COMPARATIVE WINTER ECOLOGY OF THE NORTHERN HARRIER AND RED-TAILED HAWK IN OKLAHOMA

By

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PREFACE

I truly enjoyed studying wintering raptors in Oklahoma. Studying a group of organisms of my own choice greatly enhanced my education at Oklahoma State University.

This thesis was written in a form to facilitate publication. Each chapter is a scientific paper with these sections: Introduction, Methods, Results, Discussion, Acknowledgements, and Literature Cited. The tables for each chapter are consecutively numbered through the whole thesis and are given in Appendix A. The figures are also consecutively numbered through the whole thesis and are given in Appendix B.

I would especially like to thank a number of people who withstood the wind and cold to help collect behavioral data: Tim Reid, Joe Roberts, Grant Huggins, Paul Louderback, Mark Shipley, and Lisa Cook. Their help "in the field" was as important as any I received in completing this study.

David Branecky of Oklahoma Gas and Electric Company (OG&E) provided weather data from the OG&E weather tower on my study site. I would also like to thank OG&E for the permission to use their land surrounding the Sooner Generating Station.

Thanks are extended to my graduate committee: Dr. Scott Shalaway, Dr. Stanley Fox, and Dr. Larry Talent. Special thanks go to Dr. Shalaway, my major adviser, for his insightful discussions about this study and on other aspects of graduate school. Dr. Jim Lish edited my

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I am grateful for financial assistance from the Oklahoma State University Department of Zoology, Oklahoma Cooperative Wildlife Research Unit, and Payne County Audubon Society.

Finally and most importantly, thanks go to the people close to me. My parents, Larry and Margaret Carter, profoundly successful as individuals and parents, continue to be an inspiration to me. Thanks go to my wife, Joanne, who hypothesized with me regarding why hawks do what they do. We completed our theses together; she appreciated my support in her decision to return to school, but not nearly as much as my statistical help. I also appreciate her support, but not nearly as much as her help in the typing and editing of my manuscripts.

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CHAPTER I

WEATHER AND WINTERING NORTHER HARRIERS AND RED-TAILED HAWKS IN OKLAHOMA

Introduction

A variety of weather factors affect flight behavior of raptors (Craighead and Craighead 1956, Schnell 1967, Ueoka and Koplin 1973, Grubb 1977a, Bildstein 1978, Wakeley 1978). However, these studies used univariate analyses to determine each weather variable's effect on raptor behavior. Schnell (1967) suggested that a multidimensional analysis might permit a more precise determination of the relative importance of several weather variables as well as their interaction with each other. Schnell (1967) concluded Rough-legged Hawks (*Buteo lagopus*) reacted to the end product of several related and interacting variables, but wind speed had the most marked effect on Rough-leg flight behavior. Henty (1977) studied the soaring of several tropical raptors. Soaring increased as ambient temperature increased. In one of the few multivariate approaches, Preston (1981) found Red-tailed Hawks (*Buteo jamaicensis*) soared more as wind velocity and solar radiation increased and as cloudiness and relative humidity decreased. Although Preston (1981) did not differentiate between different types of soaring (declivity and thermal, Cone 1962), he reported the association of soaring and wind may be due to the Red-tails using declivity air currents to soar. Cone (1962) listed several prerequisites for thermal soaring to occur, including low wind speeds. In contrast, high winds and variations in habitat structures (hills, tree rows, etc.) create declivity currents exploited by soaring birds. Soaring above hillsides is especially common among raptors (Pennycuick 1972). Preston (1981) concluded that studies designed to determine the effect of both thermal and declivity soaring opportunities on Buteo species distributions would prove useful in evaluating the importance of soaring as an adaptive activity.

Although soaring is conspicuous in raptors, other behaviors may have equally important adaptive advantages in relation to weather conditions. For example, Black-billed Magpies (Pica pica) perch on the ground on windy and cold days to minimize heat loss (Mugaas and King 1981).

The objective of this study was to examine the effect of weather conditions on a relatively large number of behaviors recorded for two raptor species wintering in northcentral Oklahoma. Northern Harriers (Circus cyaneus) and Red-tailed Hawks were observed to determine how weather affected their daily activities. The Northern Harrier is a widely foraging predator (Pianka 1983) that hunts with a low coursing flight (Trautman 1944, Schipper et al. 1975), frequently pouncing on prey located via visual and acoustical cues (Rice 1982, 1983). The Red-tailed Hawk is a sit-and-wait predator (Pianka 1983) that visually scans the ground for prey and makes short directional flights from a perch to capture prey.

Methods

Behavioral Observations

I observed Northern Harriers and Red-tailed Hawks in Noble County, Oklahoma, during winter (November-February) in 1982-1983 and 1983-1984. The study site was composed of a mosaic of tallgrass prairie, mowed prairie, grazed fields and bottomland woods. Behavioral observations were conducted from hills on the study site which allowed me to view hawks at long distances with a 25x spotting scope and 8x binoculars. Activity budgets consisted of 15 minute focal samples (Altmann 1974) during which I recorded durations of all behaviors to the nearest second. Durations were timed with a stopwatch attached to binoculars. Cumulative time for each behavior was dictated into a tape recorder as the focal bird changed behaviors. I continued to collect 15 minute samples on a bird until it was lost from view, and only complete samples were analyzed for this paper.

Hourly means of wind velocity, ambient temperature, percent solar radiation, precipitation and centimeters snow on the ground were later coded with the appropriate behavioral sample. These weather data were obtained from a National Weather Service tower located on the study site.

Statistical Analysis

Multivariate discriminant analyses were used to determine the effects and interaction of weather variables on the frequency of occurrence of behaviors. In this analysis, durations of behaviors were reclassified into frequencies (e.g., a behavior lasting 120 seconds was assigned a frequency of two). The conversion to minute point samples (Altmann 1974) was made to avoid assigning a frequency of one to behaviors lasting for different lengths of time.

Discriminant analysis was used to plot behavioral relationships within canonical space. Canonical variates analysis refers to classical discriminant analysis with the goal of dimension reduction and description of group relationships (Neff and Marcus 1980). Each derived new canonical variate summarizes the most among group variance (Cooley and Lohnes 1971). Each successive canonical variate summarizes the most among groups variation left over. Canonical variates analysis is analagous to discriminant analysis in a two behavior comparison. As the relationships of more behaviors are examined, the analysis should properly be called canonical variates analysis (Neff and Marcus 1980).

The assumptions and decisions necessary for canonical analysis have long been known (Green 1971, 1974) but rarely adhered to in ecological studies (Williams 1983). In the cases where violation is possible in this study (multiple behavior comparisons), I do not report multivariate test statistics. To confirm some behavioral relationships I conducted two group multivariate analysis of variance (MANOVA) and plotted the two behaviors in frequency histograms over the single canonical variate. In these cases the assumptions of multivariate discriminant analysis were met and test statistics are reported. In cases of multiple behavioral comparison, behavior centroids with 95% confidence circles were plotted in canonical space (Overall and Klett 1972, Pimentel and Frey 1978, Neff and Marcus 1980). Their area is a function of sample size for each behavior (Pimentel and Frey 1978, Neff and Marcus 1980). Each of the bivariate graphs contains original variable vectors which indicate magnitude (length) and direction of "push" for each variable (Overall and Klett 1972, Pimentel and Frey 1978). In general a group centroid located just beyond a long variable vector will represent a group having large measurements for that variable. A group occurring in the opposite direction of the vector is associated with small values for the variable (Pimentel and Frey 1978).

