatially distinct areas along transects within which Harris' hawks were either observed (H) or never observed (NoH). For this study, I assumed NoH areas were not used by Harris' hawks at that time. Using ArcGIS software, the classified imagery under the circles was clipped and analyzed. The metrics used previously were calculated and compared between all H and NoH areas and within sites using a Mann-Whitney U-test and across sites using Wilcoxon signed ranks test.

Mean annual rainfall differs between eastern and western study sites (Le Houerou and Norwine 1987, Norwine 1995, National Oceanic and Atmospheric Administration 1999), and the vegetation that influences landscape structure is influenced by this trend (Blair 1950, Scifres 1980, Diamond et al. 1987, Archer et al. 1988). Therefore, I

combined data for H and NoH areas for the four eastern study sites and the four western study sites separately. Then, I compared H and NoH areas using a U-test while controlling for regional trends. Unless otherwise stated, data are presented as mean \pm SE.

RESULTS

General Observations.-Harris' hawk relative abundance across all study sites was 17.7 ± 4.1 hawks/100 km, and index of grouping was 0.113 ± 0.037 groups/observation (see Appendix A for site-specific data). Relative abundance exhibited a strong positive correlation with grouping across sites (Fig. 2, Kendall's Tau corrected for ties, $\tau = 0.539$, $P = 0.062$). Three of the five sites with highest abundance were in the drier western region (FR-W, CH-W, KM-W). Two sites, RN-E and CU-W did not cluster with other sites in their regions. Landscape structure varied across sites (Fig. 3, Table 2), and grouping was correlated with some landscape metrics, but abundance was not ($P > 0.10$).

Grouping and Landscape Structure At Study Sites.- Significant correlations ($P < 0.05$) existed for bare ground ED ($\tau = 0.643$) and MNN ($\tau = -0.718$). Strong correlations ($P < 0.10$) also occurred for bare ground MSI ($\tau = 0.539$), %Herbaceous ($\tau = -0.491$), herbaceous PD ($\tau = 0.491$), herbaceous MPS ($\tau = -0.491$), landscape PD ($\tau = 0.567$), and landscape MPS ($\tau = -0.539$). Significant ($P < 0.05$) negative correlations also existed between grouping and bare ground lacunarity at $r = 32$ ($\tau = -0.718$) and $r = 64$ ($\tau = -0.643$). Strong correlations ($P < 0.10$) also existed between grouping and woody lacunarity at both $r = 32$ ($\tau = -0.491$) and $r = 64$ ($\tau = -0.567$). Also worth noting is that although water lacunarity did not correlate with grouping at $r = 32$ and 64 , water lacunarity was greatest at the five sites where grouping occurred for $r = 1-16$ (Fig. 3). Thus, Harris' hawks were generally observed in groups at study sites with particular

landscape structural characteristics: more evenly distributed bare ground with more bare ground edge and less distance between more complex-shaped bare ground patches, more homogeneous woody distribution, more small patches in general (particularly herbaceous), and less herbaceous cover.

Multi-Scale Spatial Heterogeneity At Study Sites.-Heterogeneity varied among sites and between landscape classes (Fig. 3). In particular, woody pixels were more clumped and made up less of the landscape at DR-E and LA-E resulting in higher heterogeneity across scales. Similarly, at FR-W, herbaceous pixels were more clumped and made up less of the landscape than other sites. Herbaceous pixels also made up relatively little of KM-W and CH-W, but they were evenly distributed through the landscape resulting in relatively low heterogeneity at all but the finest scales, particularly CH-W. The DR-E and RN-E sites had nearly identical amounts of bare ground (Table 2), but it was more randomly distributed throughout RN-E (concave curve) and more clumped in DR-E (convex curve), resulting in much lower bare ground heterogeneity for RN-E at all scales (Plotnick et al. 1996). Furthermore, the sites where grouping was never observed (DR-E, NSG-E, LA-E) had convex bare ground lacunarity curves while the other sites had more concave-shaped curves. At smaller and intermediate scales, water heterogeneity varied greatly among sites with some sites (FR-W, CH-W, and CU-W) having less but more clumped water than others, but water heterogeneity at all sites converged at the broader scales

Landscape Use and Vegetative Strata At Study Sites.-Three-dimensional structure (Appendix B) differed to some extent between random point (presence) and Harris' hawk (use) locations along transects at the four study sites with the most grouping and the

study site with the fewest Harris' hawks (Fig. 2, Table 3). Furthermore, hawks at the two sites with the most grouping (FR-W and RN-E) exhibited the most strata use/presence differences. At FR-W, Harris' hawks used locations with less bare ground ($\chi^2 = 19.34$, $df = 5$, $P < 0.01$) and brush cover ($\chi^2 = 18.28$, $P < 0.01$) and more tall herbaceous cover ($\chi^2 = 12.80$, $P < 0.05$) in greater proportions than at random points. Hawks at RN-E used locations with more tall herbaceous cover ($\chi^2 = 12.30$, $P < 0.05$) and intermediate brush ($\chi^2 = 23.91$, $P < 0.001$) and tree ($\chi^2 = 23.91$, $P < 0.001$) cover than was proportionately available. At CH-W, Harris' hawks used locations with less bare ground ($\chi^2 = 17.14$, $P < 0.01$) disproportionately more than they were available. The KM-W hawks disproportionately used locations with low to intermediate amounts of tall herbaceous cover ($\chi^2 = 11.34$, $P < 0.05$). At LA-E, Harris' hawks generally used locations with more brush ($\chi^2 = 27.58$, $P < 0.001$) and tree ($\chi^2 = 12.33$, $P < 0.05$) cover disproportionate to their availability.

While distributions of hawk observations varied from site to site, most hawks tended to be located in similar types of locations. At a relatively fine scale (i.e., 50 m radius circle), Harris' hawks in southern Texas generally used locations with approximately 25% tree cover, 50% brush cover, 25-50% tall herbaceous cover, 25% short herbaceous cover, and 25-50% bare ground (Appendix B). The same mode was observed for tree cover at all sites (6-25%), and six sites had a mode for brush cover at 26-50% (51-75% at the other two sites). Six sites had modes at 26-50% for tall herbaceous cover, and five sites had modes for short herbaceous at 6-25% (26-50% at the other three sites). The results were less consistent for bare ground (modes ranging 6-25% to 76-95%).

Landscape Structure At Hawk Locations: Across Sites.-Pooling data for all H ($n = 99$) and NoH ($n = 102$) areas revealed only MPFD at the landscape level as significantly different (U-test, $P < 0.05$) with H areas having less complex patches, but MSI did not corroborate those results ($P > 0.60$). A paired comparison across sites ($n = 8$) also revealed few differences between H and NoH areas. Bare ground MPS (Wilcoxon signed rank test, $P < 0.05$) was smaller in H areas (0.987 ± 0.289 ha) than in NoH areas (1.777 ± 0.617 ha). Other notable ($P < 0.10$) differences between H and NoH areas included woody MNN (27.2 ± 1.06 m and 39.9 ± 8.7 m, respectively) and herbaceous MPFD (1.065 ± 0.005 and 1.075 ± 0.008). These results suggest that across sites Harris' hawks were located in territory-sized areas (i.e., 500 m radius circle) with smaller bare ground patches, less complex herbaceous patches, and less fragmented woody patches.

Landscape Structure At Hawk Locations: East versus West.-In general, H and NoH areas differed more in eastern sites than in western sites (Table 4). Eastern sites had 6.5 ± 0.9 significant metrics as opposed to 2.3 ± 1.0 metrics at western sites. Furthermore at the four levels of examination (i.e., landscape, woody, herbaceous, bare ground), western sites had 2.3 ± 0.6 non-significant levels with eastern sites having 0.8 ± 0.3 non-significant levels. However, in western sites, where herbaceous cover was less than at eastern sites (Table 2), more herbaceous metrics differed than at eastern sites (Tables 4 and 5). In all eastern cases (Table 5), the differences in H areas from NoH areas were in the direction approaching H (and usually NoH) values from western sites (Appendix C). The converse was not true for differences at western sites. In eastern sites, Harris' hawks tended to be located in areas with more small patches located close

together with more edge, particularly woody. They also were in areas with more herbaceous edge. In western sites, Harris' hawks tend to be located in areas with less complex patches, particularly with more and simpler herbaceous patches

DISCUSSION

Relative abundance and grouping of Harris' hawks varies among locations in southern Texas. The range reported here is greater than abundances reported in southeastern New Mexico (9.8-18.9 hawks/100 km; Bednarz 1995). The mean of this study (17.7 hawks/100 km) approached the maximum reported in New Mexico. My observations support previous suggestions that grouping is less common in southern Texas (Bednarz 1995) than that reported in Arizona (84%; Dawson and Mannan 1991a) and New Mexico (49%; Bednarz and Ligon 1988). The observations of grouping in a non-breeding context reported here (0-23%) ranged more widely than previous Texas studies during the breeding season (5%; Griffin 1976 and 13%; Brannon 1980). In New Mexico, grouping tended to increase during the non-breeding season (Bednarz 1995). A study comparing grouping in a breeding and non-breeding context at the same site is needed to determine whether a similar seasonal trend exists in Texas.

The data collected for this study suggest Harris' hawk grouping is associated with their fine scale use within a study site. Use and presence differences in strata at a study site were generally most pronounced in sites where grouping was observed. These results help generate hypotheses for examining relationships between grouping and limitation or localization of particular landscape characteristics associated with resources or habitat quality (Brown and Balda 1977, Koenig and Pitelka 1981, Stacey and Ligon 1987, Stacey and Ligon 1991, Koenig et al. 1992). Similar differences were observed at LA-E where

no groups were observed, but abundance was lowest of all the study sites. One hypothesis for future testing is that density only influences grouping when suitable areas are limited. Therefore, while suitable areas might have been limited spatially at LA-E, too few individuals may have been present for suitable areas to be limiting for dispersing young (i.e., no habitat saturation, Koenig et al. 1992, Komdeur 1992)

Relationships between landscape structure and grouping (and possibly relative abundance) might be underestimated here because I observed a sharp decrease in Harris' hawk abundance and grouping at CU-W between 1999 and 2000. During preliminary work on 13-15 July, 1999 (Appelt unpubl. data), I made 19 observations of Harris' hawks (1-4 hawks/observation) over approximately 240 km traveled (~14 hawks/100 km) with 4 observations being of groups (0.211 groups/observation). No major landscape changes occurred at the site, but one explanation might be a decrease in lagomorph abundance (Appelt pers. obs.). Furthermore, monthly surveys conducted from February to October 2001 (Chapter 3) suggest relative abundance began to increase (10.7 ± 2.2 hawks/100 km) and continued to increase, being greater the last four months (14.8 ± 2.6 hawks/100km). A similar trend was not observed for grouping at the same time (0.100 ± 0.100 groups/observation, Chapter 3). These data are similar to those for other western sites. Preliminary work at NSG-E (~65 km southeast of CU-W) on 14-15 June 1999, suggests changes at CU-W did not represent a region-wide trend because data were similar to those from 2000 - 11 observations (1-2 hawks/observation) over approximately 120 km (~12 hawks/100 km) with no observations of groups (Appelt unpubl. data).

Both Harris' hawk relative abundance and landscape structure vary across southern Texas, but none of the landscape structure variables examined in this study were

related to Harris' hawk relative abundance. Abundance may not be related to landscape structure at all, or abundance may not be related to landscape structure at the spatial scale (i.e., extent) of my study sites (Turner 1989). The results at finer (i.e., 50 m and 500 m radius) and broader (i.e., eastern and western regions) scales demonstrate a relationship between landscape structure and areas where Harris' hawks are located (see discussion below). These results suggest landscape structure probably interacts with other factors (e.g., prey abundance, prey availability, seasonal rainfall) that likely contribute to Harris' hawk abundance, and it may not exert a detectable influence by itself. While McGarigal and McComb (1995) found landscape to be related to abundance in several of the 15 species they studied, they could not conclude it was the dominant factor due to a large amount of unexplained variation.

Although I found no quantitative relationship with abundance, landscape structure is associated with the presence of Harris' hawks at particular locations within study sites. My results demonstrate differences in landscape structure between locations used or not used by Harris' hawks and between what is used and what is present at broader and finer scales (grain and extent), respectively. This information provides insight into composition and configuration of areas used by Harris' hawks in southern Texas and identifies characteristics associated with Harris' hawk occupancy. Future studies should employ manipulative experiments to determine whether the observed relationships between landscape structure and occupancy are one of cause and effect. The strata composition data suggests specific ranges of cover are present in areas immediately surrounding (50 m) Harris' hawks. These ranges sometimes are used disproportionately more or less than they are present in a larger area, particularly where grouping occurs.

Again, future work should employ manipulative techniques to test cause and effect. The broader scale (500 m) analysis yielded composition results generally similar to those at the finer scale (e.g., FA-W brush strata mode was 26-50% and mean woody cover for H areas was 36.3%).

The results indicate other structural features are associated with Harris' hawk presence in an area. Specific characteristics differing between areas with and without hawks vary among sites (Table 4), but some conflicting observations seem easily explained. For example, NSG-E hawks appear to have been located in areas with much more bare ground in large patches with more edge and less woody cover and edge. A large area containing brush and trees was root plowed and became bare ground covered with litter shortly before initial surveys. Consequently, I used a GPS unit to record the outline of the affected area for reclassification to bare ground in the GIS. During the first surveys, four observations of Harris' hawks were made at the edge of that area. In subsequent surveys occurring throughout the next year, I never observed Harris' hawks in that area again (Appelt pers. obs.). I suspect individuals that had occupied the area were taking advantage of a temporary increase in prey availability resulting from decreased cover. Another example is that woody cover results for RN-E appear to contradict those of other sites. However, Table 2 clearly shows woody cover at RN-E is more fragmented (many small patches) than any other site, and the areas where RN-E hawks were located are similar to those used by hawks at other sites (Appendix C).

Furthermore, eastern and western study sites have different landscape structural characteristics (Table 2), and the direction and degree of structural differences between H and NoH areas are related to east/west differences (discussed below). However, results

from paired and east-west analyses both suggest that Harris' hawks in southern Texas tended to occupy areas with more woody patches that are close together, resulting in more woody edge, smaller bare ground patches, and less complex shaped herbaceous patches. These results are reasonable for a species that forages from perches and requires some open space for seeing and capturing prey, which require adequate food and cover (Janes 1985, Malan and Crowe 1997, Malan 2001). Such locations with woody patches juxtaposed with open and herbaceous patches are also used by cottontail rabbits (Davis and Schmidly 1994), the primary prey of Harris' hawks (Bednarz 1995). Thus, a hypothesis for future testing would be that the landscape structural characteristics observed in this study result in higher abundance and availability of Harris' hawk prey.

These results suggest western sites are more homogeneous for landscape structure associated with Harris' hawk use at the scale I examined (500 m radius), and eastern sites are more heterogeneous and fragmented. Variation in landscape structure across southern Texas appears to be associated, at least in part, with the steep east-west rainfall gradient that exists in the region (Le Houerou and Norwine 1987, Norwine 1995). Awareness of this not only made results easier to interpret and further highlighted structural elements associated with Harris' hawk occupancy, but it also helped to generate new hypotheses about rainfall patterns and Harris' hawk grouping (e.g., more grouping when less rainfall). In general, the areas around Harris' hawk locations vary in more ways from unused areas in eastern sites than western sites. Furthermore, across eastern sites, characteristics of hawk locations differed from those without hawks in the direction approaching hawk locations of western sites.

Structural elements associated with Harris' hawk use of areas are strongly associated with geographic region, but relative abundance does not share this relationship (Appendix A, but see below). However, the characteristics associated with grouping are typified by most of the western sites (i.e., homogeneously distributed woody and bare ground cover, less fragmented bare ground patches, less herbaceous cover with smaller patches), and grouping occurred most frequently in western sites (Chapter 3). The results of this study have helped to generate hypotheses about potential influences of landscape structure, resource availability and quality, climate, and Harris' hawk density on grouping. These potential relationships could explain geographic variation in grouping for this species. Geographic variation in grouping also has been observed in Mexican jays (*Aphelcoma ultramarina*, Strahl and Brown 1987, Brown and Horvath 1989), scrub jays (*A. coerulescens*, Peterson and Burt 1992), and Galápagos mockingbirds (*Nesomimus* spp., Curry 1989). Suggestions for these observed variations have included differences in climate (Curry 1989), habitat limitation (Curry 1989), habitat quality (Strahl and Brown 1987), phylogeny/genetics (Brown and Horvath 1989, Peterson and Burt 1992), and predation (Brown and Horvath 1989, Curry 1989). More work based on hypotheses generated from this study is necessary to identify the factors associated with geographic variation in Harris' hawk grouping.

Previous reports have suggested Harris' hawk abundance is diminishing in southern Texas (Oberholser 1974, Bednarz et al. 1988; Bednarz 1995), and this has been attributed to changes in land use, particularly fragmentation of woody (primarily mesquite) areas (Oberholser 1974, Bednarz 1995). I did not find a relationship between woody fragmentation and abundance across sites. I did find a relationship between areas

occupied by Harris' hawks and lower woody fragmentation. Therefore, my data suggest Harris' hawk presence could decrease in response to woody fragmentation. Future work testing this hypothesis should examine more areas over time to determine Harris' hawk population and prey population responses to changes in landscape structure, particularly through manipulative experiments.