Although the robustness of these techniques is thought to be good, actual documentation is poor (Williams 1983). I chose this analysis for five reasons:

1. the weather parameters I collected fit criteria for parameter selection for a multivariate analysis (Green 1971, Pimentel and Frey 1978).
2. a multidimensional analysis of this specific problem has been suggested (Schnell 1967). The method also avoids assigning complete behavioral control to one weather variable (Preston 1981).
3. univariate analysis proved cumbersome in reporting results but generally agrees with the multivariate analysis.
4. reliance can be placed on these statistics as an aid in interpreting relationships even under failure of the assumptions (Pimentel and Frey 1978).
5. the data determine the outcome of the analysis (Pimentel and Frey 1978).

Results and Discussion

Fourteen behaviors were cataloged for both species (Table 1). Five of these behaviors (flight with prey, perching with prey, prey handling, successful strikes, and unsuccessful strikes) occurred infrequently and were related. These five behaviors were lumped into one category called prey associated behaviors. A total of 514 hours of behavioral data was collected for the two winters. Seventy of these hours were used to establish the behavioral catalogs (Fagen 1978) of both species and were not used in this analysis. The remaining hours consisted of 831 15 minute samples for the Northern Harrier and 944 for the Red-tailed Hawk.

A wide range of weather values were observed during behavioral observations (Table 2). Weather variables were correlated indicating a multivariate analysis should be used to judge their individual and interacting effect on raptor behavior (Table 3). Observations were attempted during snow and rain storms, but due to visibility problems, few samples were collected. Thus precipitation's effect on behavior was not analyzed. In general raptor activity was depressed during periods of precipitation. Craighead and Craighead (1956), Schnell (1967) and Bildstein (1978) found the same to be true in their studies.

Red-tailed Hawks and Weather

The bivariate plot of Red-tail behaviors shows four distinct behavioral groups (Figure 1). Structure coefficients indicate solar radiation is positively correlated with canonical variate I (Table 4). Wind speed is highly correlated with canonical variate II (Table 4). The most frequently observed Red-tail behaviors, perched and directional flight, show no association with weather variables. They are located about the grand centroid (0,0) which represents a multivariate mean for all weather variables. Since these two behaviors occur on a daily basis, their occurrence is expected to coincide with weather averages. Red-tails spend a large portion of the day perched (84%); when moving between perches, they fly directionally (2%). I call these two behaviors primary behaviors, because they occupy 86% of the Red-tailed Hawks' daily activity budget.

The other Red-tail behaviors are located away from the grand centroid indicating a relationship with a single or multiple weather effect. Hovering, perching on the ground, and declivity soaring are located together away from the grand centroid along the wind velocity vector (Figure 1). Red-tails rarely perch on the ground, but they may when wind speeds are high. Warmer temperatures and lower wind velocities exist at ground level (Mugaas and King 1981). Red-tails may exploit this effect to conserve energy on windy days. Red-tails also declivity soar and hover more often on windy days. Again, Red-tails do not habitually hover, but on windy days more Red-tails are seen hovering when searching for prey. Rough-legged Hawks habitually hover and use these hovers as "mobile perches" to search for prey (Johnson 1981). Ospreys (_Pandion_ _haliaetus_) also hunt while hovering with the same method, only over water (Grubb 1977b). On windy days Red-tails exploit the wind to inspect the ground for prey. Hovering during high winds is energetically less expensive than on calm days (Tarboton 1978). The longest Red-tail hover I observed lasted 72s and occurred at 42 kph. Located in the same canonical space, declivity soaring also requires high wind velocities (Cone 1962).

Thermal soaring is located away from the primary behaviors along the solar radiation vector (Figure 1). As Cone (1962) stated, thermal soaring requires high solar radiation and low wind velocity. To test whether wind velocity controlled the occurrence of both thermal and declivity soaring, I conducted multivariate analysis of variance (MANOVA) and plotted the frequencies of both behaviors on the new single canonical variate. The two types of soaring were associated with different weather conditions ($F=42.05$, $p < 0.0001$). The percent thermal and declivity soaring histogram shows the separation along the canonical axis (Figure 2). Structure coefficients confirm the separation is largely due to wind velocity with a lesser effect from solar radiation (Table 5). This relationship suggests Red-tails may declivity soar on windy days. However, thermal soaring requires low wind velocities and high solar radiation. Thus, thermal soaring is separated from the primary behaviors by a synergistic effect of low wind speeds and high solar radiation (Figure 1).

Also located away from the primary behaviors are prey associated behaviors. These behaviors are located opposite the wind speed vector, indicating Red-tails are seen more often with prey at lower wind velocities. In addition, the location may be due to the combined "push" of the solar radiation and temperature vectors. However, since Red-tails are visual hunters, I would expect them to be more successful in capturing prey on calm days. The Red-tail hovering seems to be a response to the difficulty of searching for prey from a perch on windy days. They often drop off a perch, glide to a spot to search, hover while looking down and then either attack the prey or return to the perch. These mobile perches seem particularly adaptive considering their low energetic cost during high winds (Tarboton 1978).

Northern Harriers and Weather

Northern Harrier behaviors showed some of the same relationships as Red-tailed behaviors (Figure 3). Again wind velocity and solar radiation are most important in defining the canonical space (Table 6). The most common daily activities of the harrier are clustered together around the grand centroid. Harriers course while searching for prey, hover on occasion when spotting or hearing prey, and then pounce on the prey. Bildstein (1978) also found that hovering of harriers is associated with prey captures. While coursing, harriers often drop to the ground to perch and preen. All five of these primary behaviors account for a large portion of harrier daily activities (93%) and are clustered together in the same canonical space.

Harriers spent most of the day perched on the ground, however they did perch and preen on structures such as fence posts. Harriers perched on structures more with snow on the ground and during low wind velocities (Figure 3). Presumably harriers perch on structures to avoid the snow on the ground and on calm days when an exposed perch does not subject them to wind. Additionally, preening on structures is associated with less wind and more snow on the ground than perching on structures.

As with the Red-tail, thermal and declivity soaring in the harrier are separated from daily behaviors by solar radiation and wind velocity (Figure 3). Again, I conducted a MANOVA ($F=55.79$, $p < 0.0001$) and plotted the percent occurrence of each soaring behavior over the single canonical axis (Figure 4). The relationship was similar to the Red-tail histogram, i.e., wind velocity controls whether thermal or declivity soaring occurs (Table 7).

Harriers and Red-tails Compared

Since both species had similar relationships between weather variables and behaviors, I plotted their behaviors in the same canonical space (Figure 5). The primary behaviors that comprise daily activities for both species were again clustered about the grand centroid. These are the behaviors I saw on a daily basis regardless of weather conditions.

Behaviors for both species associated with high wind velocities were located together to the far right along canonical axis I. Canonical axis I is highly correlated with wind velocity (Table 8). Thermal soaring for both species was separated from other behaviors along canonical axis II which is highly correlated with solar radiation (Table 8). I conducted MANOVA to determine if different weather conditions are associated with Red-tail and Northern Harrier thermal soaring. Both species exploit the same conditions for thermal soaring (F=0.83, p = 0.5098). Again, harrier perching on structures and preening on structures was located away from the primary behaviors, separated mainly by lower wind velocities and more snow on the ground.

Raptor Behavior and Weather

As Preston (1981) pointed out, a multivariate analysis avoids oversimplification of weather's effect on raptor behavior, especially attributing behavioral control to only one weather variable. However, in doing so the actual complexity of weather's effect on raptor behavior is fully exposed. In general, both species exhibit primary or daily behaviors. The primary activities do not exploit weather conditions, instead they are performed at regular intervals, regardless of weather conditions. However, both species also exhibit other behaviors that specifically exploit certain weather conditions.

The Northern Harrier actively hunts prey and exhibits a wide variety of primary behaviors. The Red-tailed Hawk passively hunts prey and exhibits only two primary behaviors, perching and directional flight. Perching Red-tails may carry out additional primary functions that may go undetected by a human observer. While perched, Red-tails may search for prey, search for mates, thermoregulate, and occasionally preen. Their presence in an area may also signify a territory to keep other birds out. Conversely, the harrier has a definite periodicity in daily activities where coursing and hovering are mixed with bouts of loafing on the ground and preening on the ground (see also Bildstein 1978). Thus, it is unlikely the harrier can carry out daily activities while hunting and must allocate portions of the day to complete other activities. This periodicity is composed of a series of primary behaviors which are used for a specific purpose when the harrier is not flight hunting.

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I would like to thank a number of people who withstood the wind and cold to help collect behavioral data: Tim Reid, Joe Roberts, Grant Huggins, Paul Louderback, Mark Shipley, and Lisa Cook. David Branecky of Oklahoma Gas and Electric Company (OG&E) provided weather data from the OG&E tower on my study site. I would also like to thank OG&E for the permission to use their land surrounding the Sooner Generating Station.

Thanks are extended to my graduate committee: Scott Shalaway, Stanley Fox, and Larry Talent. Their comments along with Jim Lish's improved the study. My wife, Joanne, greatly helped in typing and editing the manuscript.

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LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 49:227-265.

Bildstein, K. L. 1978. Behavioral ecology of Red-tailed Hawks (Buteo jamaicensis), Rough-legged Hawks (B. lagopus), Northern Harriers (Circus cyaneus), American Kestrels (Falco sparvarius) and other raptorial birds wintering in south-central Ohio. Ph.D. diss., Ohio State Univ., Columbus, Ohio.

Fagen, R. M. 1978. Repertoire analysis. Pages 25-42 in P. W. Colgan, editor. Quantitative Ethology. John Wiley and Sons, New York, New York.

Cooley, W. W. and P. R. Lohnes. 1971. Multivariate data analysis. John Wiley and Sons, Inc. New York, New York.

Cone, C. D. Jr. 1962 Thermal soaring of birds. Am. Scientist 50:180-209.

Craighead, J. J. and F. C. Craighead. 1956. Hawks, owls, and wildlife. Dover Publ. Inc. New York, New York.

Green, R. H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. Ecology 52:543-556.

Green, R. H. 1974. Multivariate niche analysis with temporally varying environmental factors. Ecology 55:73-83.

Grubb, T. C. Jr. 1977a. Weather-dependent foraging in ospreys. Auk 94:146-149.

Grubb, T. C. Jr. 1977b. Why ospreys hover. Wilson Bull. 89:149-150.

Henty, C. S. 1977. Thermal soring of raptors. Br. Birds 70:471-475.

Johnson, D. R. 1981. The study of raptor populations. The Univ. Press of Idaho. Moscow, Idaho.

Mugaas, J. N. and J. R. King. 1981. The annual variation in daily energy expenditure of the Black-billed Magpie: a study of thermal and behavioral energetics. Stud. Avian. Biol. 5:1-78.

Neff, N. A. and L. F. Marcus. 1980. A survey of multivariate methods for systematics. Privately published. New York, New York.

Overall, J. E. and C. J. Klett. 1972. Applied multivariate analysis. McGraw Hill Co., New York, New York.

Pimentel, R. A. and D. F. Frey. 1978. Multivariate analysis of variance and discriminant analysis. Pages 247-274 in P. W. Colgan, editor. Quantitative ethology. John Wiley and Sons, New York, New York.

Pennycuick, C. J. 1972. Animal flight. Edward Arnold, London, England.

Pianka, E. R. 1983. Evolutionary ecology. 3rd ed. Harper and Row, Publishers, New York, New York.

Preston, C. R. 1981. Environmental influence on soaring in wintering Red-tailed Hawks. Wilson Bull. 93:350-356.

Rice, W. R. 1982. Acoustical location of prey by the Marsh Hawk: adaptation to concealed prey. Auk 99:403-413.

Rice, W. R. 1983. Sensory modality: an example of its effect on optimal foraging behavior. Ecology 64:403-406.

Schipper, W. J. A., L. S. Buurma, and P. H. Bossenbroek. 1975. Comparative study of hunting behavior of wintering hen-harriers Circus cyaneus and marsh harriers Circus aeruginosus. Ardea 63:1-29.

Schnell, G. D. 1967. Environmental influence on the incidence of flight in the Rough-legged Hawk. Auk 84:173-182.

Tarboton, W. R. 1978. Hunting and energy budget of the Black-shouldered Kite. Condor 80:88-91.

Trautman, M. B. 1944. Flight hunting of a marsh hawk. Wilson Bull. 56:117.

Ueoka, M. L. and J. R. Koplin. 1973. Foraging behavior of ospreys in northwestern California. Raptor Res. 7:32-38.

Wakeley, J. S. 1978. Hunting methods and factors affecting their use by Ferruginous Hawks. Condor 80:327-333.

Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64:1283-1291.

CHAPTER II

ENERGETICS OF WINTERING NORTHERN HARRIERS AND RED-TAILED HAWKS

Introduction

Recent raptor studies have stressed the importance of determining energy budgets from activity budgets of free-living raptors (Mosher and Matran 1974, Tarboton 1978, Wakeley 1978a, 1978b, Johnson 1981, Bessinger 1983, and Stalmaster 1983). Koplin et al. (1980) compared time budget energetic calculations to independent measures of energy metabolism of captive raptors with acceptable accuracy (Walsberg 1983). Sensitivity analyses on variables that are estimated in energy budget calculations from time budgets also suggest the method is robust and sufficiently accurate (Ettinger and King 1980, Wakeley 1978a, 1978b, and Stalmaster 1983). The accuracy of these models depends primarily on estimates of flight coefficients (FC) since small variations in flight time produce large variations in daily energy expenditure (Mugaas and King 1981). A flight coefficient is the multiple of the basal metabolic rate expressing energy expenditure of each type of flight (Koplin et al. 1980). However, since actual measurements of flight coefficients for a number of flight types are few, most investigators estimate coefficients for unmeasured flight types. In some studies all flight types were lumped into one category and assigned one flight coefficient (Tarboton

1978, FC = 17.2, Koplin et al. 1980, FC = 13.7). In both of these studies the species studied exhibited few flight behaviors and a single FC assignment seems reasonable. However, Tarboton (1978) emphasized different types of flight have different costs. In cases where raptors' activities are composed of larger periods of soaring or other types of energetically inexpensive flight, the assignment of one flight coefficient to all behaviors will unnecessarily overestimate flight expenditures. Some investigators have assigned different flight coefficients to different flight types (Wakeley 1978a, 1978b, Stalmaster 1983).

In this study, I used published energetic formulae to calculate daily winter energy budgets of two raptor species using different hunting strategies. The Northern Harrier is a widely foraging predator (Pianka 1983) that hunts with a low coursing flight (Trautman 1944, Schipper et al. 1975), frequently pouncing on prey that is located via visual and acoustical cues (Rice 1982, 1983). The Red-tailed Hawk is a sit-and-wait predator (Pianka 1983) that visually scans the ground for prey and uses short directional flights from a hunting perch to capture prey.