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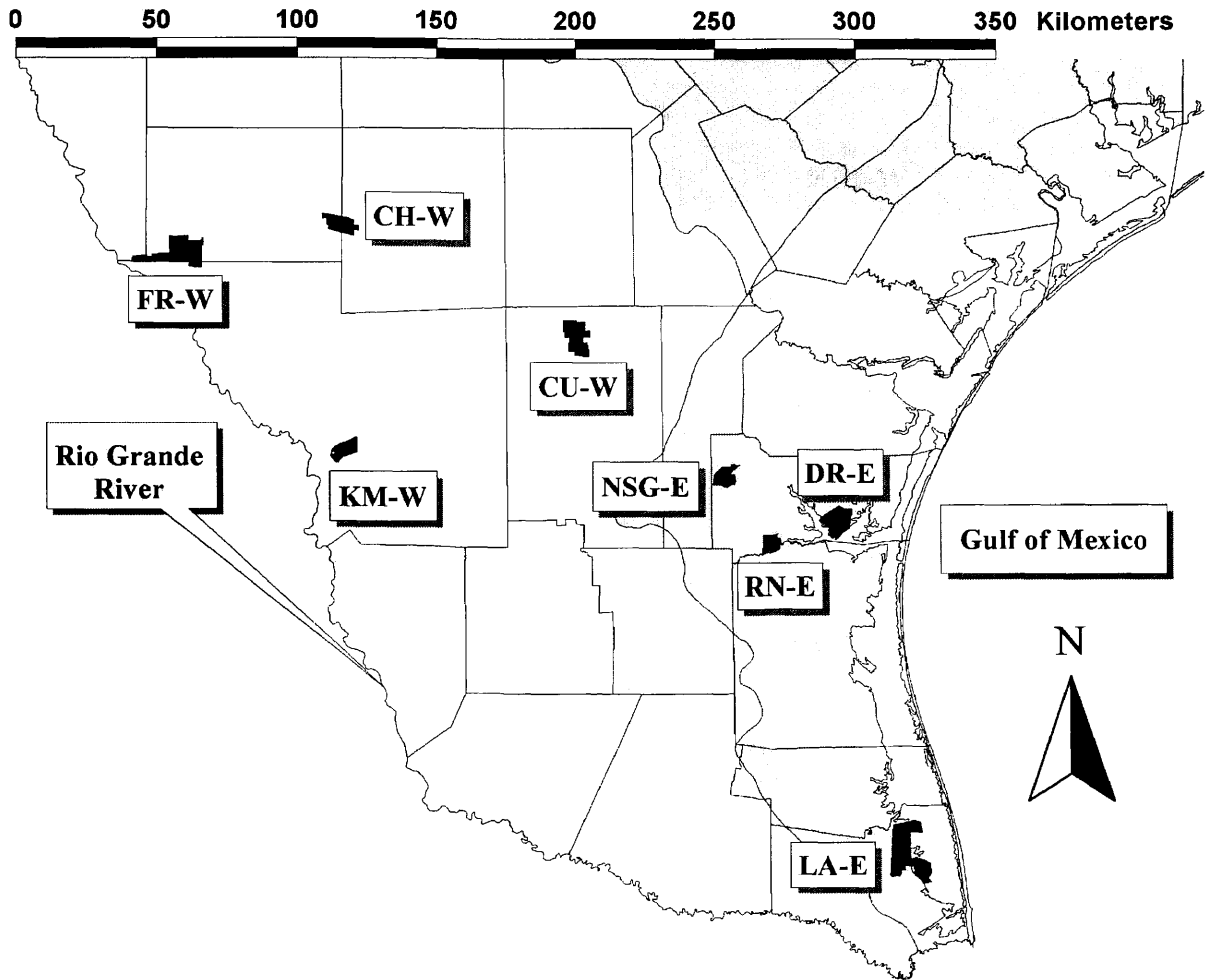


Figure 1. Map of southern Texas and locations of study sites (black) for a Harris' hawk study, 2000. The shaded area has a relatively higher mean annual rainfall than the white area. Sizes of study sites are to scale. Site codes as follows: FR-W = Faith, CH-W = Chaparral, KM-W = Killam, CU-W = Calcasieu, NSG-E = North Santa Gertrudis, RN-E = Rincon, DR-E = Don Ricardo, LA = Laguna Atascosa.

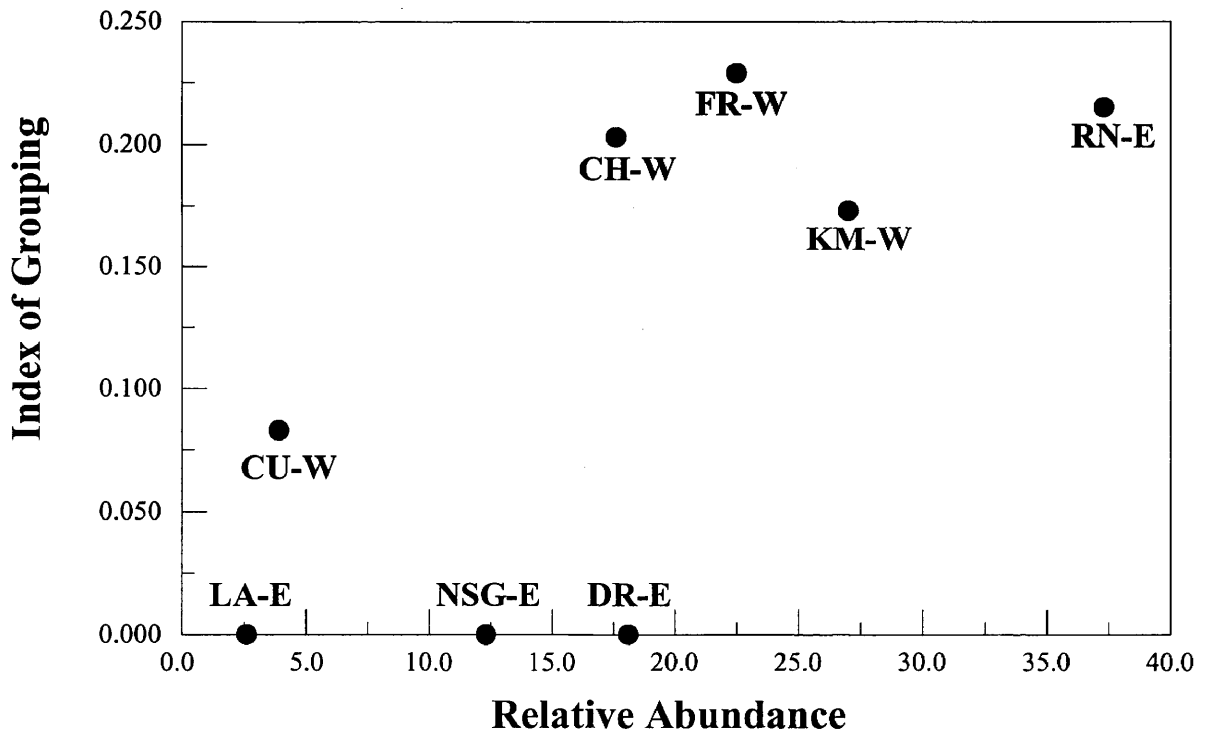


Figure 2. Relative abundance of Harris' hawks (number of hawks/100 km for a survey, mean of surveys for study site) at eight study sites, fall 2000, was positively correlated with an index of grouping (number of groups/number of observations during a survey, mean of surveys for study site). See Figure 1 for site codes.

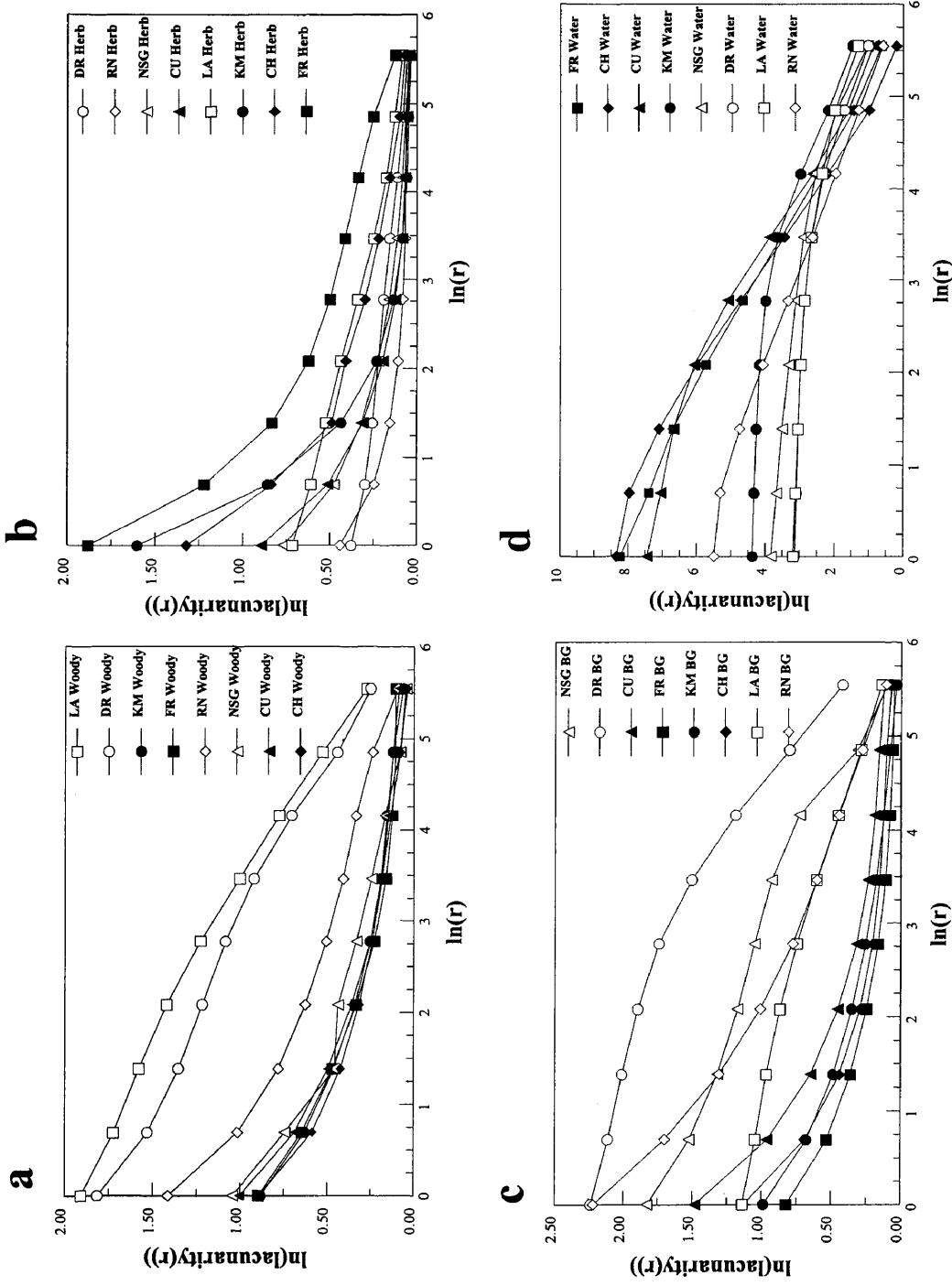


Figure 3. Lacunarity curves for (a) woody, (b) herbaceous, (c) bare ground, and (d) water at eight study sites in a Harris' hawk study, southern Texas, 2000. See Figure 1 for site codes.

Table 1. Descriptions of landscape structure metrics, their ranges, scales of use, and the information yielded^a for a Harris' hawk study, southern Texas, 2000.

Landscape Information	Metric(s) Used	Level of Examination	Range	Description
Relative Abundance	%Woody, %Herbaceous, %Bare Ground, %Water	Class	0-100%	Proportion of landscape represented by a class
Fragmentation	Patch Density (PD)	Class/Landscape	0-∞#/ha	Patches per unit area
	Mean Patch Size (MPS)	Class/Landscape	0-∞ ha	Mean size of patches in landscape
	Mean Nearest Neighbor (MNN)	Class/Landscape	0-∞ m	Mean closest distance to patch of same type
Heterogeneity	Lacunarity	Landscape	1-∞	1+(variance)/(mean) ² of box mass
Patch Shape Complexity	Mean Shape Index (MSI)	Class/Landscape	1-∞	Based on mean of perimeter to area ratios of patches
	Mean Patch Fractal Dimension (MPFD)	Class/Landscape	1-2	Mean of patch fractal dimension (D) of patches. Perim.= (Area ^D) ^{1/2}
Edge	Edge Density (ED)	Class/Landscape	0-∞ m/ha	Length of edge in area (based on class or for all classes)
Interspersion	Interspersion/ Juxtaposition Index (IJI)	Class/Landscape	0-100%	Based on ratio of edge length of class types and number of patches in landscape
Diversity	Shannon's Diversity Index (SDI)	Landscape	0-∞	Based upon proportion of landscape occupied by each class
	Shannon's Evenness Index (SEI)	Landscape	0-1	SDI divided by ln(#classes) to control for influence of rare class types

^aSee McGarigal and Marks (1995) for more detailed descriptions, but for lacunarity see Plotnick et al. (1993).

Table 2. Landscape and class level metrics calculated for eight study sites, southern Texas, 2000. See Table 1 for metric codes and Figure 1 for site codes.

Level of Analysis	Site	%Cover	PD	MPS	ED	MSI	MPFD	MNN	IJI	SDI	SEI
Landscape	FR-W		1.70	0.59	357.25	1.28	1.05	26.5	58.61	1.02	0.73
	RN-E		1.08	0.93	314.39	1.34	1.05	30.9	46.27	0.89	0.64
	CH-W		1.80	0.56	424.75	1.37	1.05	24.5	61.30	1.08	0.78
	KM-W		1.77	0.56	393.15	1.38	1.06	24.7	62.27	1.11	0.80
	CU-W		1.62	0.62	420.08	1.37	1.05	25.0	58.94	1.07	0.77
	DR-E		0.38	2.65	142.45	1.33	1.05	36.7	39.88	0.93	0.67
	NSG-E		0.98	1.02	330.59	1.34	1.05	29.4	51.07	1.10	0.79
	LA-E		0.28	3.61	139.05	1.37	1.05	44.0	53.07	1.13	0.81
Woody	FR-W	40.77	0.45	0.91	228.63	1.28	1.04	24.6	56.16		
	RN-E	24.38	0.60	0.41	203.16	1.32	1.05	27.6	20.31		
	CH-W	40.89	0.43	0.96	276.39	1.39	1.05	24.0	62.72		
	KM-W	41.22	0.26	1.57	236.20	1.37	1.05	26.0	63.54		
	CU-W	36.67	0.54	0.68	252.68	1.30	1.05	24.2	56.95		
	DR-E	16.31	0.23	0.70	101.84	1.35	1.05	30.4	1.67		
	NSG-E	35.22	0.33	1.06	232.26	1.41	1.06	24.3	30.10		
	LA-E	14.87	0.11	1.39	61.39	1.38	1.06	44.6	5.86		
Herbaceous	FR-W	15.25	0.97	0.16	192.68	1.23	1.04	26.4	59.14		
	RN-E	64.33	0.09	7.25	294.82	1.44	1.05	23.1	59.52		
	CH-W	26.68	0.91	0.29	265.90	1.31	1.05	23.4	62.87		
	KM-W	20.20	1.15	0.18	278.65	1.36	1.06	22.3	63.09		
	CU-W	40.92	0.37	1.10	337.05	1.48	1.06	22.0	63.68		
	DR-E	68.69	0.05	13.41	132.88	1.32	1.05	27.8	50.38		
	NSG-E	46.50	0.23	1.98	303.20	1.36	1.05	23.6	61.79		
	LA-E	48.95	0.08	6.10	126.49	1.32	1.05	32.0	68.98		
Bare Ground	FR-W	43.95	0.28	1.56	287.26	1.47	1.06	23.3	62.48		
	RN-E	10.89	0.39	0.28	117.22	1.32	1.05	32.5	38.28		
	CH-W	32.41	0.46	0.70	300.07	1.47	1.06	23.5	63.31		
	KM-W	37.32	0.36	1.03	260.89	1.46	1.06	24.4	64.39		
	CU-W	22.35	0.71	0.31	244.02	1.37	1.06	24.8	57.68		
	DR-E	10.68	0.07	1.45	36.31	1.31	1.05	47.1	45.00		
	NSG-E	16.10	0.41	0.40	109.72	1.27	1.05	33.7	50.07		
	LA-E	32.05	0.08	4.25	70.08	1.39	1.06	44.6	33.80		
Water	FR-W	0.03	0.00	0.25	0.35	1.30	1.06	1384.1	54.26		
	RN-E	0.41	0.00	0.92	4.29	2.25	1.14	502.5	51.89		
	CH-W	0.02	0.00	0.15	0.20	1.21	1.05	1506.7	79.52		
	KM-W	1.26	0.00	4.44	1.93	1.21	1.04	934.9	61.19		
	CU-W	0.06	0.00	0.34	0.42	1.20	1.04	997.4	63.13		
	DR-E	4.32	0.02	2.05	6.86	1.22	1.04	91.6	34.55		
	NSG-E	2.18	0.00	7.55	7.43	1.86	1.09	479.4	74.71		
	LA-E	4.13	0.01	2.81	9.43	1.39	1.06	101.9	49.88		

Table 3. Percent of observations within each percent cover category for bare ground, tall herbaceous, brush and trees in a Harris' hawk study, southern Texas, 2000. Only strata coverages differing (X^2 test, $P < 0.05$) between hawk and random point locations are presented (see Appendix B for complete data set). See Figure 1 for site codes.

%Cover	Study Sites									
	FR-W		RN-E		CH-W		KM-W		LA-E	
	Points (n=30)	Hawks (n=94)	Points (n=30)	Hawks (n=112)	Points (n=30)	Hawks (n=63)	Points (n=30)	Hawks (n=89)	Points (n=30)	Hawks (n=10)
	Tall				Tall				Brush	
	Bare Ground		Herbaceous		Bare Ground		Herbaceous		Brush	
0-5%	0	0	0	0	0	0	40.0*	27.0	16.7	20.0
6-25%	0*	3.2	20.0	3.6*	3.3*	30.2*	16.7*	46.1*	50.0*	0*
26-50%	3.3*	24.5*	40.0	35.7	23.3*	39.7	23.3	21.3	30.0	10.0
51-75%	13.3*	34.0	33.3*	57.1	46.7*	20.6	20.0*	5.6*	0*	70.0*
76-95%	56.7*	23.4*	6.7	3.6	23.3*	7.9	0	0	3.3	0
>95%	26.7*	14.9	0	0	3.3	1.6	0	0	0	0
	Tall				Tall				Trees	
	Herbaceous		Brush		Herbaceous		Brush		Trees	
0-5%	50.0*	25.5*	10.0*	0*					73.3*	10.0*
6-25%	33.3	22.3	40.0*	19.6					20.0*	70.0*
26-50%	16.7*	38.3	30.0*	64.3*					6.7	20.0
51-75%	0*	10.6	16.7	16.1					0	0
76-95%	0*	3.2	3.3*	0*					0	0
>95%	0	0	0	0					0	0
	Brush		Trees		Brush		Trees		Trees	
0-5%	6.7	1.1	10.0*	0*						
6-25%	10.0	17.0	60.0	50.9						
26-50%	23.3*	54.3*	16.7*	45.5*						
51-75%	50.0*	26.6*	13.3*	3.6						
76-95%	6.7*	1.1	0	0						
>95%	3.3*	0*	0	0						

*denotes cells contributing to X^2 significance

Table 4. Landscape structure metrics differing (U-test, $P < 0.10$) between areas with (H) and those without (NoH) Harris' hawks for eight study sites, southern Texas, 2000. The symbols ">" or "<" designate how H areas differ from NoH areas. See Table 1 for metric codes and Figure 1 for site codes.