Methods

Behavioral observations were conducted in northcentral Oklahoma during the winters of 1982-1983 and 1983-1984. The study site consisted of tallgrass prairie, mowed prairie, grazed pasture, and bottomland woods. Observations were limited to a 4.5 km^2 area north of the Sooner Generating Station of Oklahoma Gas and Electric in Noble County. During the first winter the study site was predominantly tallgrass prairie; however, the study site was mowed for hay in September of the 1983-1984 field season. Observations were collected throughout the day from November through February. Time budget data were collected from hills on the study site which allowed me to view hawks at long distances with a 25x spotting scope and 8x binoculars. Activity budgets consisted of 15 minute focal samples (Altmann 1974) during which I recorded the durations of all behaviors to the nearest second. A total of 514 hours of behavioral data was collected for the two winters. Seventy of these hours were used to establish the behavioral catalogs (Fagen 1978) of both species and were not used in the analysis. The remaining hours consisted of 831 samples on the Northern Harrier and 944 on the Red-tailed Hawk. Fourteen behaviors were cataloged for both species; however, only six were used to calculate energy budgets (Table 9).

The two species' energy budgets were calculated with a modified formula from Koplin et al. (1980) so as to incorporate different flight coefficients for each flight type. I chose a flight coefficient (FC) of 13.7 for hovering, since 13.7 represents maximum steady state power output for flying birds (King 1974, Koplin et al. 1980). A minimum value of 3.5 was used for soaring based on gliding and soaring flight measurements on a Herring Gull (Larus argentatus) (Bartholomew 1977, Stalmaster 1983). Having assigned FC to the most expensive and least expensive flight types from actual measurements, I made assignments to the three intermediate flight types based on relative amount of flapping for each behavior. Declivity soaring (Cone 1962) consists of occasional flapping and occurs in turbulent air and probably requires two or more times the power input of flight in smooth air (Bartholomew 1977). Therefore, I assigned declivity soaring a FC value of 7.0 (2 times thermal soaring, 3.5). Harriers primarily course into the wind but flap more than when using declivity soaring. I chose a FC of 9 for coursing. Directional flight is used by both birds and consists of flapping and gliding flight. Because directional flight requires more flapping than coursing, I used a FC of 10. Although the flight coefficients for coursing, directional, and declivity soaring are somewhat arbitrary, calculation of expenditures using one flight coefficient is even less accurate (see discussion). I used mean mass of Northern Harriers (570g) and Red-tailed Hawk (1122g) from Craighead and Craighead (1956) in the energetic calculations.

The daily observed intake of prey is balanced against daily energy expenditures. During behavioral observations, I recorded successful strikes (prey capture attempts) and noted where the prey was eaten. After the focal bird had finished eating and left the site, I tried to find prey remains to identify the prey. Of the prey items I saw captured, I identified 13 of 21 prey (62%) for the Northern Harrier and 9 of 23 prey (39%) for the Red-tailed Hawk. In all cases the prey was a hispid cotton rat (Sigmodon hispidus). I snap trapped and weighed cotton rats on the study site during the first week in March of both winters to determine biomass available to the hawks. I chose this period to trap rodents to avoid affecting raptor behavior (observations ceased in February) and to avoid trapping raptor prey populations. Total energetic content of each rodent was calculated with an assimilation coefficient of 0.82 (Koplin et al. 1980) and a caloric density of live rodent biomass of 2.14 kcal/g (Brisbin 1970).

Results

Northern Harriers were seen with prey at a rate of 0.1685 prey/hour, and Red-tailed Hawks at 0.1907 prey/hour. Thus, total energy consumed (TEC) is a product of the length of time I saw hawks hunting in hours (10), mass of consumed portion of prey (66.7 - 12.7 = 54g), assimilation efficiency, capture rate, and caloric density of prey:

$$\text{TEC} = 10 \times 54\text{g} \times 0.82 \times (0.1685 \text{ or } 0.1907) \times 2.14 \text{ kcal/g}.$$

Based on these calculations harriers assimilated 159.67 kcal/day (280.12 $\text{kcal}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$) and the Red-tail assimilated 180.71 kcal/day (161.06 $\text{kcal}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$).

Both hawk species exhibited most behaviors for different lengths of time (Table 10). The length of time spent coursing per sample was not different between species ($p = 0.85$) but Red-tails rarely coursed ($N=28$). Because of the infrequent use of coursing by Red-tails, I lumped coursing with directional flight. Harrier behavior is largely composed of coursing (15.05%), while Red-tail behavior is mostly thermal soaring (6.22%) and declivity soaring (7.47%).

Since energetic budgets are calculated from activity budgets, I tested the difference in behavior durations between winters for both species (Table 11). Because I detected statistical differences in activity budgets between winters, I calculated energy budgets separately for both winters. Energy budget differences between winters proved trivial so activity budgets were pooled between winters for energetic calculations.

Based on these calculations, Northern Harriers expended 138.17 kcal/day (242.40 $\text{kcal}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$) while Red-tailed Hawks expended 186.84

kcal/day (166.52 $kcal \cdot kg^{-1} \cdot day^{-1}$). This 24 hour budget is composed of energy spent at standard metabolism at night, existence metabolism during the day, and expenditure due to flight (Table 12). The daytime activity expenditures are composed of behaviors which account for the most expenditures (Table 12).

DISCUSSION

Major portions of both species' energy budgets are affected by flight activities. Coursing by the Northern Harrier accounts for 74.5% of the total flight budget and 19.9% of the daily budget. Declivity soaring and thermal soaring by the Red-tail accounts for 77.9% of the total activity budget and 13.2% of the total daily budget. Estimation of flight coefficients and the use of different coefficients for each behavior is critical since one or two flight types account for large portions of daily budgets. For example, calculating energy budgets using just one flight coefficient (13.7) inflated harrier flight budgets and total budgets by a factor of 1.69 and 1.18 respectively. Since the Red-tail budget is composed largely of energetically inexpensive soaring, the flight budget inflation (2.27) and daily budget inflation (1.22) are larger. Using more than one flight coefficient may not be as important in species that exhibit mostly one flight type. However, it is important in species exhibiting a number of flight types such as the Northern Harrier and Red-tailed Hawk.

Energetic Balances

With both species I calculated an approximate energetic balance between intake and output. The Red-tailed Hawk expends 166.5 $kcal \cdot kg^{-1} \cdot day^{-1}$ and consumes 161.06 $kcal \cdot kg^{-1} \cdot day^{-1}$. Using the same methods, the Northern Harrier expends 242.40 $kcal \cdot kg^{-1} \cdot day^{-1}$ and consumes 280.12 $kcal \cdot kg^{-1} \cdot day^{-1}$ (13.5% difference). I used the same methods for both species so that discrepancies in the energetic balance could be attributed to particular estimates for one of the species. The discrepancy in the harrier budget is probably due to an overestimation of prey consumption and/or an underestimation of activity (especially flight) expenditures. My prey consumption estimate (112.39g/day) for the Northern Harrier is larger than an empirical value (100.0g/day) from Craighead and Craighead (1956). The Red-tail estimate (127.77g/day) was much closer to the measured value (134.8g/day) from Craighead and Craighead (1956). It may be possible harriers are capturing smaller prey. This is unlikely since cotton rats dominated my study site and all prey capture remains I found were cotton rats. It is also possible that harriers did not use all of the 54g of a 66.7g rodent that I calculated. However, I could not statistically detect a difference in the amount of prey left by both species. An underestimate of one of the flight coefficients (probably coursing) could also account for the discrepancy.

Overall, there are many more reasons for the discrepancy, but it is probably an artifact of the estimates mentioned above. Harriers may actually assimilate less prey biomass and/or some activities may cost more than I estimated. Finally, this discrepancy may be a bias of the energetic formulae and dogma which are developed to end with balances in energetic calculations. Northern Harriers that hunt in the winter on tallgrass prairie habitat may store energy for migration and the nesting season. Red-tailed Hawks are not as migratory; in fact, I observed the same pair of Red-tails over two winters on my study site. In February of the second winter they were observed copulating and probably remained in the area to breed. In contrast, harriers began leaving the area in February, and all were gone by mid-March.

Energy Expenditures and Hunting Strategy

The Northern Harrier is a widely foraging predator while the Red-tailed Hawk is a sit-and-wait predator (Pianka 1983). The Northern Harrier expends 1.46 times more energy than the Red-tail per kilogram of body weight. Flight expenditures comprise 26.7% of the harrier's daily budget while only 17.0% of the Red-tail's budget is spent in flight. In addition, the largest portion of Red-tail flight (thermal and declivity soaring) is not used to capture prey. I did not observe attempts at prey by Red-tails from soaring behaviors in two winters. Other authors (Wakeley 1978b) found soaring to be used more often than expected based on prey captures using soaring. Soaring is also used in thermoregulation, territorial displays, and exploratory flights (Wakeley 1978b). Additionally, soaring is used for regional or seasonal migrations. It is not uncommon to see a Red-tail "catch" a thermal, gain altitude, then leave the thermal in a long directional glide. Harrier coursing alone accounts for 19.9% of total daily expenditures. It is clear the harrier expends more energy in hunting prey, but is the increased expenditure balanced by increased prey captures?

Harriers contact prey more often (1.88 strikes/hour) than Red-tails (0.49 strikes/hour). But harriers have a very low success ratio (5.66%) while Red-tails have a relatively high success ratio (25.00%). The actual rate of prey capture is comparable, but because the Northern Harrier is so much smaller, intake per gram body mass is much higher. Thus, harriers do capture more prey to balance the increased cost of active foraging.

I have calculated energy budget balances over two winters using the same methods for both species. However, on any given day the proportions of time and energy devoted to each behavior within a strategy may change. Both of these species exploit low wind speeds and high solar radiation to soar on thermals. These favorable conditions cause an increase in energetic expenditures, but because the conditions are conducive to soaring the cost is minimal. On windy days, both species exploit declivity air currents to declivity soar, since soaring on thermals is no longer possible. Associated with this behavioral change is an increased energetic cost. Since the actual cost will vary with the conditions, future studies should concentrate on determining the cost of a variety of behaviors under many conditions. Factors that may alter energy budgets of wintering raptors include weather, availability of perches, prey vulnerabilty, and interactions between raptors.

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LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-265.

Bartholomew, G. A. 1977. Energy and metabolism. Pages 57-110 in M. S. Gordon, ed. Animal physiology: principles and adaptations. MacMillan Co., New York, New York.

Beissinger, S. R. 1983. Hunting behavior, prey selection, and energetics of Snail Kites in Guyana: consumer choice by a specialist. Auk 100:84-92.

Brisbin, I. L. 1970. A determination of live-weight caloric conversion factors for laboratory mice. Ecology 51:541-544.

Craighead, J. J. and F. C. Craighead. 1956. Hawks, owls and wildlife. Dover Publ. Inc., New York, New York.

Cone, C. D. Jr. 1962 Thermal soaring of birds. Am. Scientist 50:180-209.

Ettinger, A. O. and J. R. King. 1980. Time and energy budgets of the Willow Flycatcher (Empidonax traillii) during the breeding season. Auk 97:535-546.

Fagen, R. M. 1978. Repertoire analysis. Pages 25-42 in P. W. Colgan, ed. Quantitative ethology. John Wiley and Sons, New York, New York.

Johnson, D. R. 1981. The study of raptor populations. The Univ. Press of Idaho. Moscow, Idaho.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp 4-85 in Avian Energetics (R. A. Paynter, Ed.). Publ. Nuttall Ornithol. Club, No.15.

Koplin, J. R., M. W. Collopy, A. R. Brammann, and H. Levenson. 1980. Energetics of two wintering raptors. Auk 97:795-806.

Mosher, J. A. and P. E. Matran. 1974. Size dimorphism: a factor in energy savings for Broad-winged Hawks. Auk 91:325-341.

Mugaas, J. N. and J. R. King. 1981. The annual variation in daily energy expenditure of the Black-billed Magpie: a study of thermal and behavioral energetics. Stud. Avian Biol. 5:1-78.

Pianka, E. R. 1983. Evolutionary ecology. 3rd ed. Harper and Row, New York, New York.

Rice, W. R. 1982. Acoustical location of prey by the Marsh Hawk: adaptation to concealed prey. Auk 99:403-413.

Rice, W. R. 1983. Sensory modality: an example of its effect on optimal foraging behavior. Ecology 64:403-406.

Schipper, W. J. A., L. S. Buurma, and P. H. Bossenbroek. 1975. Comparative study of hunting behavior of wintering hen-harriers Circus cyaneus and marsh harriers Circus aeruginosus. Ardea 63:1-29.

Stalmaster, M. V. 1983. An energetics simulation model for managing wintering Bald eagles. J. Wildl. Manage. 1983.

Trautman, M. B. 1944. Flight hunting of a Marsh Hawk. Wilson Bull. 56:117.

Tarboton, W. R. 1978. Hunting and energy budget of the Black-shouldered Kite. Condor 80:88-91.

Wakeley, J. S. 1978a. Activity budgets, energy expenditures, and energy intakes of nesting Ferruginous Hawks. Auk 95:667-676.

Wakeley, J. S. 1978b. Hunting methods and factors affecting their use by Ferruginous Hawks.

Walsberg, G. E. 1983. Ecological energetics: what are the questions. in A. H. Brush and G. A. Clark, Jr. Perspectives in ornithology. Cambridge Univ. Press, New York, New York.

CHAPTER III

STRATEGIES OF SIT-AND-WAIT AND WIDELY FORAGING RAPTORS

Introduction

The premise that different foraging activities are adaptive based on their relative costs and benefits is a common theme in ecology (Lack 1946, Schoener 1971, Norberg 1977, Pyke et al. 1977, Krebs et al. 1983). The relative fitness incurred by the performance of an act is measured with energy or time as the "currency". The relationship between time and energy is inseparable (Mugaas and King 1980), but usually not proportional (Winterhalder 1983). Activities may last for short periods and be energetically expensive or last for long periods and be relatively inexpensive. Organisms foraging during the winter may be constrained by both time and energy because the shorter photoperiod may limit time to perform all activities (Mugaas and King 1981).

Among carnivorous predators, sit-and-wait versus widely foraging methods of prey capture are evident. The dichotomy of sit-and-wait and widely foraging predators has widespread practical appeal among ecologists (Pianka 1983). Each of these foraging modes has a series of correlates associated with the strategy (Huey and Pianka 1981, Pianka 1983). In addition, other authors have listed core adaptations and other adaptations associated with "searchers" and "pursuers" (Eckhardt

1979). Originally the dichotomy was addressed by Schoener (1969) with Type I and Type II predators. Eckhardt (1979) tested the universality of these classification schemes with foraging guilds of insectivorous birds, and suggested other taxa must be tested. In addition, other foraging strategy adaptations may be found in other taxa (Eckhardt 1979).