Site	Level of Examination			
	Landscape	Woody	Herbaceous	Bare Ground
FR-W	ns	ns	<IJ ^a	>ED ^c
RN-E	<PD ^b >MPS ^b >MSI ^b >SDI ^b >SEI ^b	<PD ^b , >MPS ^a	<%Cover ^c	ns
CH-W	ns	>MPFD ^a	<MPFD ^b <MSI ^a	>MNN ^c <%Cover ^a
KM-W	ns	ns	ns	ns
CU-W	<MPFD ^b	ns	ns	>MNN ^b
DR-E	>PD ^b <MPS ^b	>PD ^c >IJ ^b	>ED ^a	ns
NSG-E	>IJ ^b >SDI ^b >SEI ^b	<%Cover ^b <ED ^b	>IJ ^c	>%Cover ^c >MPS ^b >ED ^c <MNN ^b <IJ ^b
LA-E	<MNN ^a	>%Cover ^b >ED ^b <MNN ^b	ns	<ED ^b

^aP < 0.10; ^bP < 0.05; ^cP < 0.01

Table 5. Landscape structure metrics differing (U-test, $P < 0.10$) between areas with (H) and without (NoH) Harris' hawks in eastern and western study sites, southern Texas, 2000. See Table 1 for metric codes.

Level of Analysis	Metric	Eastern Sites		Western Sites		
		H ($n=39$)	NoH ($n=46$)	Metric	H ($n=60$)	NoH ($n=56$)
Landscape	MNN ^a	32 ± 1 m	46 ± 4 m	MPFD ^b	1.055 ± 0.001	1.058 ± 0.001
	PD ^c	0.83 ± 0.05	0.73 ± 0.07			
		patches/ha	patches/ha			
	MPS ^c	1.42 ± 0.10	2.15 ± 0.23			
		ha	ha			
	ED ^c	294 ± 15	252 ± 16			
		m/ha	m/ha			
Woody	PD ^a	0.40 ± 0.03	0.32 ± 0.04	ns		
		patches/ha	patches/ha			
	ED ^c	179 ± 13	144 ± 16			
		m/ha	m/ha			
	MNN ^c	29 ± 1 m	57 ± 11 m			
Herbaceous	ED ^b	266 ± 14	219 ± 15	PD ^b	1.02 ± 0.04	0.91 ± 0.04
		m/ha	m/ha		patches/ha	patches/ha
				MPFD ^b	1.052 ± 0.001	1.058 ± 0.002
				MSI ^c	1.33 ± 0.02	1.39 ± 0.03
Bare Ground	ns			ns		

^a $P < 0.01$; ^b $P < 0.05$; ^c $P < 0.10$

CHAPTER III

CAN A HARSH ENVIRONMENTAL CONSTRAINTS MODEL EXPLAIN GEOGRAPHIC VARIATION IN HARRIS' HAWK GROUPING?

Introduction

Emlen (1982) presented an ecological constraints model explaining why young of some species delay dispersal. It has subsequently been included in the broader delayed-dispersal threshold model (Koenig et al. 1992) that incorporates both constraints resulting in and benefits of delaying dispersal (Emlen 1994). The original constraints model remains useful because it identifies several factors resulting in constraints to dispersal. One of these is based on the harshness or unpredictability of the environment (Emlen 1982, Emlen and Vehrencamp 1983). While habitat may not become saturated, variable or unpredictable fluctuations of resources can result in the equivalent of increasing or decreasing areas available for dispersal (Emlen 1982, 1984).

Emlen (1982) used low rainfall and food availability in white-fronted bee-eaters (*Merops bullockoides*) to demonstrate increased grouping in response to harsh conditions. In Australia, distribution patterns of cooperatively breeding birds, which delay dispersal, match geographic patterns of aseasonal areas, which may have unpredictable resources from year to year (Ford 1989). Du Plessis et al. (1995) demonstrated in South Africa that facultative cooperative breeding occurred most frequently in semi-arid areas with the greatest variability in both amount and timing of rainfall. Observations of dispersal and philopatry in common mole-rats (*Cryptomys hottentotus hottentotus*) in arid and mesic

environments were similar to that expected by a harsh environment model (Spinks et al. 2000).

Harris' hawks (*Parabuteo unicinctus*) facultatively form groups usually as a result of delayed dispersal (but see Dawson and Mannan 1991a) and exhibit cooperative breeding and hunting behaviors (Bednarz 1995). Grouping also occurs outside of a breeding context with groups being larger during the "non-breeding" season (Bednarz 1988, Faaborg and Bednarz 1990, Bednarz 1995). Harris' hawks use the same areas throughout the year (Dawson and Mannan 1991b, Bednarz 1995), and most breeding occurs in spring (March-June) with additional breeding in summer and early fall, but they may breed during any month of the year (Bednarz 1995).

Harris' hawks occupy a broad range from the southwest USA to Argentina and central Chile (del Hoyo et al. 1994, Bednarz 1995), and grouping behavior and climate, particularly normal annual precipitation (NAP), vary with geography. Proportions of nests attended by groups were 84% in Arizona (NAP = 280 mm, Dawson and Mannan 1991a), 49% in New Mexico (NAP = 302.5 mm, Bednarz and Ligon 1988) and 5% (NAP = 380 mm, Griffin 1976) to 13% (no NAP reported, Brannon 1980) in Texas. Little is known about this species in Central and South America, but a study in central Chile (Jiménez and Jaksić 1993) reported no observations of cooperative breeding or hunting (NAP = 400 mm, Jiménez and Jaksić 1989). Thus, a geographic trend appears to exist, an inverse relationship between NAP and degree to which Harris' hawks form groups. However, these studies were conducted at the northern and southern extents of the Harris' hawk range (del Hoyo et al. 1994) and may not be representative of all populations.

Southern Texas provides a unique opportunity to examine variation in Harris' hawk grouping under different rainfall conditions within a relatively small geographic region. A strong gradient in annual precipitation (~ 1 mm/km) exists over a relatively short distance (Le Houerou and Norwine 1987, Norwine 1995). Closer to the Gulf of Mexico, annual rainfall is ~ 150 - 200 mm greater than that of areas 200 - 250 km inland (west). Furthermore, variability in annual rainfall is greater in the west than the east (Le Houerou and Norwine 1987, Norwine 1995). As a result, Harris' hawks in southern Texas occupy areas with different levels of environmental harshness and vary in their tendencies to form groups (Chapter 2). Rainfall seems an appropriate measure of environmental harshness for Harris' hawks, because they tend to occupy semi-arid to arid areas, they seem dependent upon free water (Bednarz et al. 1988, Dawson and Mannan 1991b; Bednarz 1995) and their prey abundances fluctuate with rainfall (Sowls 1957, Lechleitner 1959, Brown and Zeng 1989, Davis and Schmidly 1994, Windberg 1998, Ernest et al. 2000). However, Bednarz and Ligon (1988) suggested a harsh environment model might not explain Harris' hawk cooperative breeding based on different criteria for environmental harshness (lagomorph abundance and group age composition).

Thus, rainfall might influence, either directly or indirectly, the tendency for Harris' hawks to form groups. Because a steep rainfall gradient extends across southern Texas, the region is particularly appropriate for exploring the viability of the harsh or unpredictable environment model for explaining geographic variation in facultative grouping of Harris' hawks in a non-breeding context. I used rainfall as a measure of environmental harshness to determine two things: 1) whether Harris' hawks are more likely to form groups in a region with more variable and lower long-term annual rainfall

than a region with more rainfall and less variability and 2) whether current and recent annual and seasonal rainfall amounts correlate with Harris' hawk grouping as predicted by Emlen's model (1982).

Methods

Study Sites

This study included 8 sites (36.5 km² – 210.5 km²) in southern Texas, USA ranging from the Gulf of Mexico in the east to the Rio Grande Valley in the west and south (Chapter 2, Fig. 1). Western and central portions of southern Texas are relatively drier (~560 mm annually) with more variable annual rainfall than the area near the Gulf Coast (~700 mm; Le Houerou and Norwine 1987, Norwine 1995). These regions also represent at least 2 distinctive ecoregions, descriptively named here as the humid Coastal Grasslands and the drier South Texas Brushland (Diamond et al. 1987, Olson et al. 2001).

Study sites included ranches and wildlife management areas inhabited by Harris' hawks. Ranch sites included 3 locations (Rincon, Don Ricardo, and North Santa Gertrudis) on the King Ranch (Kleberg County) near the coast, and the Calcasieu (Duval County), Killam (Webb) and Faith (Dimmitt, Webb and Maverick Counties) ranches located in the drier brushland region. The 2 wildlife management areas were Laguna Atascosa National Wildlife Refuge (Cameron County) near the coast and the state-owned Chaparral Wildlife Management Area (Dimmitt and LaSalle Counties) in the drier Brushland. Sites were assigned codes (Chapter 2) based on their name and east (E) or west (W) location: Calcasieu (CU-W), Chapparal (CH-W), Faith (FR-W), Killam (KM-

W), Don Ricardo (DR-E), Laguna Atascosa (LA-E), North Santa Gertrudis (NSG-E) and Rincon (RN-E).

Hawk Data Collection

Survey methods were the same as described previously (Chapter 2), plus an additional set of monthly surveys (see below). I conducted road transect surveys (Andersen et al. 1985; Fuller and Mosher 1987) at each site to estimate the degree to which groups (> 2 hawks) were present.

During the first non-breeding season (September – November 2000), the study design was to visit each of 8 sites on 2 occasions, for 2 days per visit, with a morning and late afternoon survey on each day. However, at 2 coastal sites (DR-E and NSG-E), heavy rains in early November made a second visit unfeasible. Thus, the sample size varied between the Coastal Grasslands ($n = 24$ surveys) and South Texas Brushland ($n = 32$ surveys). Study sites were not accessible during the hunting season (December – January). The following year (February – October 2001), a single morning survey was conducted each month at 2 sites (RN-E and CU-W) to examine the variation in grouping data during a breeding season and an additional non-breeding season.

Transect lengths were 38.54-57.56 km (mean = 48.24 km) and incorporated paved roads, unimproved roads, fence lines and utility rights-of-way (see Chapter 2 for selection criteria). I conducted surveys by truck (25 kph) noting all observations of Harris' hawks.

When possible, I recorded the age of each individual as either < 1 year old (heavily streaked plumage and possibly dependent upon adult birds) or > 1 year old (lightly streaked or adult plumage and potentially capable of dispersing, Bednarz 1995).

The number of birds at each observation was noted and classified as a group (> 2 hawks) or non-group (pair or individual). Groups consisted of individuals within 300 m of one another because Harris' hawks frequently space themselves along 2-4 telephone/power poles (~100 m apart, Appelt pers. obs.).

Indices of Harris' Hawk Grouping

I used several continuous and categorical variables as indices of Harris' hawk grouping. I measured the relative presence of groups two ways. The first was the proportion of observations consisting of groups (POG), which was a continuous variable and calculated as the number of group observations divided by total observations during a survey. The second measure was a categorical variable based on the number of groups and non-groups observed within each ecoregion. I calculated mean group size, which was a continuous variable, as the mean size of group observations at a study site. I measured a categorical variable based on group age composition by determining the number of group and non-groups with hawks aged < 1 year. I measured the number of hawks per observation two ways. The first was a continuous variable calculated by dividing the total number of hawks observed during a survey by the number of observations. The second measure was a categorical variable based on the number of observations of sizes 1-5 hawks in each ecoregion.

Comparisons Between Ecoregions

To determine the effect of ecoregion (i.e., long-term annual rainfall amount and variability) on Harris' hawk grouping, I used a binomial z-test to determine whether the

probability of observing groups (categorical) was higher than expected by chance in South Texas Brushland. I also compared the distribution of hawks per observation (categorical) between the two ecoregions with a G-square test of equal probabilities, and I tested whether observations of 3 or more hawks occurred more often than expected by chance using a binomial z-test. To determine whether groups in either ecoregion had individuals < 1 year greater than expected by chance, I used a binomial z-test.

To estimate the degree to which groups were present at a given study site, I calculated the mean POG and number of hawks per observation (continuous) based on surveys at each site ($n = 4$ or 8 surveys, fall 2000). Because the categorical data were not entirely independent, I compared the continuous POG, number of hawks per observation, and mean group size data of the 4 Coastal Grassland and 4 South Texas Brushland sites using a Mann-Whitney U-test. The continuous data are presented as mean \pm SEM.

Relationships Between Indices of Grouping and Rainfall

I calculated indices of rainfall to examine the effect of a continuous variable representing a gradient of environmental harshness in contrast to the categorical variable, ecoregion, used in the above analyses. I tested whether a relationship existed between mean POG and number of hawks per observation (continuous) and rainfall at study sites using Kendall's non-parametric rank correlation. I obtained annual and monthly rainfall data from the National Oceanic and Atmospheric Administration National Climatic Data Center (NOAA-NCDC, <http://lwf.ncdc.noaa.gov/oa/ncdc.html>) for weather stations located near each site (Appendix D). Because DR-E and LA-E each lie between 2 stations, I used their averages to estimate rainfall at those sites.

For each site, I calculated 2 indices of rainfall, Total Year and Breeding Season (February – June), for the year before (e.g., Total Year – Previous) and the year during which surveys were conducted (e.g., Total Year – Same). Bednarz and Ligon (1988) proposed a potential time-lag effect on grouping based on Harris' hawk and prey abundance, which is likely influenced by time-lag effects in vegetation and prey abundance to rainfall (Ernest et al. 2000). Thus, I calculated correlations between hawk indices and rainfall indices from both the same (2000) and previous (1999) years to determine possible time-lag effects of rainfall (a driving variable).

Results

Effect of Ecoregion on Grouping Indices

Groups of 3 hawks were observed more frequently in South Texas Brushland (Fig. 1a; binomial z-score = 2.34, $P < 0.05$) and less frequently in Coastal Grasslands (binomial z-score = -2.34, $P < 0.05$) than expected by chance, but groups of 4 and 5 hawks did not differ from expected (binomial z-scores = -0.58 and 0.04, respectively, $P > 0.05$). Similarly groups in general were not sighted significantly more often in the South Texas Brushland than expected by chance (binomial z-score = 1.65, $P > 0.05$) and the distribution of number of hawks per observation did not differ between the 2 ecoregions (Fig. 1a; $G^2 = 7.3$, $P > 0.05$). Difficulty in detecting differences was due primarily to a single Coastal Grassland study site (RN-E), which was the only coastal site where groups were observed (Fig. 1b). This may be due in part to its relative dryness compared to other coastal sites (see below). The study site exerted similar influence on the continuous data with brushland POG (0.172 ± 0.032) and hawks per observation (1.7 ± 0.1) not

differing significantly (Mann-Whitney U-test, $P = 0.139$ and 0.149 , respectively) from grassland POG (0.054 ± 0.054) and hawks per observation (1.4 ± 0.1). Because I could not calculate mean group size for the 3 coastal sites without groups (DR-E, LA-E, NSG-E, Chapter 2), I could not statistically compare the continuous mean group size data. Mean group size at each site was as follows: FR-W = 3.6 ± 0.2 ($n = 11$), CH-W = 3.5 ± 0.2 ($n = 9$), KM-W = 3 ± 0 ($n = 11$), CU-W = 3 ($n = 1$), and RN-E = 3.7 ± 0.2 ($n = 13$).

Grouping occurs during both breeding and non-breeding seasons in southern Texas (Fig. 2), and therefore observations of groups included individuals hatched the previous year. For observations where ages were estimated, young hawks (< 1 year) were infrequently observed in both grassland (5/111 observations) and brushland (5/164 observations) areas. Furthermore, groups did not include young hawks more often than expected by chance in either Coastal Grasslands or South Texas Brushland (binomial z-score = 0.40 and -0.40 , respectively, $P > 0.05$).

Non-Breeding Season Variation in Grouping and Rainfall

A strong negative correlation existed between same year rainfall and indices of Harris' hawk grouping. The mean POG at study sites was negatively correlated with both Breeding Season - Same (τ corrected for ties = -0.718 , $P = 0.013$, Fig. 3a) and Total Year - Same (τ corrected for ties = -0.567 , $P = 0.050$, Fig. 4a). The number of individuals per observation yielded similar relationships with Breeding Season - Same ($\tau = -0.571$, $P = 0.048$, Fig. 3b) and Total Year - Same (τ corrected for ties = -0.571 , $P = 0.048$, Fig. 4b). A weak negative correlation existed between Total Year - Previous and POG (τ corrected for ties = -0.416 , $P = 0.150$) but not with Breeding Season - Previous

($P > 0.60$). No correlations existed between number of individuals per observation and either rainfall index for the previous year ($P > 0.45$).

Discussion

Data from this study support the predictions based on Emlen's (1982) harsh environment hypothesis. Harris' hawks also appear to occupy the types of areas and exhibit the types of responses to rainfall that Du Plessis et al. (1995) observed for facultative cooperative breeding birds in South Africa. Harris' hawk grouping in southern Texas is negatively correlated with recent rainfall trends (Figs. 3 and 4 similar to Fig. 1 in Emlen 1982), and is not associated with rainfall from the previous year (i.e., no one-year time-lag). Grouping, particularly groups of 3, varies between ecoregions with differing long-term annual rainfall patterns. Two study sites influenced these results: RN-E, the only Coastal Grassland site with groups and CU-W, the South Texas Brushland site with the least grouping (but see Chapter 2 for possible explanation). These differences likely cannot be completely explained with rainfall data alone, but breeding season rainfall at RN-E was more like brushland than grassland sites (Fig. 3).