I chose two species of raptors, one a sit-and-wait predator, and the other a widely foraging predator, to test this model. The Northern Harrier (_Circus cyaneus_) is a widely foraging predator that hunts with a low coursing flight frequently pouncing on prey that is located via visual and acoustical cues (Rice 1982, 1983). The Red-tailed Hawk (_Buteo jamaicensis_) is a sit-and-wait predator that visually scans the ground for prey and uses short directional flights from a hunting perch to capture prey. Both of these species' behaviors were studied during two winters (1982-1983 and 1983-1984) in northcentral Oklahoma.

Methods

I tested a series of predictions from past authors in relation to the Northern Harrier and Red-tailed Hawk as widely foraging and sit-and-wait predators (Schoener 1969, Eckhardt 1979, Huey and Pianka 1981, Pianka 1983). I conducted focal behavioral observations on both species noting behaviors and prey captures. Energetic calculations were done using formulae I modified from Koplin et al. (1980). More complete descriptions of methods and energetic calculations are addressed elsewhere (Carter 1984).

Results

I generated a list of 13 correlates from previous studies that apply to raptors (Schoener 1969, Huey and Pianka 1981, Eckhardt 1979) (Table 13). Some of these predictions are generalizations and can only be substantiated by citing relevant sources. Other predictions have been quantitatively confirmed by others who collected data on aspects of the Northern Harrier and Red-tailed Hawk which I did not study (Craighead and Craighead 1956, Evans 1982, Johnson 1981, Rice 1982, 1983).

DISCUSSION

Red-tailed Hawks, Northern Harriers and Their Prey

Because they are more active, widely foraging predators should capture and consume more prey than sit-and-wait predators. Huey and Pianka (1981) determined food intake of widely foraging lizards should be 1.3-1.5 times more than sit-and-wait lizards. The weight of prey per kilogram of hawk captured by Northern Harriers was 1.74 times that of the Red-tail (Table 13). Since harriers capture more prey, they should also contact prey (Huey and Pianka 1981) more often or have a higher foraging intensity (Eckhardt 1979) based on their widely foraging habits. As reflected by successful and unsuccessful strikes, harriers contact prey 3.84 times more often than Red-tails. Even though harriers contact prey more often, they are less successful (5.66%, 21 successes of 371 attempts) than Red-tails (25.00%, 23 successes of 92 attempts). This converse relationship suggests the two predators may capture prey at similar rates. Actual capture rates (success ratio x contacts rate) show that the Northern Harrier contacts and captures prey at a rate (0.1064 captures / hour) which is comparable to the Red-tailed Hawk (.1225 captures / hour). Although both species' capture rate is nearly the same, their different strategies may exploit different prey with different activities.

Sit-and-wait predators should eat active prey, while widely foraging should eat sedentary or clumped prey (Huey and Pianka 1981, Eckhardt 1979). I do not have data on prey activity immediately before they are captured. However, Red-tails do seem to "key-in" on moving prey as visual hunters. Northern Harriers when hunting drop on anything that appears "rodent-like." I have observed harriers capture small brown objects only to let them go. The objects blow away in the wind and appear to be old nests, "cow chips," or other debris. These observations suggest that harriers concentrate their hunting efforts on relatively sedentary or clumped prey. However, I did observe harriers making up to seven strikes during a prey encounter, with each strike occurring at a different location, suggesting a rodent moving along the ground. In general though, Northern Harriers do not capture agile prey (Craighead and Craighead 1956).

Widely foraging predators should be food specialists while sit-and-wait predators are food generalists. Although raptors are opportunistic, Craighead and Craighead (1956) considered the Northern Harrier a restrictive feeder while the Red-tail was considered a generalist (Table 13). More recently, other studies have determined that raptor "behavior and morphology are simply adequate, not specialized for particular kinds of prey" (Jaksic and Braker 1983). However in the case of the Northern Harrier and Red-tailed Hawk, their morphology and behavior allow them to be "adequate" in different ways.

Foraging Behavior

Eckhardt (1979) predicted active searchers should have high velocity (perch changes/minute) and high search intensity (perch changes/attack). It is difficult to tell when a Red-tail is actually hunting or just perching. This is a common problem when studying sit-and-wait predators because many daily activities are carried out while perched, and these activities are mixed with actual hunting bouts (Winterhalder 1983). I calculated a general parameter (flights/hour) that better describes raptor hunting strategies. Harriers fly more often (8.49 flights/hour) than do Red-tails (4.18 flights/hour). Although not all these flights are associated with prey, they do reflect the relative sit-and-wait versus widely foraging activity patterns in raptors (Table 13).

The attack radius (Eckhardt 1979) is much smaller for the Northern Harrier than the Red-tail (Table 13). Harriers pounce on prey immediately below them, while Red-tails make long directional flights out to capture prey. These flights on occasion exceed 75 meters in length.

The foraging space (Eckhardt 1979) of both species overlap, however on my study site harriers actively hunted creek bottoms with tallgrass prairie on both sides. After a large portion of the study site was mowed, harriers did not hunt these mowed areas. The Red-tail seemed to hunt all microhabitats, although its distribution on the study site seemed related to the availability of suitable perches. Schnell (1968) found the same to be true in his study of Red-tail perch site and habitat selection. He attributed Red-tailed Hawks' distribution within a general locality to their finding "suitable" perch sites.

Morphological Characteristics

Huey and Pianka (1981) predicted widely foraging lizards should be streamlined while sit-and-wait should be stocky with short tails. This correlate also applies to raptors (Table 13). Harriers are streamlined with long rounded wings and long tails; Red-tailed Hawks have a robust body with short rounded wings and short rounded tails. Johnson (1981) reported the Red-tail has wing loading 1.68 times that of the Northern Harrier (Table 13). Although wing loading has many implications in raptors, one would expect widely foraging predators to have relatively lighter bodies and more wing area.

Sexual dimorphism should be prevalent among widely foraging (active pursuit) predators (Schoener 1969, Snyder and Wiley 1976). Again, the implications of sexual dimorphism in raptors abound (Hill 1944, Storer 1966, Reynolds 1972, Amadon 1975, Von Schantz and Nilsson 1981), but female harriers are 1.4 times larger than male harriers (Evans 1982).

Sensory mode of sit-and-wait predators should be largely visual, while widely foraging predators should use visual and olfactory cues to capture prey (Huey and Pianka 1981, Pianka 1983). In addition to visual cues, widely foraging harriers also use acoustical location to capture prey (Rice 1982, 1983). This trait seems particularly adaptive considering the foraging space of the harrier on my study site in Oklahoma. Harriers actively hunted areas with >450-500 g/m^2 of dry standing prairie biomass. In Oklahoma, Birney et al. (1976) found rodents (Microtus spp.) avoided areas with <450-500 g/m^2 of dry prairie biomass. In such dense areas locating prey via acoustical cues would be adaptive since visual sightings of prey may be few.

Daily Metabolic Expense

Most important to the aforementioned correlates of foraging modes are the energetic costs associated with each strategy. Specifically, are the costs of foraging widely balanced by increased prey consumption? The Northern Harrier expends 242.40 $kcal \cdot kg^{-1} \cdot day^{-1}$, while the sit-and-wait Red-tail expends 166.52 $kcal \cdot kg^{-1} \cdot day^{-1}$. Balanced against these expenditures the harrier assimilates 280.12 $kcal \cdot kg^{-1} \cdot day^{-1}$ and the Red-tail assimilates 161.06 $kcal \cdot kg^{-1} \cdot day^{-1}$ (Carter 1984). The ratio of consumed over expended was 1.16 for the Northern Harrier and 0.97 for the Red-tailed Hawk. There are various possibilities why consumed does not match expended in the harrier (Carter 1984). However, instead of "adjusting" these values I chose to use the same methods for both species, and attribute any errors in agreement to estimation of variables in energetic calculations. In addition, the Northern Harrier is migratory and may store energy in the winter for the spring migration. Thus, taking the error of these estimates into account the Northern Harrier captures much more prey than than energy used in prey capture and daily activity. The Red-tail shows good agreement between prey captured and energy expended for daily activities. Both species capture and assimilate a comparable amount of energy needed for daily existence based on the cost of their respective foraging strategy.