While the observed relationships between rainfall and grouping do not demonstrate cause and effect, they help generate hypotheses about how different factors might influence these relationships. Differences in Harris' hawk grouping based on ecoregions are probably associated with different patterns of vegetation, and likely prey species, between the two regions (Blair 1950, Scifres 1980, Diamond et al. 1987, Archer et al. 1988, Chapter 2). These patterns may influence the presence of groups in western areas (Chapter 2, Chapter 4). Differences in grouping based on recent rainfall is likely

associated with proximate factors influencing whether young individuals disperse or not (Emlen 1982, Emlen and Vehrencamp 1983). The absence of a relationship between grouping and the previous year's rainfall does not support the hypothesis that grouping is associated with food availability and possibly reproductive success during the previous year (Bednarz and Ligon 1988). Because the relationship between grouping and rainfall is strongest when based on breeding season rainfall, a short (~3-4 month) time lag might influence proximate factors (e.g., herbaceous vegetation and prey availability) potentially associated with grouping during the non-breeding season, which is when dispersal typically occurs (Bednarz 1995). This study was not designed to address these proximate factors, but its results help generate hypotheses for future testing (see below).

The harsh environment model predicts temporal rather than spatial openings for dispersal (Emlen 1982, Emlen and Vehrencamp 1983, Emlen 1984); therefore, it may explain patterns observed in both New Mexico and southern Texas. Bednarz and Ligon (1988) noted breeding ranges were unoccupied every year of their study, suggesting habitat saturation was unlikely. Previously (Chapter 2), I identified differences in areas where Harris' hawks were observed and where they were never observed. In general, the western sites exhibited fewer differences between areas with and without hawks than eastern sites. Thus, if harsh or unpredictable constraints limit opportunities for dispersal rather than the availability of areas, unoccupied areas should be expected when groups form, and in Bednarz and Ligon's (1988) study, unoccupied breeding ranges varied inversely with grouping from year to year. If appropriate constraints were identified, an experiment alleviating these constraints in unused areas should result in the dissolution of nearby groups and the subsequent occupation of the treated areas.

Hypothesized Proximate Factors Influencing A Rainfall-Grouping Relationship

Free water is an important resource used by many animals living in arid and semi-arid environments (Fisher et al. 1972, Gehrt and Fritzell 1998, Rosenstock et al. 1999, DeStefano et al. 2000, Gabor et al. 2001). Harris' hawks also appear to be dependent upon open water sources (Bednarz et al. 1988, Dawson and Mannan 1991b) and water has been suggested as either an ecological constraint resulting in habitat saturation or a resource that enhances territory quality, thereby influencing philopatry, particularly during the breeding season (Dawson and Mannan 1991b). In Arizona, Harris' hawks were historically associated with riparian areas (Whaley 1986), and anthropogenic water sources may have allowed them to expand their range into more arid areas because they regularly use these water sources (Bednarz et al. 1988). Individuals occupying areas closer to water likely spend less time and energy acquiring water than others. Therefore, proximity to water might increase the quality of an area. Locations with higher or more predictable rainfall might have more water sources. This might explain why grouping generally did not occur at eastern sites in this study.

Prey abundance and prey availability may influence Harris' hawk grouping in response to rainfall. Rainfall has been reported to influence abundance of many Harris' hawk prey species (Sowls 1957, Lechleitner 1959, Brown and Zeng 1989, Davis and Schmidly 1994, Windberg 1998, Ernest et al. 2000). Desert and semi-arid small mammal populations often increase in response to increased vegetation corresponding with increased precipitation (Lechleitner 1959, Beatley 1976, Brown and Zeng 1989, Heske et al. 1997, Lima et al. 1999 and references therein; Ernest et al. 2000). Increased

vegetation not only increases prey abundance but can also limit prey availability by providing increased cover (Brannon 1980, Janes 1985, Malan and Crowe 1997). Tall vegetation can interfere with both prey detection and capture, particularly for a perch hunting species (Janes 1985) like the Harris' hawk (Bednarz 1995). Brannon (1980) observed both cottontail rabbit (*Sylvilagus* spp.) and vegetation (< 1 m high) densities simultaneously increase, which corresponded with rainfall data for that year (NOAA-NCDC 1979). The proportion of mammal remains (including cottontails) at nests simultaneously decreased as vegetation density increased. Therefore, Harris' hawks may switch the type of prey they consume based upon cover, or alternatively, as Bednarz et al. (1988) suggest, lizards and other prey may have become more available at that time.

Regardless of the reason, switching prey types might influence grouping in Harris' hawks because they hunt cooperatively throughout the year, especially during the non-breeding season (Bednarz 1988, Bednarz and Faaborg 1990). Cooperative hunting is only directed toward larger prey like cottontail rabbits for which it yields higher success (Bednarz 1988, Malan and Crowe 1997), and with Harris' hawks the prey is subsequently shared (Bednarz 1988). Smaller prey may be difficult to share. Furthermore, because meeting daily energy requirements under harsh conditions may be difficult, cooperative hunting may be a response to those conditions because individuals in groups of 5 have a greater chance of fulfilling their energetic requirements hunting only large prey than those in smaller groups or pairs (Bednarz 1988). Harris' hawks in the two ecoregions might have been using different prey types. Coastal Grassland sites had more tall herbaceous cover (Chapter 2, Appendix B) and different types of prey are associated with more herbaceous cover, particularly cotton rats (*Sigmodon hispidus*), which are much

smaller than cottontail rabbits (Davis and Schmidly 1994). Cottontail rabbits occupy areas with more brush cover (Davis and Schmidly 1994), which is more abundant in western sites (Chapter 2, Appendix B).

Future work on Harris' hawks should examine these possible responses to rainfall as proximate factors influencing delayed dispersal. Several predictions become apparent based on these factors:

- 1) If free water is important, groups should be located in areas near water sources during particularly dry years, and grouping around water should decrease during wetter years or when additional water sources are available.
- 2) If prey abundance is important, grouping should occur when overall prey abundance is low but only in locations having high relative prey abundance.
- 3) If prey availability or prey type changes with rainfall and vegetation cover is an important factor, Harris' hawk diet should reflect the change, and groups should consume larger prey.
- 4) If larger prey increases the chance of fulfilling daily energy requirements, groups should occur more under harsher conditions, and they should consume larger prey.

Conflicting Results?

Results from two previous Harris' hawk studies appear to conflict with a harsh or unpredictable environment model but might be explainable in part by the proximate factors listed above. In central Chile, cooperative breeding and hunting has not been observed (Jiménez and Jaksić 1993), but normal rainfall there (400 mm, Jiménez and

Jaksić 1989) is less than that in southern Texas (variability may be less, though). This may be explained in part by prey size. The degu (*Octodon degus*), a gerbil-sized rodent, appears to be their primary prey (Jaksić et al. 1980, Jiménez and Jaksić 1993). While rabbits (*Oryctolagus cuniculus*) are a major constituent of their diet, other smaller prey types are frequently used (Jaksić et al. 1980, Jiménez and Jaksić 1993). Thus, Harris' hawks may not form groups in Chile because they can capture and consume sufficient small prey to fulfill their energetic requirements without employing group hunting.

In the second case (Bednarz and Ligon 1988), grouping was not always inversely related with annual rainfall and lagomorph abundance during the breeding season. Groups and pairs also did not appear to use different prey. However, analysis of prey remains at nests may result in bias against small animals (Marti 1987). Furthermore, Bednarz and Ligon (1988) reported significantly fewer woodrat (*Neotoma* spp.) nests on transects associated with pair than group nest sites with intermediate numbers associated with non-nesting sites when both lagomorph abundance and grouping were low. Prey abundance, availability, and size might explain this conflict with a harsh environment model. Woodrat populations appear to be influenced less by rainfall than other small mammals (Windberg 1998), and group nest sites had slightly higher indices of lagomorph abundance than pair sites (Bednarz and Ligon 1988). Pairs might have occupied areas less suitable for woodrats than groups, but pairs might have preyed heavily on woodrats, suppressing abundance, while groups preyed more on lagomorphs and less on woodrats, slightly elevating woodrat abundance. Perhaps by foraging on woodrats or other small prey, individuals in pairs decreased their dependence on more efficient group hunting for lagomorphs to meet their energetic needs. Finally, because my interpretations are based

on non-breeding data, they may not be completely applicable to a breeding season scenario.

Conclusions

In southern Texas, grouping in Harris' hawk generally appears to be associated with low rainfall, as consistent with predictions of a harsh or unpredictable environment model for delayed dispersal. This trend seems consistent and may at least partially explain geographic variation in Harris' hawk grouping based on long-term rainfall across the northern portion of their range. However, an alternative hypothesis that cannot be rejected at this time is that the observed Harris' hawk groups were not family groups but aggregations of related and/or unrelated individuals (Dawson and Mannan 1991b) associated with a clumped, rich resource as described in social carnivores (Macdonald 1983, Kruuk and Macdonald 1985). Future work should consider this as a possible alternative model and whether its predictions are different from those described for models of cooperative breeding in animals (Koenig and Pitelka 1981, Stacey and Ligon 1987, 1991).

Further work examining the proximate factors discussed here for testing hypotheses generated based on Emlen's model (1982) may help to explain facultative grouping in Harris' hawks. Rainfall as a measure of environmental harshness may not explain all geographic variation in Harris' hawk grouping by itself. Other factors like natal habitat quality considered within the delayed-dispersal threshold model (Koenig et al. 1992, Emlen 1994) may further highlight the constraints and benefits influencing grouping in this species.

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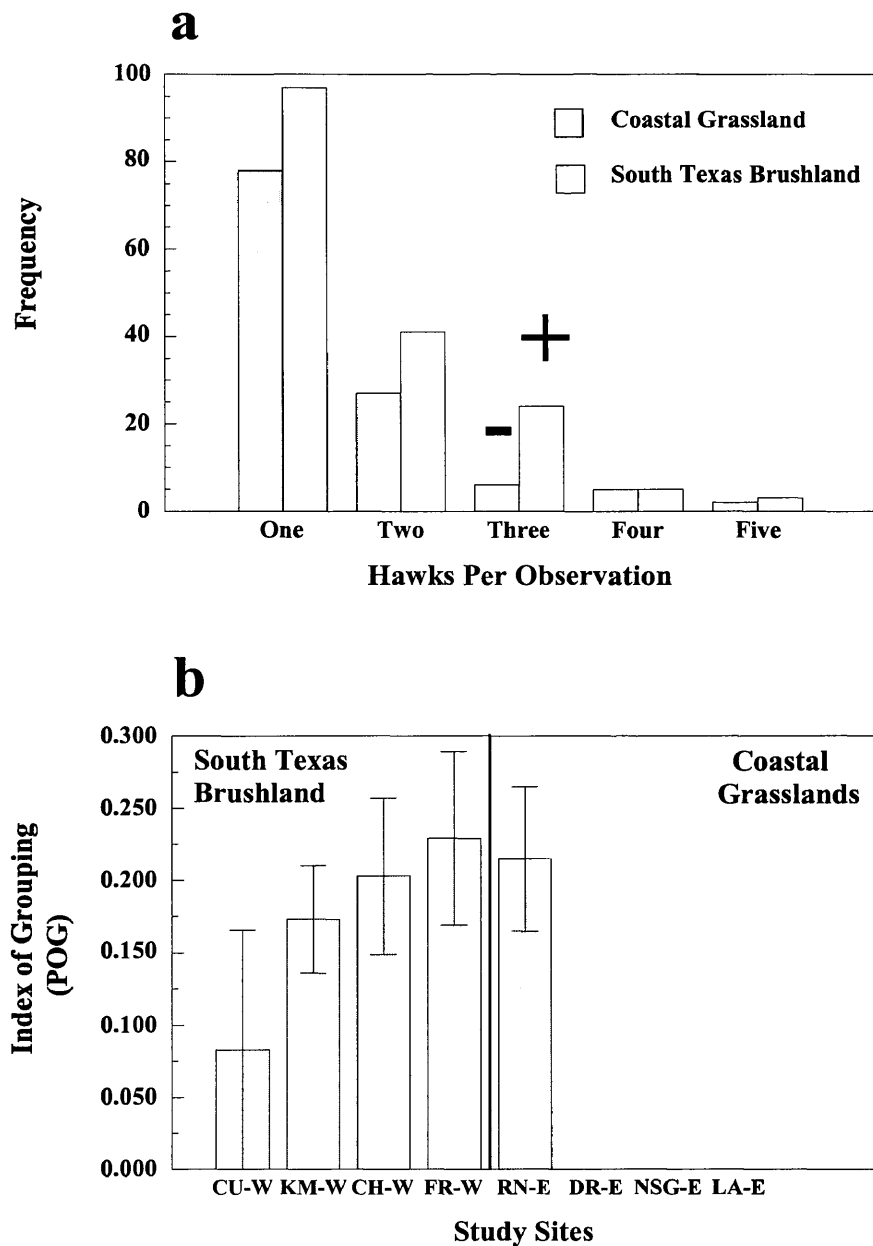


Figure 1. (a) Number of Harris' hawks per observation between ecoregions of low and high rainfall and (b) index of grouping at each site separated by ecoregion, southern Texas, 2000. Index of grouping is based on proportion of hawk observations consisting of groups (> 2 hawks) using the mean \pm SEM of all surveys at each site ($n = 8$, except DR-E and NSG-E $n = 4$). See text for site codes. + and - denote greater and less than expected ($P < 0.05$).

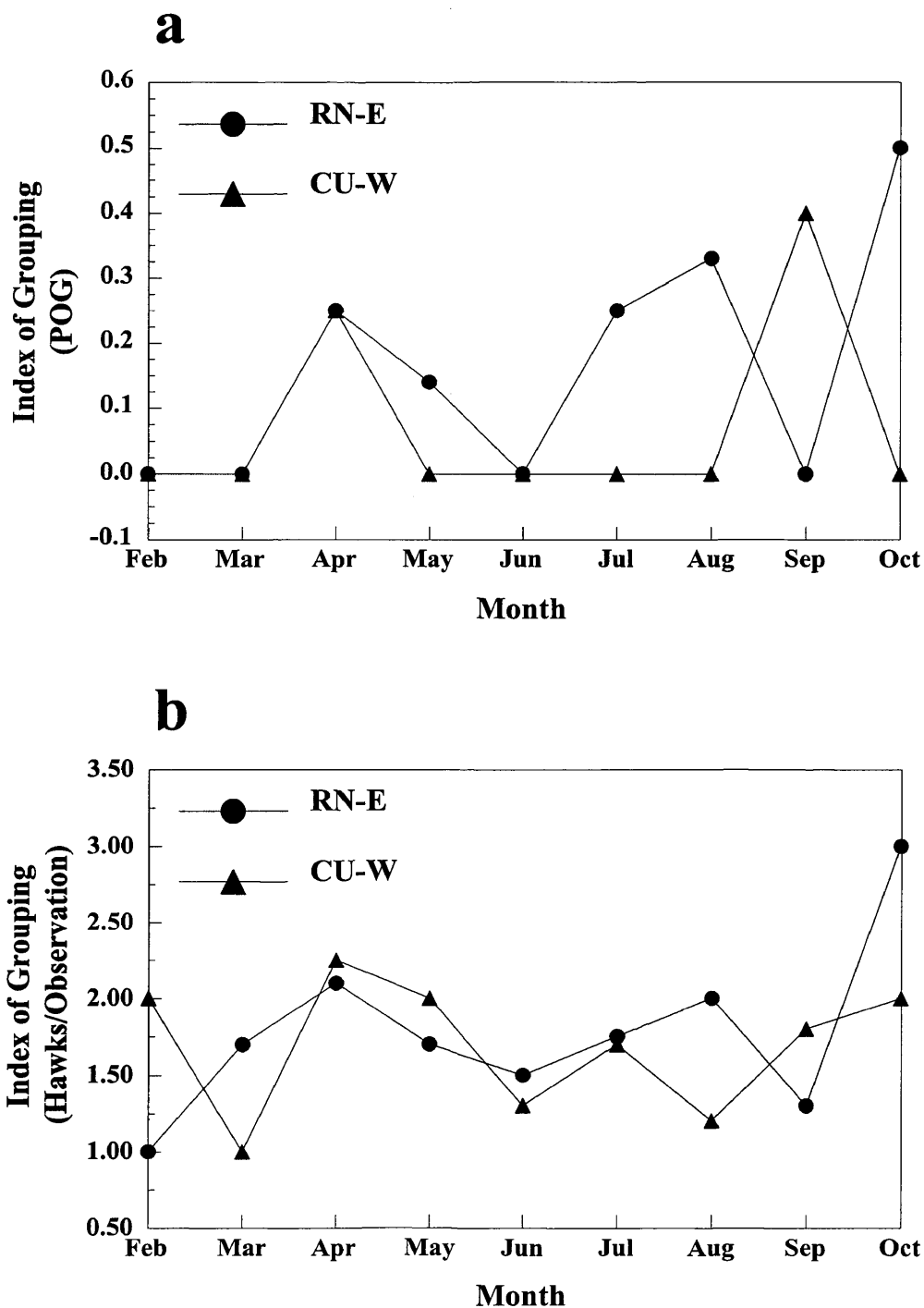


Figure 2. Monthly data for two study sites in a Harris' hawk study, southern Texas, 2001, based on two indices of grouping (a) proportion of observations consisting of groups and (b) number of hawks per observation. See text for site codes.

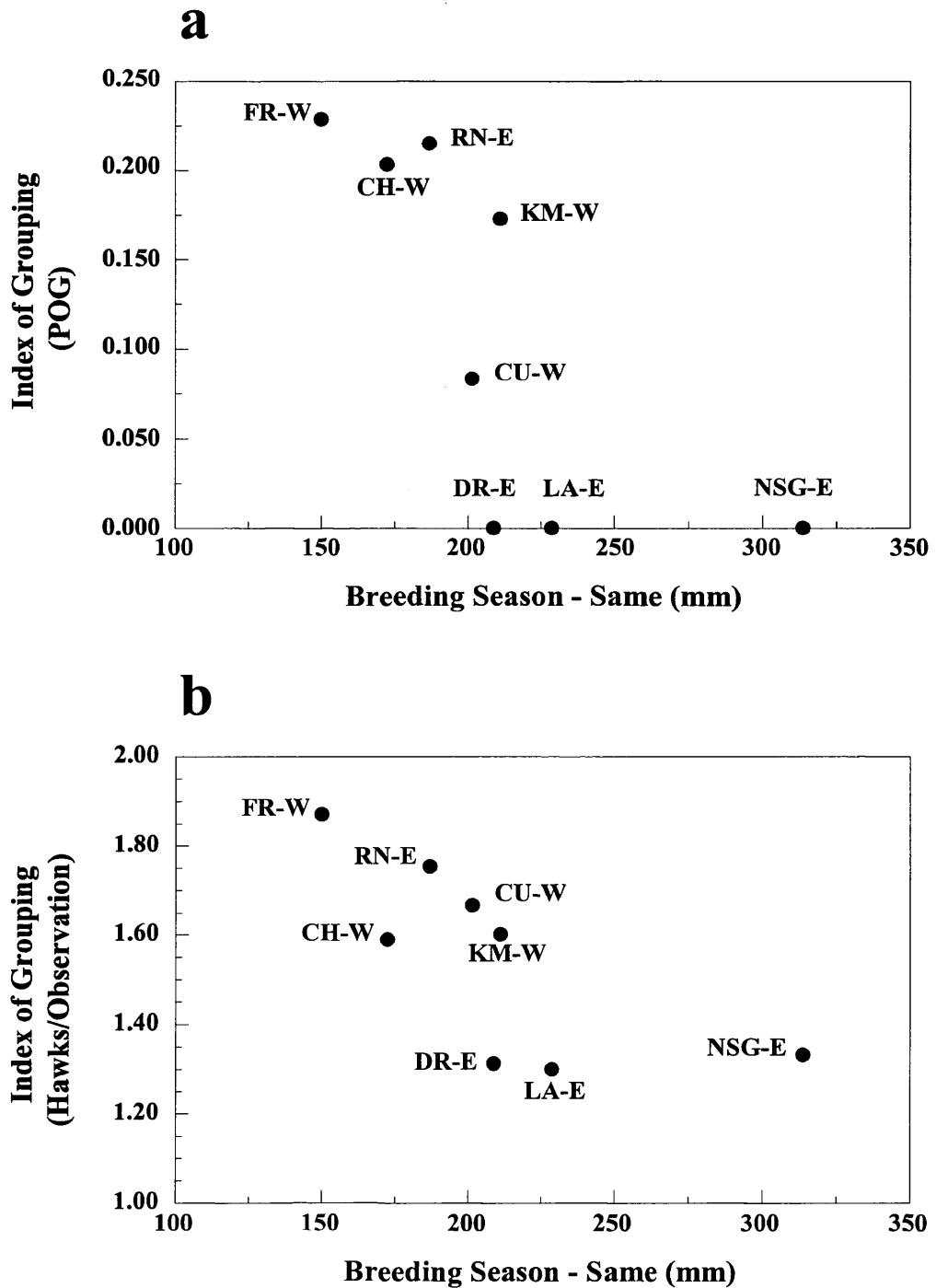


Figure 3. An index of rainfall (Breeding Season –Same) was negatively correlated with 2 indices of Harris’ hawk grouping (a) proportion of observations consisting of groups (site survey mean) and (b) number of hawks per observation (site survey mean) at eight southern Texas study sites, 2000. See text for site codes.

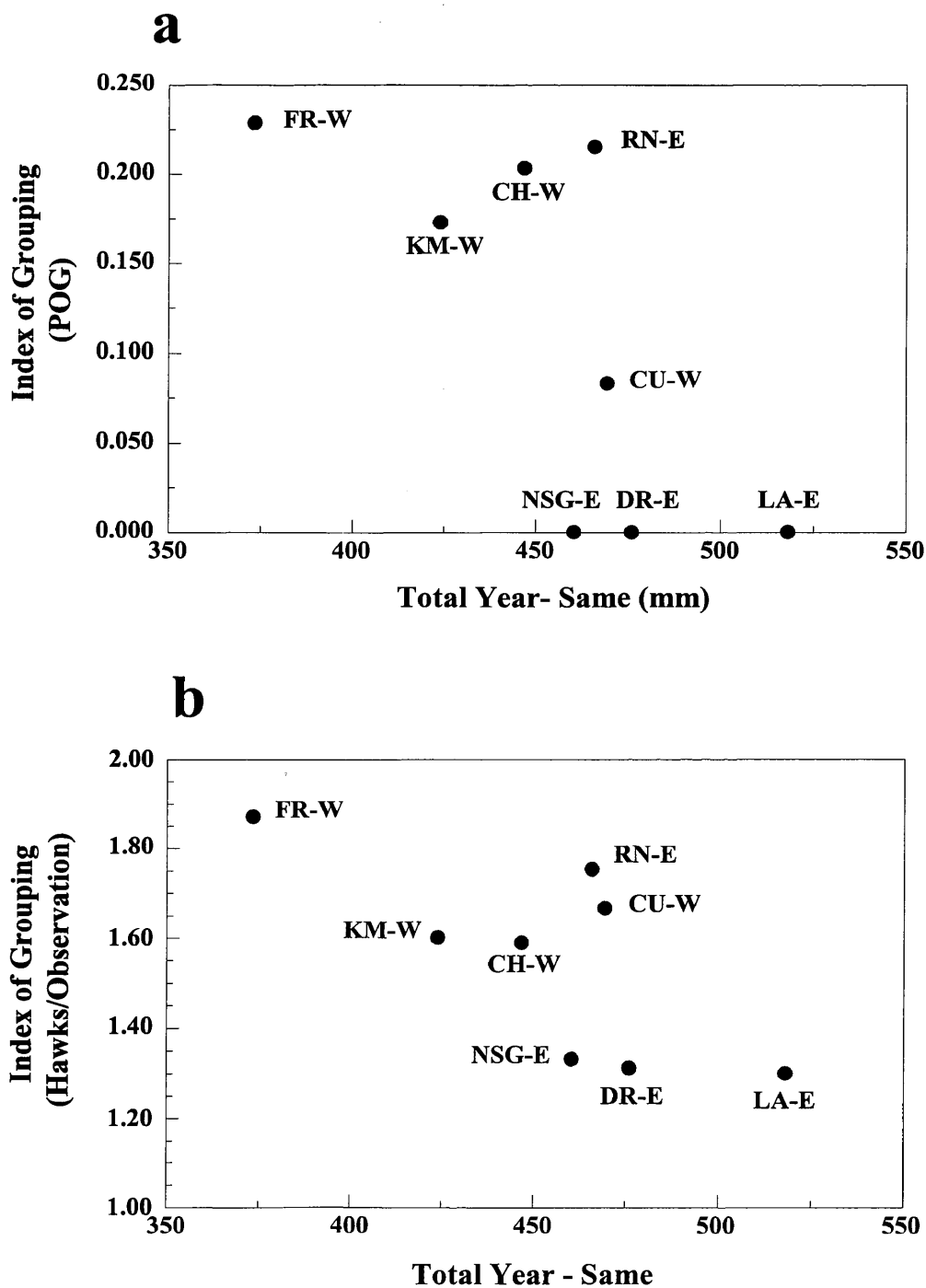


Figure 4. An index of rainfall (Total Year – Same) was negatively correlated with 2 indices of Harris’ hawk grouping (a) proportion of observations consisting of groups (site survey mean) and (b) number of hawks per observation (site survey mean) at eight southern Texas study sites, 2000. See text for site codes.

CHAPTER IV
A MULTI-SCALE EXAMINATION OF LANDSCAPE STRUCTURE IN AREAS
USED BY HARRIS' HAWK GROUPS AND NON-GROUPS IN SOUTHERN
TEXAS, USA

Scale is an important concept in ecological study (Wiens 1989, Levin 1992, Kareiva 1994, Schneider 2001), because different patterns become apparent at different scales (Levin 1992, May 1994). Scale refers to either the resolution (grain size) or extent (total size) at which a system is examined and may be either spatially or temporally based (O'Neill et al. 1986, Gustafson 1998). Conclusions of ecological studies are influenced by scale and observed patterns and processes of importance at one scale may not be important at other scales (Turner 1989). The organisms or processes being examined determine the appropriate scales of analysis (Turner 1989, Kotliar and Wiens 1990). A hierarchical approach to examining patterns in ecological studies at three or more scales broadens understanding of the effects of underlying processes (Kotliar and Wiens 1990). Such a hierarchy might include mesohabitats contained within territories located within home ranges of organisms. These adjacent levels would provide a framework within which the effects of patterns can be compared (Kotliar and Wiens 1990).

Patterns of landscape structure and its influence on presence, abundance, distribution, and behavior of fauna at single or multiple scales has been the subject considerable interest recently (McGarigal and McComb 1995, Jokimäki and Huhta 1996, Drolet and Desrochers 1999, Gros and Rejmánek 1999, Naugle et al. 1999, Saab 1999, Bajema and Lima 2001, Coppedge et al. 2001, Hewison et al. 2001, Chapter 2).

Landscape structure refers to the spatial relationships between distinctive elements in an area in relation to their composition and configuration (Forman and Godron 1986, McGarigal and McComb 1995). The structure of an area influences use by animals at different scales (Kotilar and Wiens 1990). An animal might use a home range based on structural characteristics associated with important resources. It might contain localized, non-defendable resources (e.g., water) or defendable resources associated with food (e.g., matrix of vegetation patches resulting in both abundance and vulnerability of prey) and reproduction (e.g., areas suitable for nests or dens) at a territorial level or individual mesohabitats with structure particularly suitable for foraging.

While locations of resources (e.g., food, water, nest sites, cover) in an area can influence the tendency of animals to form groups (Macdonald 1983; Kruuk and Macdonald 1985; Stacey and Ligon 1987, 1991; Woodroffe and Macdonald 1993), few studies have explicitly examined relationships between landscape structure and grouping in animals (Wigley et al. 1999, Hewison et al. 2001, Chapter 2). Spatial arrangement of elements can be more important than their relative composition, particularly escape cover for ungulates (San José et al. 1997, Hewison et al. 2001, but see Gerard and Loisel 1995). Therefore, spatial arrangements of foraging and escape cover patches (e.g., clumped in localized areas) rather than their relative composition might influence the spatial distribution of prey and could thereby result in predator grouping around a localized resource (i.e., prey, Macdonald 1983, Kruuk and Macdonald 1985). Various landscape metrics can be used to identify structural characteristics of a landscape (McGarigal and Marks 1995, Gustafson 1998), providing possible insight into the spatial arrangement of potential prey species in an area. For example, patch fragmentation may yield lower prey

abundance at finer scales or at broader scales a more heterogeneous landscape, which may result in greater prey diversity or clumping of prey (Wiens 1976). Edge might provide areas of prey vulnerability near escape cover. Interspersion of patches might influence how clumped or evenly interspersed prey might be. Although they are not spatially explicit, metrics like percent composition of a class or the diversity of classes in an area can influence the types and diversity of prey in an area.

Water could be an important resource that influences aggregations or spatial use of animals, particularly in arid and semi-arid environments (Crook 1960, Fisher et al. 1972, Gehrt and Fritzell 1998, Rosenstock et al. 1999, DeStefano et al. 2000, Gabor et al. 2001). Predators can obtain preformed water from their prey (Robbins 1993), but in Arizona, signs of terrestrial and avian predators were highest around water developments, which appeared to be used primarily for drinking rather than as foraging sites (DeStefano et al. 2000). Water may influence aggregations or grouping in animal species because it is an important (rich), difficult to defend and localized resource that may be patchily distributed (Koenig 1981, Koenig and Pitelka 1981, Macdonald 1983, Kruuk and Macdonald 1985, Stacey and Ligon 1987, 1991).

At broader landscape (36-210 km²) and finer territorial (0.79 km²) scales (Withers and Meentemeyer 1999), Harris' hawks (*Parabuteo unicinctus*), which facultatively form cooperative groups (Bednarz 1995), were more likely to be in areas with more homogeneously distributed woody cover and bare ground, less fragmented bare ground, and less herbaceous cover consisting of smaller patches (Chapter 2). Bednarz and Ligon (1988) examined the composition of selected elements near Harris' hawk group and pair nest sites at a fine scale (grain = 5-10 m, extent = 75 m). Their analysis revealed no

differences. However, none of the variables they measured were spatially explicit, and they only examined one spatial scale.

Spatial arrangement of vegetation and resources, rather than their composition, and the scale at which patterns are examined might better predict differences in areas used by groups and pairs of Harris' hawks. Harris' hawks occupy territories year-round, and grouping, which appears to be associated with cooperatively hunting relatively large prey (e.g., lagomorphs; Bednarz 1988), increases during the non-breeding season (Faaborg and Bednarz 1990, Bednarz 1995). Furthermore, they tend to occupy areas with structure that seems particularly favorable for abundance and availability of a primary prey type (Chapter 2), cottontail rabbits (*Sylvilagus* spp., Bednarz 1995). Therefore, one might predict Harris' hawks would form groups in areas with structure that enhances abundance and availability of their prey. Similarly, water is a landscape structural element that is an important resource for Harris' hawks (Bednarz et al. 1988, Dawson and Mannan 1991, Bednarz 1995), and its proximity might enhance the quality of an area by reducing energetic costs of flying long distances to obtain it. Therefore, one might predict Harris' hawk group territories to be located closer to water than those of non-groups. To date, no study has compared the landscape structure of areas used by Harris' hawk groups and non-groups (pairs and individuals).

In this study, I examined whether landscape structure differs between areas used by grouped and non-grouped Harris' hawks in a non-breeding context. Specifically, I analyzed landscape structure data based on three scales. These scales differed in extent but not grain size and approximated Harris' hawk mesohabitat, territory, and home range sizes. I identify for the first time potential landscape characteristics associated with

Harris' hawk groups and generate hypotheses for the observed relationships for future testing.

Methods

Study Sites

This study included five sites where Harris' hawk groups were observed in southern Texas, USA (Chapter 2). They ranged from the Gulf of Mexico on the eastern border to the Rio Grande River on the western border and are described in detail elsewhere (Chapter 2). These sites (36.5 km² – 210.5 km²) included the Calcasieu (Duval County), Killam (Webb County) and Faith (Dimmitt, Webb and Maverick Counties) ranches and the Rincon pastures on the King Ranch (Kleberg County). The fifth site was the state-owned Chaparral Wildlife Management Area (Dimmitt and LaSalle Counties).

Procedures

Data collection procedures have been described elsewhere (Chapter 2) and will be summarized briefly here. During the non-breeding season between 25 September and 15 November 2000, I conducted eight road line transect surveys (Andersen et al. 1985, Fuller and Mosher 1987) at each study site. Transects ranged from 38.54-55.07 km in length and included paved roads, primitive (dirt or gravel) roads, fence lines, and petroleum pipeline/power line/telephone line rights-of-way. Survey routes were designed to systematically cover the area of each site. Transect criteria and selection procedures have been described previously (Chapter 2).

I noted all Harris' hawks, classifying each observation as either a group (>2 birds) or non-group (1 or 2 birds). Groups consisted of individuals within 300 m of one another. Because Harris' hawks frequently distribute themselves along a series of up to 4 telephone/power poles (~100 m apart), 300 m seemed an appropriate distance (pers. obs). I recorded each Harris' hawk's location using a global positioning system (GPS) unit (Pathfinder, Trimble Navigation, Sunnyvale, CA, USA) with sub-meter accuracy (see Chapter 2 for more details).

I imported each hawk location into a geographic information system that included a layer of classified imagery for each study site (Chapter 2), and locations of individuals in each group or pair were merged and used as a single unit of observation. Next, I created 100 m, 500 m and 1000 m-radius circular buffers around each observation. These distances approximate mesohabitat (fine scale), territorial (intermediate scale), and home-range (broad scale) sizes for this species. For this study, I considered mesohabitat (i.e., 100 m-radius, or fine scale) to be the area around a Harris' hawk observation within which prey would be within "striking distance." Previous work in this species (Bednarz and Ligon 1988) examined smaller areas (75 m-radius), but my choice was limited by grain size (20 m, see Chapter 2). As described previously (Chapter 2), a 500 m-radius circle (intermediate scale) is a reasonable approximation of Harris' hawk territory size based on their spacing and territorial behavior (Bednarz 1987, Dawson and Mannan 1991, Bednarz 1995). Harris' hawk home range sizes range from 339 ha to 413 ha for non-breeding adult females and males, respectively (Bednarz 1995). Therefore, a 1000 m-radius circle, or 314 ha (broad scale), is less than reported home ranges but seems a

reasonable approximation given constraints of some study site sizes and maintaining spatial independence for analyses.

In many cases, buffers around separate observations overlapped. Therefore, I merged overlapping buffers for groups and repeated the process for all non-group observations. I also excluded any non-group observations with buffers overlapping group buffers at each scale. This was based on the assumption that observations of overlapping non-groups may or may not have been members of the overlapped group. The result was spatially distinct areas along transects within which Harris' hawk groups were either observed (G) or not observed (NG). The underlying assumption was that no observations of groups indicated that areas were not used by groups. However, non-groups might have been using G areas. The classified imagery (see below) within the G and NG buffers was isolated and used for landscape structure analyses.

I used 20-m resolution multi-spectral satellite imagery (SPOT Image, Reston, VA, USA) from 0-3 months before initial surveys for landscape structure analyses (Chapter 2). Imagery pixels were classified into 4 land cover classes: woody, herbaceous, bare ground, and water. Using the ArcView extensions Spatial Analyst and Patch Analyst, I calculated a number of landscape metrics (McGarigal and Marks 1995, Gustafson 1998; Chapter 2, Table 1) for G and NG areas at each site (McGarigal and Marks 1995). These metrics provide information about composition and configuration of a landscape based on the various patch types individually (class level) and together overall (landscape level) including relative abundance of each class (percent woody cover, herbaceous cover, water, bare ground), fragmentation (patch density, mean patch size, mean nearest neighbor distance), patch shape complexity (mean shape index, mean patch fractal

dimension), amount of edge (edge density), interspersions of each patch type relative to one another (interspersions/juxtaposition index), and diversity (Shannon's diversity index, Shannon's evenness index).