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LITERATURE CITED

Amadon, D. 1975. Why are female birds of prey larger than males? Raptor Research 9 1/2:1-11.

Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetative cover to cycles of Microtus populations. Ecology 57:1043-1051.

Carter, M. F. 1984. Comparative winter ecology of the Northern Harrier and Red-tailed Hawk in Oklahoma. Unpublished ms thesis. Oklahoma State University, Stillwater, Ok.

Craighead, J. J. and F. C. Craighead. 1956. Hawks, owls, and wildlife. Dover Publ. Inc. New York, New York.

Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. Ecol. Mono. 49:129-149.

Evans, D. L. 1982. Status report of twelve raptors. U.S.F.W.S. Special Sci. Report, Wildl. No. 238. Washington, D.C.

Hill, N. P. 1944. Sexual dimorphism in Falconiformes. Auk 61:228-234.

Huey, R. B. and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 55:304-316.

Jaksic, F. M. and H. E. Braker. 1981. Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. Can. J. Zool. 61:2230-2241.

Johnson, D. R. 1981. The study of raptor populations. The Univ. Press of Idaho. Moscow, Idaho.

Krebs, J. R., D. W. Stephens, and W. J. Sutherland. 1983. Perspectives in optimal foraging in A. H. Brown and G. A. Clark, Jr. Perspectives in ornithology. Cambridge Univ. Press, New York, New York.

Koplin, J. R., M. W. Collopy, A. R. Brammann, and H. Levenson. 1980. Energetics of two wintering raptors. Auk 97:795-806.

Lack, D. 1946. Competition for food by birds of prey. J. Anim. Ecol. 15:123-129.

Mugaas, J. N. and J. R. King. 1981. The annual variation in daily energy expenditure of the Black-billed Magpie: a study of thermal and behavioral energetics. Stud. Avian Biol. 5:1-78.

Norberg, R. A. 1977. An ecological theory on foraging time and energetics and choice of optimal food searching method. J. Anim. Ecol. 46:511-529.

Pianka, E. R. 1983. Evolutionary ecology. 3rd ed. Harper and Row, New York, New York.

Pyke, G. H., H. R. Pulliam, and E. L Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biol. 52:137-154.

Reynolds, R. T. 1972. Sexual dimorphism in accipiter hawks: a new hypothesis. Condor 74:191-197.

Rice, W. R. 1982. Acoustical location of prey by the Marsh Hawk: adaptation to concealed prey. Auk 99:403-418.

Rice, W. R. 1983. Sensory modality: an example of its effect on optimal foraging behavior. Ecology 64:403-406.

Schnell, G. D. 1968. Differential habitat utilization by wintering Rough-legged and Red-tailed Hawks. Condor 70:373-377.

Schoener, T. W. 1969. Models of optimal size for solitary predators. Am. Nat. 103:277-313.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

Snyder, N. F. and J. W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. Am. Ornitho. Mono. 20.

Storer, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83:423-436.

Von Schantz, T. and I. N. Nilsson. 1981. The reversed size dimorphism in birds of prey: a new hypothesis. Oikos 36:129-132.

Winterhalder, B. 1983. Opportunity-cost foraging models for stationary and mobile predators. Am. Nat. 122:73-84.

APPENDIX A

TABLES

Table 1. Northern Harrier and Red-tailed Hawk winter behaviors and definitions of behaviors cataloged in northcentral Oklahoma.

BEHAVIOR	DEFINITION
Coursing	low to the ground flapping and gliding flight also called quartering
Directional	direct flight composed of gliding and flapping e.g. (flapping flight between perches)
Hovering	vigorous flapping flight with little or no ground speed
Thermal Soaring	non-flapping flight, usually in tight circles (Cone 1962)
Declivity Soaring	soaring flight usually with birds oriented into the wind, also consists of occasional flapping (Cone 1962)
Perching and Preening on the Ground	perching or preening while perched on the ground
Perching and Preening on Structures	perching or preening while perched on structures such as fence wires and post, hay bales and vegetative structures
Prey Associated Behaviors	any behavior that the raptor appears in "contact" with prey e.g. (successful and unsuccessful strikes, flight with prey, perched with prey, and prey handling)

Table 2. Weather variable averages, standard deviations, and ranges observed during behavioral observations in November-Febuary of 1982-1983 and 1983-1984.

Weather Variable	$\bar{x}$ ± S.D.	RANGE
Temperature	3.75 ± 5.51	-9.00 - 19.00
Wind Velocity (kph)	17.93 ± 9.12	3.03 - 48.49
Snow on Ground (cm)	0.94 ± 3.25	0.00 - 15.24
Solar Radiation (Langleys/cm^2)	46.20 ± 29.60	0.00 - 100.00

Table 3. Product moment correlation coefficients between weather variables observed during behavioral observations.

Weather Variable	Wind Velocity	Snow	Solar Radiation
Temperature	0.0740*	-0.327*	0.292*
Wind Velocity		-0.008	0.115*
Snow			0.099*

* significant correlation at $p < 0.001$

Table 4. Structure coefficients between weather variables and first two canonical variables for all Red-tailed Hawk behaviors.

Weather Variable	Canonical Variate I	Canonical Variate II
Temperature	-0.3883	-0.1924
Snow	-0.1907	0.0774
Solar Radiation	0.6962	-0.3992
Wind Velocity	0.2561	0.8159

Table 5. Structure coefficients between weather variables and the single canonical variate for Red-tailed Hawk declivity and thermal soaring.

Weather Variable	Canonical Variate I
Temperature	-0.2980
Snow	0.3175
Solar Radiation	-0.4459
Wind Velocity	0.9110

Table 6. Structure coefficients between weather variables and the first two canonial variates for all Northern Harrier behaviors.

Weather Variable	Canonical Variate I	Canonical Variate II
Temperature	-0.0733	0.0228
Snow	-0.4637	-0.1260
Solar Radiation	0.3613	0.9228
Wind Velocity	0.9003	-0.1424

Table 7. Structure coefficients between weather variables and the single canonical variate for Northern Harrier thermal and declivity soaring.

Weather Variable	Canonical Variate I
Temperature	0.0735
Snow	-0.0666
Solar Radiation	-0.4717
Wind Velocity	0.9209

Table 8. Structure coefficients between weather variables and the first two canonical variates for all Northern Harrier and Red-tailed Hawk behaviors.

Weather Variable	Canonical Variate I	Canonical Variate II
Temperature	-0.2497	-0.1166
Snow	-0.3206	-0.1251
Solar Radiation	0.4507	0.7968
Wind Velocity	0.7956	-0.4343

Table 9. Behaviors, their definitions, and flight coefficients used in energetic calculations.