After calculating these metrics for G and NG areas at each scale, I pooled all G and NG area metric values (unequal sample sizes) at each scale for all sites and compared G and NG values using Mann-Whitney U-test. I did the same comparisons within each site. Using mean G and NG values for each site ($n = 5$), I made paired comparisons across sites using Wilcoxon signed ranks test.

As a first attempt at identifying potential structural characteristics differing between group and non-group areas and because these metrics may interact, I reported all differences at $P < 0.15$ significance level and specifically identified differences at $P < 0.05$. Metrics differing at $P < 0.15$ are potential candidates for further analyses (Wigley et al. 1999).

Water appears to be an important component of Harris' hawk habitat (Bednarz et al. 1988, Dawson and Mannan 1991, Bednarz 1995). Because water occurred rarely within buffer areas, I calculated the distance from each group and non-group observation to the nearest water pixel. I used the same observations from the fine scale analysis. Therefore, I excluded non-group observations with 100 m-radius circles overlapping those of groups. I compared group and non-group distances to water within sites using Mann-Whitney U-test and made a paired comparison across sites (Wilcoxon signed ranks test) using the group and non-group distance means for each site. Unless otherwise stated, data are presented as mean \pm SEM.

Results

I made 45 group and 192 non-group observations across the five study sites. Pooling metrics for G and NG areas from all sites yielded different results at different scales (Table 1). At the broad scale (1000 m), none of the metrics differed (Mann Whitney U-test; $P > 0.15$) between G ($n = 16$) and NG ($n = 19$) areas. At the intermediate scale (500 m), the only differences between G ($n = 23$) and NG ($n = 50$) areas were that G areas had lower herbaceous interspersion and greater bare ground edge density. The most differences were observed between G ($n = 33$) and NG ($n = 117$) areas at the fine scale (100 m). Herbaceous patch density was lower ($P < 0.05$) and patch size and patch shape complexity were higher in G than NG areas. Together, these results demonstrated lower herbaceous fragmentation in G areas. Landscape patch density, patch size, and patch shape complexity essentially mirrored the herbaceous results.

A paired comparison across sites ($n = 5$) similarly revealed scale-dependent differences in metrics between G and NG areas with the most differences again observed at the fine scale (Table 2). At the fine scale, groups were in areas with generally fewer and larger patches ($P < 0.05$), particularly woody patches, again demonstrating less fragmentation in G areas. Herbaceous patches were closer together ($P < 0.05$) and bare ground patches were less complex in G areas. More ($P < 0.05$) and smaller herbaceous patches were present in G areas at the intermediate scale with woody patches being more complex and bare ground patches less interspersed. At the broad scale, woody patches were present at lower densities in G areas similar to that observed at the fine scale. Herbaceous patches were more complex shaped ($P < 0.05$) at the broad scale, and bare ground patches were more fragmented and less interspersed similar to intermediate scale.

Different specific metrics differed between G and NG areas within sites (Table 3, Appendices F-H). A within site comparison was not made for Calcasieu because only one group was observed. An interesting similarity was observed in herbaceous differences (in direction not degree) between G and NG areas at the fine scale at the two sites where groups were most frequently observed (Faith and Rincon, Chapter 2). In both cases, groups were in areas with more herbaceous cover that was less fragmented than non-groups. The only other similarity between two sites was greater woody interspersion at the fine scale in G areas between the Faith and Killam sites. In two cases, differences between G and NG areas were repeated across scales (Killam G areas with greater woody interspersion and Faith G areas with more herbaceous cover in larger patches), but the rest were inconsistent.

Group observations were not significantly closer to water sources (996 ± 196 m) than non-group observations (1247 ± 133 m; Wilcoxon signed ranks test, $P > 0.30$). Similarly, no within site differences were observed (Mann-Whitney U-test, $P > 0.10$).

Discussion

In this discussion, I will first examine the relative importance of landscape structural characteristics at the fine and intermediate scales. The former is more representative of the surroundings used by a foraging hawk, and the latter represents a spatial arrangement of structural elements used for foraging as well as other activities. Few landscape metrics emerged as distinguishing habitat differences between grouped and non-grouped hawks at the broad scale used in this study. Finally, I will address the hypothesis that the distribution of water influences the distribution of Harris' hawk

groups in a semi-arid environment. Throughout the discussion I identify hypotheses generated from this study.

Fine Scale

Harris' hawk groups might be more likely to use higher quality territories containing higher quality foraging mesohabitats. This pattern has been recorded for acorn woodpeckers (*Melanerpes formicivorus*, Stacey and Ligon 1987, 1991), pale chanting-goshawks (*Melierax canorus*, Malan and Crowe 1997, Malan 2001) and some carnivore species (Macdonald 1983, Kruuk and Macdonald 1985, Beckoff and Wells 1986, Woodroffe and Macdonald 1993). Because surveys were conducted during the times of day Harris' hawks typically forage (Bednarz 1995), fine scale areas in this study likely represent areas used for foraging. Such areas require adequate perches for their primary mode of hunting (Bednarz 1995) and must be appropriate in terms of prey being present (i.e., food and cover for prey) and available (Pianka 1983, Janes 1985, Bednarz et al. 1988, Morrison et al. 1992).

I did not evaluate prey abundance or availability; however, Harris' hawk groups were located in mesohabitats with less fragmented woody and herbaceous patches, which may have higher densities and a greater variety of mammalian prey (Morrison et al. 1992, Malen 2001). Some prey species (Bednarz 1995) like the cotton rat (*Sigmodon hispidus*) generally occupy areas with mostly herbaceous cover or mixed grass-brush (Kincaid et al. 1983, Davis and Schmidly 1994). Others, like wood rats (*Neotoma micropus*) and cottontail rabbits (*Sylvilagus* spp.), tend to remain in areas with denser brush (Box 1959, Davis and Schmidly 1994), but eastern cottontails (*S. floridanus*) venture into open areas

during crepuscular hours to forage (Davis and Schmidly 1994) increasing their availability to hawks. Therefore, the results of this study suggest future studies should test the hypothesis that groups occupy higher quality areas with landscape structure providing higher prey diversity, abundance and availability.

This hypothesized pattern is similar to that of pale chanting-goshawks, which only form polyandrous groups in particular vegetation associations with a mixture of scrub and grassland (Malen et al. 1997, Malan 2001). This type of habitat mosaic not only supports high densities of two of its primary prey species (Malan and Crowe 1996), which occupy different types of patches (Malen et al. 1997, Malan 2001), but also results in high availability due to intermediate cover and numerous perches (Malan and Crowe 1997). Future studies should examine prey abundance compared with that captured and consumed by Harris' hawks among areas with specific landscape characteristics and between areas used by groups and non-groups in southern Texas. Manipulative experiments would test the response of prey abundance and use in response to changes in landscape structure.

If the hypothesis described above is true, results from this study support predictions expected for a benefits-of-philopatry explanation for grouping (Stacey and Ligon 1987, 1991) but are the opposite of those expected for a marginal habitat explanation (Koenig and Pitelka 1981). The former predicts grouping will occur where habitat quality is unevenly distributed among territories while the latter predicts territory quality is evenly distributed among territories. If the previously described characteristics (i.e., lower fragmentation of patches, especially herbaceous at Faith and Rincon) are indicative of higher quality habitat, grouping is more common where Harris' hawk fine

scale (mesohabitat) quality is more variable. At the fine scale, more differences existed between G and NG areas at those sites where groups were observed in greater proportions (Table 3). The number of differing metrics at a site was positively correlated with the proportion of observations consisting of groups at a site (Kendall's correlation, $\tau = 1.00$, $P < 0.05$). This is unlikely an artifact of those sites having more group samples because sample sizes (excluding Calcasieu, see Chapter 2 for more information) were similar among sites at this scale (Appendix F). Further work is necessary to test the hypothesis that the above criteria truly represent higher quality habitat by bestowing higher fitness to individuals occupying those areas (Koenig et al. 1992).

Intermediate Scale

Areas within the extent of the intermediate scale likely include a mosaic of suitable foraging mesohabitats. Grouped hawks were in areas with more complex woody patches and more fragmented herbaceous cover and bare ground than areas containing non-groups. The complex woody patches likely provide both suitable perching sites and cover for some prey while the more fragmented herbaceous and bare ground patches in the larger area may be associated with foraging mesohabitats with higher prey availability. Whether or not these characteristics represent higher quality habitat is uncertain. Likewise, at the broad scale, differences between group and non-group areas are difficult to interpret. As with the finer scales, woody patches are less fragmented in group areas and bare ground is more fragmented, but herbaceous does not differ much. At the broadest scale, differences likely decrease between groups and non-groups because more of the landscape is sampled resulting in less variation between them (Levin 1992).

Some limitations in study design may have resulted in difficulty identifying many strong differences between areas used by groups and non-groups. First, while I attempted to distinguish group areas from non-group areas as much as possible by removing overlapping areas, some groups could have been misidentified as non-groups (Dawson and Mannan 1989) possibly confounding results. Second, the grain size (20 m) may have been too coarse for identifying small patches at the fine scale (O'Neill et al. 1996). The most differences was observed at that scale, perhaps more were missed. Third, because factors other than landscape structure appear to influence Harris' hawk grouping (Chapter 3), relatively small differences in structure might result in slightly higher quality and shift the balance of costs and benefits of delayed dispersal (Koenig et al. 1992). In the future, manipulative studies can test for cause and effect relationships.

Water

This study did not document differences in proximity of group and non-group observations to water. However, this study cannot rule out water as a potential factor influencing Harris' hawk grouping due to a number of limitations. The coarse grain of this analysis may have influenced these results. I was only able to include water sources approximately 20 x 20 m (i.e., grain size). Therefore, smaller water sources like cattle troughs and windmills were not included in the analyses. Their influence on grouping is uncertain. The sampling method also made determining whether non-group observations were actually members of groups impossible.

Harris' hawks might fulfill much of their water requirements with preformed and metabolic water (Robbins 1993), but they may fly up to 10 km to drink water (Bednarz

1995). Therefore, areas closer to water might be higher quality, and individuals in those areas would not disperse to poorer quality areas (Koenig et al. 1992). Proximity to water may result in higher quality areas simply by reducing the time and energy required to obtain water, or it could be a resource used by prey species resulting in higher prey abundance. In areas where resources are rich and/or habitat quality is unequally distributed, groups are more likely to form (Macdonald 1983, Kruuk and Macdonald 1985, Stacey and Ligon 1987, 1991). Future work should examine the spatial arrangement of clearly identified groups and non-groups in relation to all natural and artificially supplied water sources.

Summary

For the first time, this study identifies hypotheses relating potential differences in landscape structure to Harris' hawk grouping at multiple scales, particularly at a fine scale approximating mesohabitats. Future tests of these hypotheses using manipulative experiments may contribute to measurable ways of distinguishing between good and poor habitat, based on the spatial configuration of vegetative cover as it pertains to prey diversity, abundance and availability and other resources such as water. Such quantitative approaches examining landscape structure may be useful for comparisons in other species that form groups, but few studies of this type have been conducted (Wigley et al. 1999, Hewison et al. 2001, Chapter 2). Because animals select for different habitat characteristics for different functions at different scales, use of appropriate and multiple scales is essential for studies on habitat use and selection (Orians and Wittenberger 1991).

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Table 1. Landscape and class metrics differing^a between areas with groups and non-groups of Harris' hawks at 3 scales (in m) for 5 study sites combined, southern Texas 2000. See text for sample sizes.

Scale	Level	Metric ^b	Groups		Non-Groups		<i>P</i>
			Mean ± SEM	Range	Mean ± SEM	Range	
100	Landscape	PD	2.76 ± 0.17	1.28-5.36	3.06 ± 0.08	0.89-5.19	0.061
		MPS	0.41 ± 0.03	0.19-0.78	0.37 ± 0.01	0.19-1.13	0.070
		MSI	1.41 ± 0.03	1.11-1.79	1.38 ± 0.02	1.10-2.36	0.131
	Herbaceous	PD*	1.04 ± 0.10	0.15-2.30	1.28 ± 0.06	0.19-2.69	0.046
		MPS	0.82 ± 0.22	0.04-5.08	0.49 ± 0.07	0.04-3.76	0.146
		MSI	1.58 ± 0.09	1.00-3.19	1.45 ± 0.04	1.00-3.09	0.108
		MPFD	1.08 ± 0.01	1.00-1.21	1.07 ± 0.00	1.00-1.22	0.109
500	Herbaceous	IJI	82.61 ± 3.32	47.55-99.80	85.47 ± 2.62	35.30-100	0.147
	B. Ground	ED	275 ± 19	67-382	248 ± 13	22-376	0.138
1000			None < 0.15				

^aMann-Whitney U-test, $P < 0.15$

^bPD = Patch Density; MPS = Mean Patch Size; MSI = Mean Shape Index; MPFD = Mean Patch Fractal Dimension; IJI = Interspersion/Juxtaposition Index; ED = Edge Density

*significant at $P < 0.05$

Table 2. Landscape metrics differing between areas with Harris' hawk groups and non-groups based on paired comparisons^a at three scales (in m) within study sites ($n = 5$), southern Texas, 2000.

Scale	Level	Metric ^b	Groups		Non-Groups		<i>P</i>
			Mean \pm SEM	Range	Mean \pm SEM	Range	
100	Landscape	PD*	2.67 \pm 0.27	1.90-3.41	3.05 \pm 0.25	2.12-3.43	0.043
		MPS*	0.42 \pm 0.04	0.33-0.56	0.37 \pm 0.04	0.31-0.53	0.043
	Woody	PD	0.83 \pm 0.08	0.64-1.03	1.08 \pm 0.14	0.85-1.64	0.138
	Herbaceous	MNN*	22 \pm 3	12-28	27 \pm 5	16-46	0.043
	B. Ground	MSI	1.44 \pm 0.13	1.00-1.71	1.61 \pm 0.07	1.33-1.75	0.138
		MPFD	1.06 \pm 0.02	1.00-1.10	1.09 \pm 0.01	1.05-1.10	0.080
500	Landscape		None < 0.15				
	Woody	MPFD	1.07 \pm 0.00	1.05-1.08	1.06 \pm 0.00	1.05-1.07	0.138
	Herbaceous	PD*	0.86 \pm 0.20	0.18-1.32	0.75 \pm 0.21	0.18-1.28	0.043
		MPS	0.97 \pm 0.73	0.15-3.89	1.72 \pm 1.04	0.15-5.66	0.138
	B. Ground	IJI	73.9 \pm 11.3	35.1-96.7	85.2 \pm 7.2	56.5-95.7	0.138
1000	Landscape		None < 0.15				
	Woody	PD	0.36 \pm 0.07	0.16-0.49	0.50 \pm 0.11	0.36-0.68	0.080
	Herbaceous	MPFD*	1.06 \pm 0.00	1.05-1.07	1.05 \pm 0.00	1.04-1.06	0.043
	B. Ground	MNN	27 \pm 2	24-36	26 \pm 4	24-32	0.080
		IJI	65.3 \pm 9.5	29.3-82.1	72.8 \pm 8.2	42.1-89.7	0.138

^aWilcoxon signed ranks test, $P < 0.15$

^bMNN = Mean Nearest Neighbor, See Table 1 for other abbreviations

*significant at $P < 0.05$

Table 3. Landscape metrics differing (Mann-Whitney U-test, $P < 0.15$) between areas with (G) and without (NG) Harris' hawk groups at 3 different scales (in m), 4 study sites, southern Texas, 2000. The symbols ">" or "<" designate how G areas differ from NG areas. See Tables 1 and 2 for abbreviation definitions. See Appendices F-H for sample sizes.

Site	Level of Examination and Scale											
	Landscape			Woody			Herbaceous			Bare Ground		
Faith	100	500	1000	100	500	1000	100	500	1000	100	500	1000
	>MSI ^c	ns	ns	>LJI ^b	ns	ns	>%cover ^c	>%cover ^b	ns	ns	>ED ^a	ns
	<MNN ^b						>MPS ^c	>MPS ^a				
	>SDI ^c						>ED ^b , >MSI ^c					
>SEI ^c							>MPFD ^c					
							<MNN ^b					
Rincon	<ED ^a	<PD ^b	ns	<%cover ^a	ns	ns	>%cover ^c	ns	ns	ns	<PD ^a	ns
	<SEI ^d	>MPS ^b		<MPS ^b			<PD ^c , >MPS ^c					
							>MSI ^a					
							>MPFD ^a					
Chaparral	>MPFD ^a	>PD ^b	ns	>ED ^a	<LJI ^b	ns	<LJI ^a	ns	ns	<LJI ^c	ns	ns
	<LJI ^b	<MPS ^b										
Killam	ns	<SDI ^b	ns	>LJI ^a	>LJI ^a	ns	<%cover ^a	ns	<MPS ^a	ns	<MNN ^c	ns

^a $P < 0.15$, ^b $P < 0.10$, ^c $P < 0.05$, ^d $P < 0.01$

CHAPTER V

SUMMARY

This dissertation examined potential ecological factors associated with group formation in Harris' hawks (*Parabuteo unicinctus*) based on ecoregion and landscape structure. In the second chapter, I identified some landscape patterns at a broad scale (e.g., evenly distributed bare ground and woody vegetation throughout a study site) and a fine scale (e.g., disproportionate use of particular ranges of vegetation cover) associated with locations where Harris' hawks and Harris' hawk groups were and were not observed. The third chapter examined the hypothesis that a broad regional pattern in Harris' hawk grouping appeared to be associated with constraints of a harsh or unpredictable environment. The fourth chapter identified testable hypotheses about habitat quality, examining the relationship between distribution of vegetation patches and areas where Harris' hawk groups were located at multiple spatial scales.

Together, these chapters help to add understanding of spatial patterns to a conceptual model of why Harris' hawks facultatively form groups. In this summary, I will further explain the potential relationships among landscape patterns, prey cover and water resources that provide a suite of hypotheses and predictions for future research.

CONCEPTUAL MODEL

Based on landscape structure, I found no evidence that habitat saturation alone explains why Harris' hawks form groups as suggested previously (Dawson & Mannan 1991). However, the strong observed correlation between hawk abundance and grouping

indicates density could affect the influence of other factors associated with grouping like habitat/patch quality or temporal availability of habitat associated with a harsh or unpredictable environment as seen with delayed dispersal (Koenig et al. 1992) and assemblages of carnivores (Macdonald 1983, Woodroffe & Macdonald 1993).

A Habitat Saturation Model would predict that all suitable areas are occupied and groups form because young individuals lack areas for dispersal (Emlen 1982). However, the vegetation structure data presented here indicate Harris' hawk grouping does not occur at locations with greater potential for limitation of usable areas (i.e., greater differences between areas used and not used). Conversely, in areas where groups were observed, few differences existed between occupied and unoccupied areas. This suggests suitable areas as I measured them by landscape structure were not limited spatially, and something other than saturated habitat was influencing Harris' hawk grouping. These results are congruent with observations made by Bednarz and Ligon (1988).

The second chapter points to alternative hypotheses explaining why Harris' hawks form groups. The areas used by Harris' hawks at both finer (mesohabitat) and broader (territorial) scales appeared to be associated with characteristics favorable for prey abundance and availability, but this remains to be determined. The specific characteristics appear to differ between areas within ecoregions with differing rainfall patterns. Furthermore, study sites where groups were observed tended to have landscape characteristics like those generally present in areas with lower rainfall: homogeneously distributed woody and bare ground, more bare ground edge with less complex patches closer together, and less overall herbaceous cover divided into small patches. Harris' hawks at these sites also tended to use mesohabitats that differed from random areas of

the same size. All these data suggested two things. Harris' hawks may form groups in harsher areas with less and unpredictable rainfall, and they may group at sites with more localized or clumped resources like water or possibly prey based on vegetation structure.

The results of the third chapter support the hypothesis that Harris' hawk grouping is influenced by a harsh, unpredictable environment (Emlen 1982) and does not support the hypothesis that grouping is influenced by productivity in the previous year (Bednarz & Ligon 1988). Bednarz and Ligon (1988) suggested their data supported the idea that groups are more likely to form after productive years based on the idea that high prey abundance results in higher hawk productivity. During their study, prey abundance did correspond with higher rainfall. Therefore, I would have expected to observe a positive correlation between grouping and rainfall from the previous year.

In direct contrast to that expectation, my data demonstrated not only a weak negative correlation between indices of grouping and the previous year's rainfall but also a strong negative correlation with rainfall during the same year. These observations match well with the predictions of a Harsh Environment Model. Furthermore, a harsh environment model can explain the apparent availability of unused areas because it predicts temporal rather than spatial shifts in ability for younger individuals to disperse. The influence of these temporal shifts on delayed dispersal would be further enhanced by the relationship of grouping with density observed in the second chapter (Koenig et al. 1992). Finally, a Harsh Environment Model provides a framework within which predictions can be made about the proximate factors (particularly prey type and availability) influencing delayed dispersal in this and other species. However, proximate factors provided by other types of models also must be considered.

Data from the fourth chapter suggest subtle landscape differences between areas occupied by groups and non-groups. Whether these differences result in higher quality habitat or clumped resources for groups as expected by the benefits-of-philopatry model (Stacey and Ligon 1987, 1991) or resource dispersion (Macdonald 1983) is unknown. Water may be a resource near which individuals may aggregate or delay dispersal, but the data did not demonstrate a significant difference between proximity of group and non-group observations to water. The structure of areas occupied by groups and non-groups differed in few ways, but the most differences were found at the fine scale approximating mesohabitat size. Groups appeared to occupy mesohabitats with structure particularly suitable for hunting cottontail rabbits (e.g., patches of woody cover with hunting perches near patches with less woody cover and more herbaceous cover).

Differences at the intermediate scale approximating territory size suggest a mosaic of mesohabitats with groups having more complex woody patches with fragmented herbaceous and bare ground patches for foraging. Differences at the broad scale approximating home range size are few and similar to those described for territories. Overlap probably occurs between group and non-group areas at this scale.

The fourth chapter also highlights some difficulties in using landscape structure to examine grouping while helping to generate hypotheses for future study. First, the data demonstrate that any analysis of landscape pattern in areas occupied by groups and non-groups may be specific to the study site. Results from one place may be difficult to extrapolate to other areas. Second, examining different spatial scales yields different results. Therefore, studies conducted at one scale may provide limited interpretations. Third, while results of landscape analyses can provide quantitative information about the

structure of areas occupied by groups and non-groups, it can only provide clues about the underlying processes (e.g., groups in an area result from higher prey abundance and availability associated with landscape structural characteristics). These observed patterns help to build a conceptual model for generating hypotheses for future work.

The results of this study help to generate a conceptual model for understanding why Harris' hawks form groups (Fig. 1). If Harris' hawks form groups based on the harshness of their environment related to rainfall and to meet their nutritional requirements based on quality of habitat (i.e., food and water) and the types of prey available in areas they occupy, several predictions can be made. Grouping will occur when conditions are harsh and will fluctuate from year to year, and previously occupied areas will be unoccupied in harsh years. Harris' hawks occupying harsh or unpredictable environments will delay dispersal or aggregate under harsh conditions but only in areas of higher quality, or likely to result in higher fitness, than anything else available at that time. Therefore, groups will only form in higher quality areas, which will have more abundant and available prey and be near water. Groups will tend to use larger prey and tend to occupy areas with mesohabitats suitable for foraging for that prey type. Group size will be related to the relative abundance of larger prey and approach an optimum for energetic return (Nudds 1978). If the abundance and availability of smaller sized prey is high and that of larger prey is low in territories, groups will not form. Presence of nearby water may further enhance territory quality and encourage aggregations or philopatry. Finally, the above predictions will all be influenced by density of hawks. Because different responses are employed by different individuals within the same population, environmental harshness, prey availability and type, and presence of water may not

individually be sufficient to result in delayed dispersal or aggregations of Harris' hawks. Rather, these proximate factors likely influence the difference in potential fitness at a given time between forming groups, by delaying dispersal or simply aggregating, and maintaining separate territories.

FUTURE RESEARCH DIRECTIONS

The conceptual model presented here provides a framework for future study on Harris' hawk grouping behavior. Future studies must determine the accuracy of the different components of the model by focusing on determining the following:

1. Whether and how landscape structure, particularly herbaceous and woody cover, influences abundance, availability and diversity of Harris' hawk prey species.
2. Whether prey use differs between groups and non-groups particularly between ecoregions with differing rainfall patterns.
3. Whether prey use within an area changes in response to patterns of rainfall and herbaceous vegetation.
4. Whether prey abundance and availability differs between areas occupied by groups and non-groups.
5. Whether spatial arrangement of water sources influences the spatial arrangement of groups and non-groups.
6. Whether prey type and availability and proximity to water translate into increased fitness and thus influence habitat quality.

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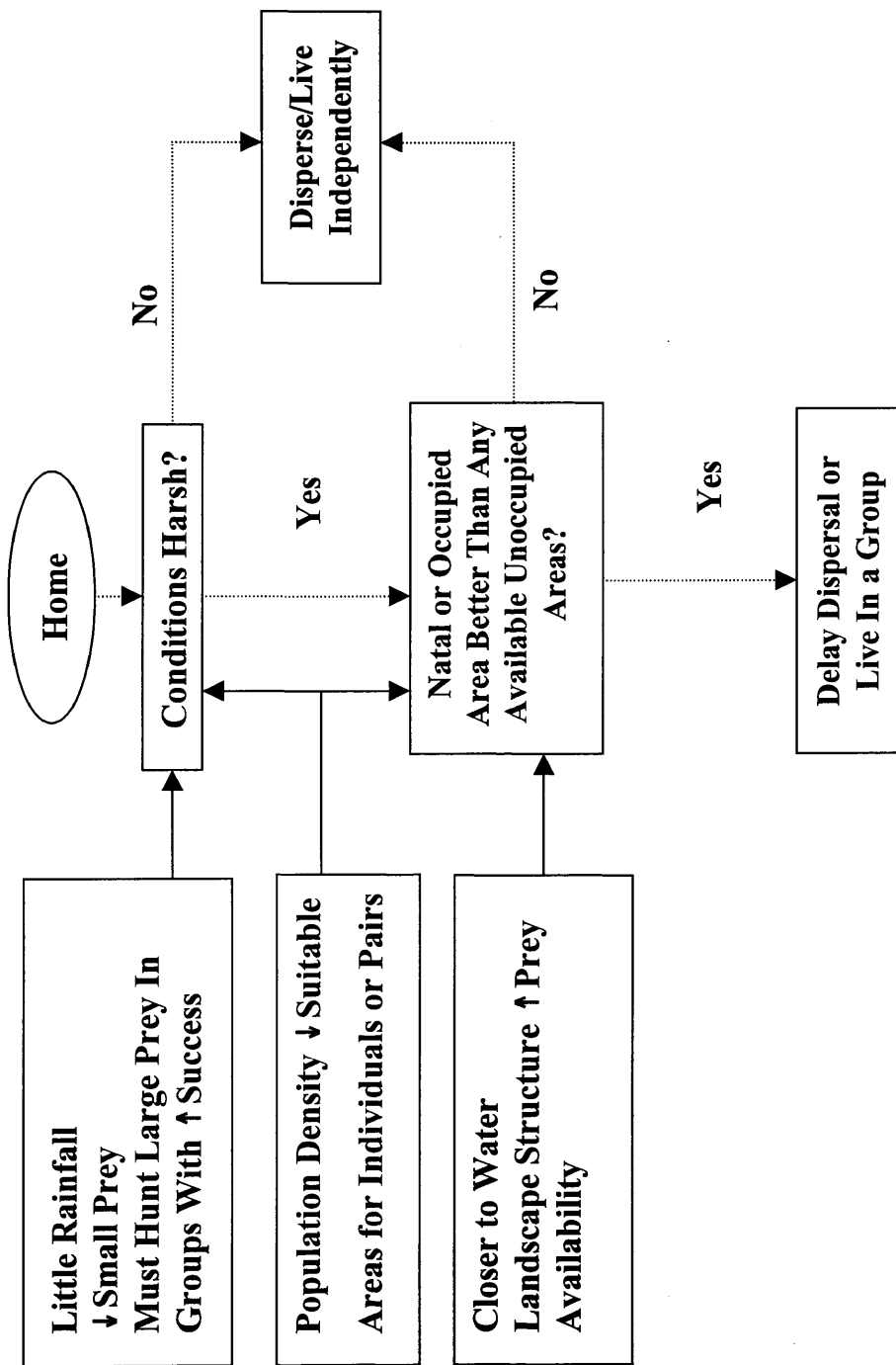


Figure 1. A graphical representation of an integrative conceptual model illustrating how environmental harshness, population density and habitat quality (boxes on left) might influence (solid arrows) decisions (dotted arrows) about whether young Harris' hawks disperse to live independently or delay dispersal (or aggregate in groups with unrelated individuals).

APPENDICES

Appendix A. Relative abundance and grouping at each of 8 Harris' hawk study sites, southern Texas, fall 2000. See Chapter 2 for methods and site codes (Fig. 1).

Study Site	Relative Abundance (#Hawks/100km) ^a	Index of Grouping (#Groups/#Observations) ^a
FR-W (n = 8)	22.47 ± 1.57	0.229 ± 0.060
RN-E (n = 8)	37.30 ± 4.10	0.215 ± 0.050
CH-W (n = 8)	17.58 ± 2.93	0.203 ± 0.054
KM-W (n = 8)	27.00 ± 2.92	0.173 ± 0.037
CU-W (n = 8)	3.94 ± 1.05	0.083 ± 0.083
DR-E (n = 4)	18.13 ± 3.44	0
NSG-E (n = 4)	12.32 ± 4.36	0
LA-E (n = 8)	2.61 ± 0.87	0

^amean value of all surveys at a site

Appendix B. Percent of observations in each percent cover category at various strata levels at 8 study sites for 50 m radius circles around random points and Harris' hawk locations, southern Texas, 2000. See Chapter 2 for methods and site codes (Fig. 1).

Cover Type	%Cover	FR-W		RN-E		CH-W		KM-W		CU-W		DR-E		NSG-E		LA-E		
		Points (n=30)	Hawks (n=94)	Points (n=30)	Hawks (n=112)	Points (n=30)	Hawks (n=63)	Points (n=30)	Hawks (n=89)	Points (n=30)	Hawks (n=16)	Points (n=30)	Hawks (n=26)	Points (n=30)	Hawks (n=24)	Points (n=30)	Hawks (n=30)	
Bare	0-5%	0	0	6.7	15.2	0	0	0	0	0	0	0	40.0	15.4	20.0	20.8	36.7	0
Ground	6-25%	0*	3.2	60.0	53.6	3.3*	30.2*	0	1.1	0	12.5	30.0	46.2	20.0	45.8	23.3	20.0	0
	26-50%	3.3*	24.5*	20.0	27.7	23.3*	39.7	30.0	12.4	23.3	37.5	23.3	26.9	43.3	16.7	20.0	60.0	0
	51-75%	13.3*	34.0	13.3	3.6	46.7*	20.6	33.3	32.6	40.0	43.8	6.7	11.5	13.3	8.3	6.7	10.0	0
	76-95%	56.7*	23.4*	0	0	23.3*	7.9	23.3	48.3	6.3	36.7	0	0	0	8.3	6.7	10.0	0
Short	>95%	26.7*	14.9	0	0	3.3	1.6	13.3	5.6	0	0	0	0	3.3	0.0	6.7	0	0
	0-5%	43.3	18.1	0	0	13.3	9.5	16.7	9.0	6.7	0	30.0	0	3.3	0	36.7	0	0
	6-25%	56.7	71.3	13.3	27.7	76.7	66.7	63.3	70.8	66.7	50.0	16.7	42.3	36.7	25.0	26.7	40.0	0
	26-50%	0	10.6	60.0	63.4	6.7	20.6	16.7	20.2	20.0	25.0	50.0	38.5	50.0	45.8	23.3	60.0	0
Herb	51-75%	0	0	23.3	8.9	3.3	3.2	3.3	0	6.7	25.0	3.3	19.2	6.7	25.0	10.0	0	0
	76-95%	0	0	3.3	0	0	0	0	0	0	0	0	0	3.3	4.2	3.3	0	0
	>95%	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0-5%	50.0*	25.5*	0	0	3.3	1.6	40.0*	27.0	13.3	0	0	0	3.3	0	10.0	10.0	0
Tall	6-25%	33.3	22.3	20.0	3.6*	40.0	15.9	16.7*	46.1*	43.3	31.3	10.0	23.1	16.7	25.0	13.3	10.0	0
	26-50%	16.7*	38.3	40.0	35.7	40.0	52.4	23.3	21.3	33.3	62.5	23.3	34.6	33.3	45.8	23.3	60.0	0
	51-75%	0*	10.6	33.3*	57.1	16.7	25.4	20.0*	5.6*	10.0	6.3	30.0	34.6	26.7	16.7	20.0	20.0	0
	76-95%	0*	3.2	6.7	3.6	0.0	4.8	0	0	0	0	10.0	7.7	16.7	4.2	26.7	0	0
Herb	>95%	0	0	0	0	0	0	0	0	0	0	26.7	0	3.3	8.3	6.7	0	0

*cells contributing to χ^2 significance between random points and hawk locations within a study site (Freeman-Tukey deviate test).

Appendix B. Continued.

Cover Type	%Cover	FR-W		RN-E		CH-W		KM-W		CU-W		DR-E		NSG-E		LA-E	
		Points (n=30)	Hawks (n=94)	Points (n=30)	Hawks (n=112)	Points (n=30)	Hawks (n=63)	Points (n=30)	Hawks (n=89)	Points (n=30)	Hawks (n=16)	Points (n=30)	Hawks (n=26)	Points (n=30)	Hawks (n=24)	Points (n=30)	Hawks (n=30)
Brush	0-5%	6.7	1.1	10.0*	0*	0	0	3.3	0	0	0	26.7	0	10.0	16.7	16.7	20.0
	6-25%	10.0	17.0	40.0*	19.6	30.0	12.7	13.3	9.0	10.0	6.3	23.3	26.9	43.3	41.7	50.0*	0*
	26-50%	23.3*	54.3*	30.0*	64.3*	50.0	54.0	46.7	57.3	30.0	56.3	23.3	19.2	30.0	41.7	30.0	10.0
	51-75%	50.0*	26.6*	16.7	16.1	16.7	30.2	20.0	28.1	46.7	37.5	20.0	34.6	13.3	0	0*	70.0*
	76-95%	6.7*	1.1	3.3*	0*	0	3.2	16.7	5.6	13.3	0.0	6.7	19.2	3.3	0	3.3	0
	>95%	3.3*	0*	0	0	3.3	0	0	0	0	0	0	0	0	0	0	0
Trees	0-5%	60.0	35.1	10.0*	0*	13.3	1.6	40.0	30.3	36.7	12.5	53.3	19.2	13.3	12.5	73.3*	10.0*
	6-25%	26.7	53.2	60.0	50.9	53.3	41.3	26.7	40.4	56.7	81.3	26.7	42.3	46.7	54.2	20.0*	70.0*
	26-50%	10.0	11.7	16.7*	45.5*	26.7	34.9	16.7	23.6	6.7	6.3	10.0	19.2	23.3	25.0	6.7	20.0
	51-75%	3.3	0	13.3*	3.6	3.3	17.5	13.3	5.6	0	0	10.0	19.2	10.0	8.3	0	0
	76-95%	0	0	0	0	3.3	3.2	3.3	0	0	0	0	0	6.7	0.0	0	0
	>95%	0	0	0	0	0	1.6	0	0	0	0	0	0	0	0	0	0

*cells contributing to X^2 significance between random points and hawk locations within a study site (Freeman-Tukey deviate test).

Appendix C. Mean landscape structure metrics calculated for areas with (H) and without Harris' hawks (NoH) at each of 8 study sites, southern Texas, 2000. See Chapter 2 for methods, site codes (Fig. 1) and metric codes (Table 1).

Level of Analysis	Site	%Cover		PD		MPS		ED		MSI		MPPD		MNN		IJI		SDI		SEI		
		H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H
Land-scape	FR-W	n=17	n=16	1.87	1.74	0.54	0.60	391.24	354.06	1.327	1.323	1.048	1.051	26.60	28.01	87.20	90.12	0.96	0.88	0.854	0.796	
	RN-E	n=13	n=6	1.03	1.34	1.00	0.79	366.51	353.34	1.460	1.380	1.058	1.055	29.19	28.48	52.84	55.35	0.87	0.76	0.748	0.667	
	CH-W	n=19	n=13	2.00	2.00	0.51	0.51	446.10	459.88	1.399	1.412	1.057	1.058	24.65	23.72	93.67	93.87	1.02	1.04	0.908	0.934	
	KM-W	n=18	n=12	2.04	2.04	0.49	0.49	432.86	438.07	1.399	1.413	1.060	1.063	23.76	23.88	91.65	90.64	1.02	1.00	0.898	0.888	
	CU-W	n=6	n=15	1.63	1.87	0.67	0.55	418.94	445.55	1.407	1.427	1.053	1.060	27.35	24.55	74.89	86.56	0.93	1.04	0.820	0.905	
	DR-E	n=12	n=9	0.58	0.37	1.81	3.20	207.48	157.83	1.398	1.406	1.056	1.058	34.42	58.62	36.34	31.69	0.58	0.47	0.498	0.531	
	NSG-E	n=9	n=12	1.06	1.12	1.06	1.07	351.39	360.08	1.492	1.458	1.063	1.060	27.93	33.53	71.67	56.53	1.02	0.89	0.876	0.762	
	LA-E	n=5	n=19	0.46	0.45	2.25	2.77	209.35	195.29	1.420	1.453	1.054	1.061	38.88	52.61	36.26	53.57	0.76	0.82	0.728	0.693	
	Woody	FR-W	36.33	42.55	0.55	0.43	0.92	1.37	232.86	220.23	1.376	1.410	1.052	1.058	26.21	27.11	80.93	81.48				
		RN-E	28.35	19.43	0.50	0.79	0.66	0.25	211.00	209.61	1.414	1.317	1.061	1.053	28.67	27.61	31.18	28.08				
CH-W		41.66	36.24	0.46	0.52	1.34	0.98	288.80	272.64	1.547	1.469	1.066	1.058	24.93	24.89	94.11	95.24					
KM-W		40.35	38.56	0.33	0.36	1.58	1.91	252.10	249.91	1.573	1.635	1.066	1.071	25.82	26.87	92.05	91.53					
CU-W		38.77	40.30	0.62	0.55	1.42	0.89	281.34	267.60	1.480	1.392	1.058	1.051	22.77	25.09	67.90	84.59					
DR-E		19.17	17.07	0.38	0.18	0.52	1.05	145.35	93.46	1.371	1.389	1.057	1.059	29.93	87.01	3.29	0.48					
NSG-E		27.00	38.09	0.37	0.44	0.88	0.98	201.49	265.09	1.516	1.520	1.069	1.068	27.24	29.64	42.91	37.79					
LA-E		28.47	15.62	0.26	0.17	1.61	1.22	133.22	71.86	1.370	1.372	1.050	1.056	32.20	70.90	2.21	6.70					

Appendix C. Continued.

Level of Analysis	%Cover		PD		MPS		ED		MSI		MPFD		MNN		IJI		SDI		SEI			
	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH	H	NoH		
Herbaceous	FR-W	15.39	12.08	1.01	0.97	0.18	0.12	198.53	173.30	1.245	1.231	1.045	1.043	27.36	28.71	85.03	86.74					
	RN-E	55.75	69.71	0.18	0.10	5.12	12.44	334.69	324.54	2.064	2.658	1.077	1.097	22.48	20.40	65.78	71.02					
	CH-W	27.57	27.18	0.96	0.97	0.51	0.33	262.52	280.21	1.326	1.355	1.049	1.056	24.39	23.16	93.94	92.06					
	KM-W	20.00	20.90	1.29	1.25	0.16	0.17	284.46	291.36	1.330	1.352	1.058	1.062	22.73	22.55	90.78	88.79					
	CU-W	44.62	37.05	0.41	0.51	1.72	0.88	325.11	329.80	1.587	1.636	1.060	1.072	23.16	22.75	75.69	88.06					
	DR-E	76.17	70.94	0.07	0.08	21.37	52.52	191.58	137.96	1.950	2.321	1.081	1.114	22.17	12.47	52.05	39.15					
	NSG-E	48.06	48.01	0.26	0.32	2.97	1.91	308.74	315.30	1.809	1.629	1.076	1.065	22.86	26.12	88.24	64.25					
	LA-E	64.08	52.57	0.11	0.12	6.86	8.15	191.11	162.46	1.796	1.858	1.076	1.087	26.12	26.49	55.82	75.53					
	Bare	FR-W	48.23	45.35	0.31	0.33	2.21	5.61	304.45	263.24	1.666	1.819	1.066	1.078	23.06	24.66	90.88	94.70				
	Ground	RN-E	15.78	10.72	0.35	0.44	0.50	0.30	140.57	119.73	1.354	1.338	1.050	1.053	36.18	36.93	49.89	46.42				
CH-W		30.77	36.56	0.58	0.51	0.67	0.88	292.13	315.53	1.526	1.578	1.067	1.066	24.39	22.26	92.49	93.34					
KM-W		39.60	40.46	0.41	0.42	1.15	1.91	283.17	282.87	1.546	1.674	1.068	1.071	24.30	24.44	91.70	91.14					
CU-W		16.61	22.57	0.59	0.82	0.34	0.32	182.72	244.47	1.360	1.377	1.053	1.061	33.86	24.82	87.31	85.93					
DR-E		2.84	21.06	0.13	0.17	0.21	1.10	27.86	95.93	1.220	1.336	1.043	1.048	46.15	84.23	23.50	19.46					
NSG-E		21.03	12.67	0.41	0.35	0.85	1.38	136.47	84.80	1.339	1.251	1.050	1.042	33.67	48.23	56.54	69.79					
LA-E		7.45	21.69	0.09	0.15	1.97	2.72	30.40	83.24	1.338	1.413	1.060	1.063	71.35	76.92	10.60	22.23					

Appendix D. Eight Harris' hawk study sites, southern Texas, 2000, and corresponding NOAA weather stations used for precipitation data in Chapter 3. See Chapter 2, Figure 1 for site codes.

Study Site	Weather Station(s)	Normal Annual Rainfall (mm)	2000 Departure From Normal (mm)
RN-E	Sarita 7 E	647	-182
DR-E	Chapman Ranch	749	-263
	Sarita 7 E	647	-182
NSG-E	Kingsville	701	-240
LA-E	Harlingen	707	-196
	Port Isabel	699	-173
FR-W	Carrizo Springs	550	-177
CH-W	Cotulla	587	-140
KM-W	Laredo 2	544	-120
CU-W	Freer 18 WNW	561*	-92

*denotes value based on average of available years 1979-1999 (n=12).

Appendix E. Total year (T) and breeding season (B) rainfall (mm) 1999-2001 at 8 southern Texas Harris' hawk study sites used in Chapter 3. See Chapter 2, Figure 1 for site codes.

Study Site	2001T	2001B	2000T	2000B	1999T	1999B
RN-E	633	172	466	187	785	224
DR-E	739	200	476	209	783	229
NSG-E	727	138*	461	314	807	186
LA-E	**	**	518	229	580	259
FR-W	**	**	373	150	456	206
CH-W	**	**	447	173	464	236
KM-W	**	**	424	211	420	202
CU-W	355+	98	469	201	473	300

*denotes no Harris' hawks were observed during fall surveys.

**denotes no Harris' hawk data collected at site during that time.

+denotes incomplete data for November, during which significant rainfall occurred

Appendix F. Mean landscape metric values for Harris' hawk group (G) and non-group (NG) areas at a fine (100 m) scale.

Land- scape	Site	%Cover		PD		MPS		ED		MSI		MPFD		MNN		LJI		SDI		SEI	
		G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG
Woody	Faith	n=10	n=25	2.82	3.00	0.39	0.37	565.93	545.67	1.39	1.30	1.06	1.05	26.85	36.88	87.05	81.37	0.92	0.85	0.84	0.77
	Rincon	n=8	n=24	1.90	2.12	0.56	0.53	492.82	547.90	1.46	1.53	1.07	1.08	37.54	29.51	45.76	40.71	0.65	0.78	0.61	0.80
	Chaparral	n=9	n=28	3.41	3.42	0.33	0.31	644.65	628.00	1.45	1.38	1.07	1.06	26.16	25.90	77.11	88.70	0.93	0.95	0.82	0.87
	Killam	n=5	n=33	2.97	3.43	0.36	0.31	545.42	606.60	1.34	1.36	1.06	1.06	25.36	28.99	95.00	88.42	0.82	0.95	0.75	0.85
	Calcasieu	n=1	n=7	2.24	3.28	0.45	0.32	512.82	595.97	1.33	1.34	1.05	1.06	23.60	32.64	58.17	83.03	0.79	0.89	0.72	0.81
Herb- aceous	Faith	29.32	37.72	0.93	1.02	0.37	0.58	266.19	291.18	1.32	1.36	1.05	1.06	26.32	24.58	80.94	72.55				
	Rincon	20.82	30.75	1.03	0.98	0.23	0.50	234.12	299.73	1.32	1.53	1.06	1.08	31.37	25.98	26.06	28.03				
	Chaparral	39.61	36.94	0.88	0.91	0.72	0.61	355.85	335.95	1.66	1.57	1.09	1.09	20.37	20.80	90.95	89.55				
	Killam	37.42	35.60	0.67	0.85	0.71	0.62	271.70	299.01	1.48	1.53	1.08	1.08	24.47	29.80	97.99	91.70				
	Calcasieu	43.59	22.11	0.64	1.64	0.68	0.14	358.97	282.69	1.63	1.23	1.09	1.05	20.00	25.53	50.33	67.26				
Bare Ground	Faith	22.58	13.38	1.05	1.14	0.27	0.16	274.67	187.31	1.41	1.23	1.07	1.04	28.37	46.12	82.16	85.45				
	Rincon	70.09	56.57	0.31	0.68	2.68	1.35	414.74	426.07	2.28	1.93	1.15	1.11	11.87	16.14	58.14	46.74				
	Chaparral	24.46	27.05	1.41	1.59	0.22	0.26	302.77	314.00	1.35	1.29	1.06	1.05	24.67	25.16	69.26	88.71				
	Killam	15.54	20.97	1.49	1.71	0.10	0.13	248.97	312.96	1.24	1.28	1.04	1.05	23.67	25.68	90.89	85.83				
	Calcasieu	53.85	57.70	0.96	0.62	0.56	1.41	358.97	433.96	1.35	2.05	1.07	1.14	22.76	23.18	50.33	90.96				
Bare Ground	Faith	48.10	48.90	0.83	0.83	0.80	0.97	372.87	367.79	1.56	1.64	1.09	1.09	20.57	23.97	90.14	82.79				
	Rincon	9.09	12.01	0.55	0.44	0.22	0.62	112.28	136.71	1.27	1.70	1.04	1.09	44.73	25.24	41.17	56.82				
	Chaparral	35.70	36.01	1.09	0.93	0.55	0.52	382.83	357.60	1.65	1.62	1.10	1.09	21.10	21.84	67.27	84.20				
	Killam	47.04	43.18	0.81	0.87	1.28	1.10	341.58	356.97	1.71	1.75	1.09	1.10	13.54	24.53	95.23	86.72				
Calcasieu	2.56	20.19	0.64	1.02	0.04	0.24	51.28	228.44	1.00	1.33	1.00	1.05	28.28	51.72	100.00	77.97					

Appendix G. Mean landscape metric values for Harris' hawk group (G) and non-group (NG) areas at an intermediate (500 m) scale.

Site	%Cover		PD		MPS		ED		MSI		MPFD		MNN		IJI		SDI		SEI	
	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG
Land- scape	Faith	n=7	0.23	1.83	0.53	0.55	410.06	378.07	1.34	1.32	1.05	1.05	26.34	26.78	86.03	88.02	0.99	0.94	0.87	0.84
	Rincon	n=4	0.22	1.09	1.12	0.95	351.87	373.02	1.49	1.45	1.06	1.06	29.63	29.00	53.09	52.73	0.89	0.86	0.76	0.74
	Chaparral	n=6	0.20	1.90	0.46	0.54	479.26	430.80	1.41	1.40	1.06	1.06	24.02	24.94	85.93	97.25	1.05	1.01	0.89	0.92
	Killam	n=5	0.17	2.03	0.49	0.49	436.77	431.36	1.40	1.40	1.06	1.06	23.92	23.70	97.21	89.51	0.98	1.04	0.90	0.90
	Calcasieu	n=1	0.08	1.59	0.56	0.69	359.26	430.87	1.33	1.42	1.05	1.05	30.50	26.72	58.52	78.16	0.84	0.95	0.60	0.86
Woody	Faith	32.68	38.89	0.58	0.52	0.73	1.06	227.70	236.48	1.37	1.38	1.05	27.48	25.32	83.04	79.45				
	Rincon	27.19	28.86	0.49	0.50	0.60	0.69	197.01	217.22	1.40	1.42	1.06	29.70	28.21	21.94	35.29				
	Chaparral	42.24	41.38	0.47	0.45	1.37	1.32	325.95	271.66	1.64	1.51	1.07	23.88	25.42	86.78	97.49				
	Killam	37.22	41.56	0.36	0.32	1.76	1.51	243.49	255.41	1.59	1.57	1.07	26.89	25.41	99.58	89.15				
	Calcasieu	67.81	32.96	0.12	0.73	5.89	0.53	279.94	281.62	1.94	1.39	1.08	20.92	23.14	61.47	69.19				
Herb- aceous	Faith	18.72	13.05	1.02	1.01	0.22	0.15	225.39	179.73	1.27	1.23	1.05	26.02	28.29	81.17	87.73				
	Rincon	55.02	56.07	0.18	0.18	3.89	5.66	325.90	338.60	1.84	2.16	1.07	22.48	22.49	71.59	63.19				
	Chaparral	26.26	28.17	1.09	0.90	0.27	0.62	275.51	256.53	1.30	1.34	1.05	24.14	24.50	85.99	97.60				
	Killam	19.16	20.32	1.32	1.28	0.15	0.16	278.85	286.61	1.33	1.33	1.06	23.13	22.57	94.88	89.20				
	Calcasieu	21.49	49.24	0.67	0.36	0.32	1.99	229.79	344.17	1.42	1.62	1.07	30.61	21.67	55.22	79.78				
Bare Ground	Faith	48.54	48.00	0.32	0.30	1.57	2.66	320.79	293.01	1.59	1.72	1.06	23.35	22.86	89.75	91.68				
	Rincon	17.72	14.92	0.22	0.41	0.77	0.38	138.79	141.36	1.46	1.31	1.06	36.54	36.02	35.12	56.45				
	Chaparral	31.47	30.45	0.65	0.55	0.60	0.71	308.34	284.65	1.50	1.54	1.06	23.64	24.74	85.62	95.66				
	Killam	43.62	38.05	0.38	0.42	1.49	1.02	304.37	275.02	1.61	1.52	1.07	22.18	25.11	96.71	89.78				
	Calcasieu	10.64	17.80	1.00	0.51	0.11	0.38	156.60	187.94	1.19	1.39	1.04	31.58	34.31	62.24	92.33				

Appendix H. Mean landscape metric values for Harris' hawk group (G) and non-group (NG) areas at a broad (1000 m) scale.

Land- scape	Site	%Cover		PD		MPS		ED		MSI		MPFD		MNN		III		SDI		SEI	
		G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG	G	NG
Woody	Faith	38.98	41.69	0.49	0.48	1.02	0.96	229.67	242.16	1.30	1.32	1.04	1.05	25.19	24.25	70.27	65.59				
	Rincon	18.86	29.27	0.46	0.48	0.42	0.65	153.30	216.57	1.34	1.36	1.05	1.06	30.26	28.17	25.96	25.29				
	Chaparral	36.95	39.08	0.44	0.50	0.85	0.88	294.34	261.29	1.48	1.40	1.06	1.06	24.15	24.54	76.98	91.17				
	Killam	45.83	36.68	0.25	0.36	2.30	1.12	246.69	242.00	1.53	1.44	1.06	1.06	26.01	25.82	81.40	70.27				
	Calcasieu	65.75	32.55	0.16	0.68	4.11	0.67	241.14	260.01	1.41	1.35	1.04	1.05	23.12	23.49	57.24	76.97				
Herb- aceous	Faith	17.19	11.39	0.94	1.04	0.21	0.11	206.43	168.49	1.26	1.21	1.05	1.04	26.54	27.51	70.18	75.80				
	Rincon	55.77	57.16	0.18	0.13	3.28	6.20	313.26	335.95	1.58	1.77	1.06	1.06	21.88	22.85	67.36	51.49				
	Chaparral	29.24	28.28	0.94	0.86	0.37	0.34	270.93	257.38	1.32	1.31	1.05	1.05	23.21	23.97	77.70	89.62				
	Killam	18.37	21.00	1.26	1.15	0.15	0.19	266.91	283.62	1.32	1.36	1.06	1.06	22.94	22.55	80.02	68.93				
	Calcasieu	23.83	45.12	0.54	0.37	0.44	1.37	242.16	348.61	1.48	1.51	1.07	1.06	24.60	21.34	57.91	83.08				
Bare Ground	Faith	43.75	46.85	0.31	0.24	1.45	2.05	297.10	292.24	1.53	1.55	1.06	1.06	23.81	23.55	74.47	77.95				
	Rincon	24.78	12.90	0.26	0.46	0.93	0.27	176.83	144.30	1.39	1.28	1.05	1.05	36.04	32.22	29.28	42.08				
	Chaparral	33.77	32.63	0.55	0.46	0.70	0.77	304.91	291.94	1.49	1.51	1.06	1.07	23.68	23.92	77.48	89.72				
	Killam	35.35	41.59	0.44	0.33	1.09	1.50	259.93	288.09	1.45	1.48	1.06	1.06	24.50	24.24	82.14	71.90				
	Calcasieu	10.35	22.33	0.82	0.61	0.13	0.39	147.70	236.03	1.25	1.41	1.05	1.06	29.13	26.62	62.92	82.10				