BEHAVIOR	DEFINITION	FLIGHT COEFFICIENT
Coursing	low flapping and gliding flight also called quartering, used almost exclusively by harriers	10.0
Directional	flapping and gliding flight with more flapping than coursing, often used by Red-tails moving between hunting perches, also used by both birds when moving to or from the roost	9.0
Hovering	vigorous flapping flight with little or no ground speed	13.7
Thermal Soaring	non-flapping flight usually in "tight" circles (Cone 1962)	3.5
Declivity Soaring	soaring with occasional flapping, birds are oriented into the wind	7.0
Perching	all non-flight activities, calculated with Koplin et al. (1980) equation for existence metabolism of non-passerine birds	

Table 10. Duration (seconds) and frequency of the behaviors used in energetic calculations.

	NORTHERN HARRIER		RED-TAILED HAWK		
	$\bar{x}$	N	$\bar{x}$	N	P>t
Coursing	104.4	1078	110.1	28	0.8560
Directional	76.0	107	28.1	487	0.0005
Hovering	3.5	201	6.5	93	0.0021
Soaring	194.9	100	278.5	142	0.0001
Declivity	114.8	231	278.5	228	0.0001
Perching	513.1	1019	563.0	1268	0.0001

Table 11. Mean differences in duration (seconds) of behaviors between field seasons for both species.

BEHAVIOR	1982-1983		1983-1984		
	$\bar{x}$	N	$\bar{x}$	N	P>t
Harrier Coursing	109.7	837	86.1	241	0.0044
Red-tail Hovering	5.2	70	10.7	23	0.0089
Red-tail Declivity	301.7	191	158.7	37	0.0030
Red-tail Perching	550.4	976	601.7	292	0.0200

Table 12. Energy expenditures of the Northern Harrier and Red-tailed Hawk for flight behaviors and the 24 hour activity cycle.

BEHAVIOR	Northern Harrier		Red-tailed Hawk	
	% of day	kcal/day	% of day	kcal/day
Coursing	15.05	25.93		
Directional	1.09	2.21	2.01	6.70
Hovering	0.08	0.25	0.07	0.32
Thermal Soaring	2.61	1.85	6.22	7.25
Declivity Soaring	3.58	5.08	7.47	17.42
ACTIVITY TOTAL	22.41	36.84	15.77	31.69
DAY INACTIVE TOTAL	77.59	55.45	84..23	86.52
NIGHT TOTAL		45.88		68.63
DAILY ENERGY BUDGET		138.17		186.84

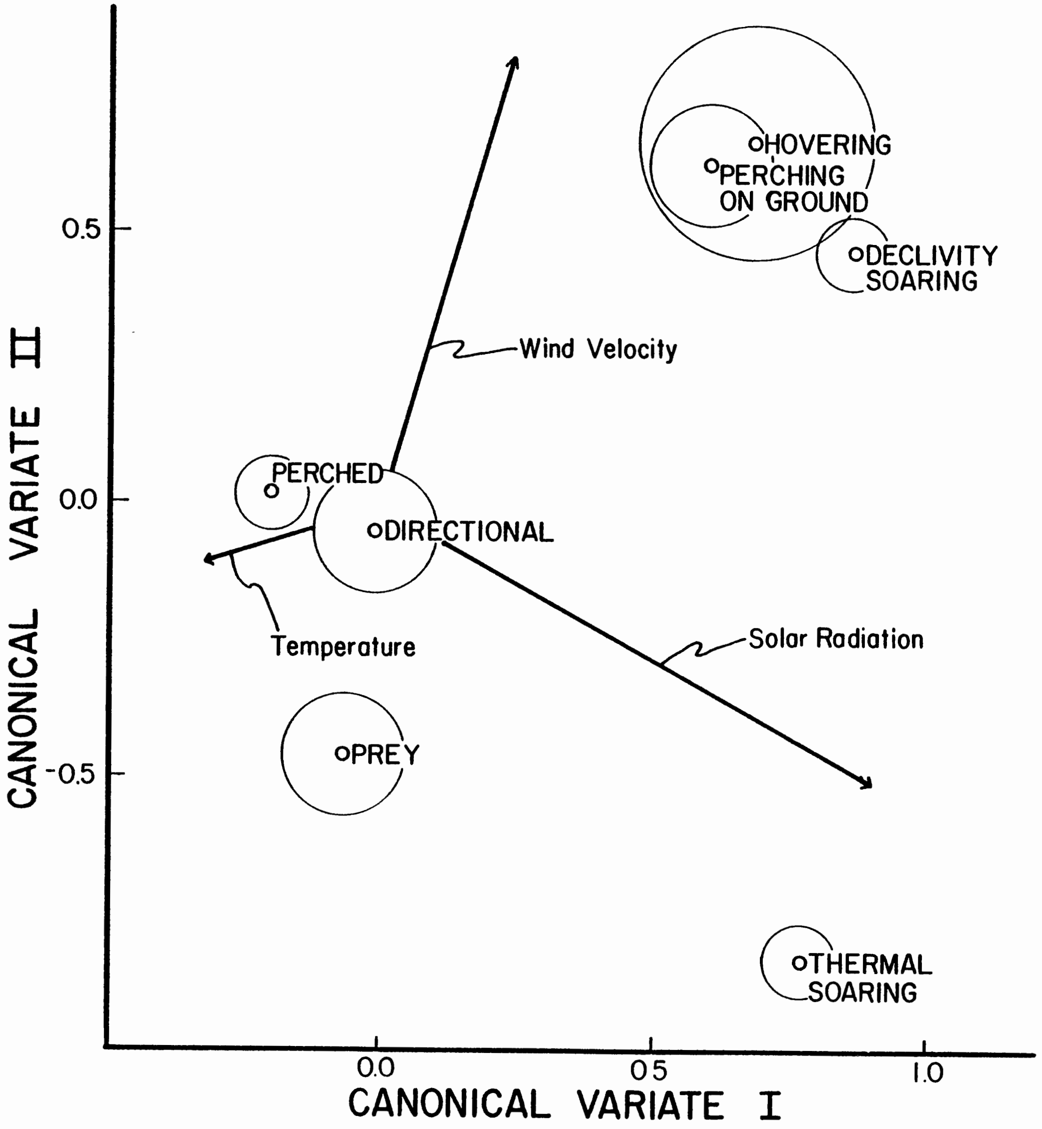
Table 13. Predicted and observed correlates of sit-and-wait (Red-tailed Hawk) and widely foraging (Northern Harrier) raptors.

CORRELATE	SIT-AND-WAIT	WIDELY FORAGING
Volume of prey captured/day	LOW 89.73g/kg of hawk	HIGH 127.68g/kg of hawk
Foraging intensity Encounter rate	LOW 0.49 strikes/hour	HIGH 1.88 strikes/hour
Success ratio	HIGH 25.0%	LOW 5.6%
Contacts x Success	EVEN 0.1225	EVEN 0.1064
Prey Activity	EAT ACTIVE PREY	EAT SEDENTARY OR CLUMPED PREY
Prey Type	SPECIALIST	GENERALIST
Flight Rate (flights/hour)	LOW 4.18	HIGH 8.49
Attack Radius	LARGE	SMALL
Foraging Space	LARGE	SMALL
Morphology	STOCKY broad rounded wings robust body,broad tail	STREAMLINED slim, long wings, long tail
Sexual Dimorphism	LOW	HIGH
Sensory Mode	VISUAL visual	VISUAL, OLFACTORY, and ACOUSTICAL visual and acoustical
Daily Metabolic Expense	LOW $166.5 \mathrm{kcal} \cdot \mathrm{kg}^{-1} \cdot \mathrm{day}^{-1}$	HIGH $242.4 \mathrm{kcal} \cdot \mathrm{kg}^{-1} \cdot \mathrm{day}^{-1}$

APPENDIX B

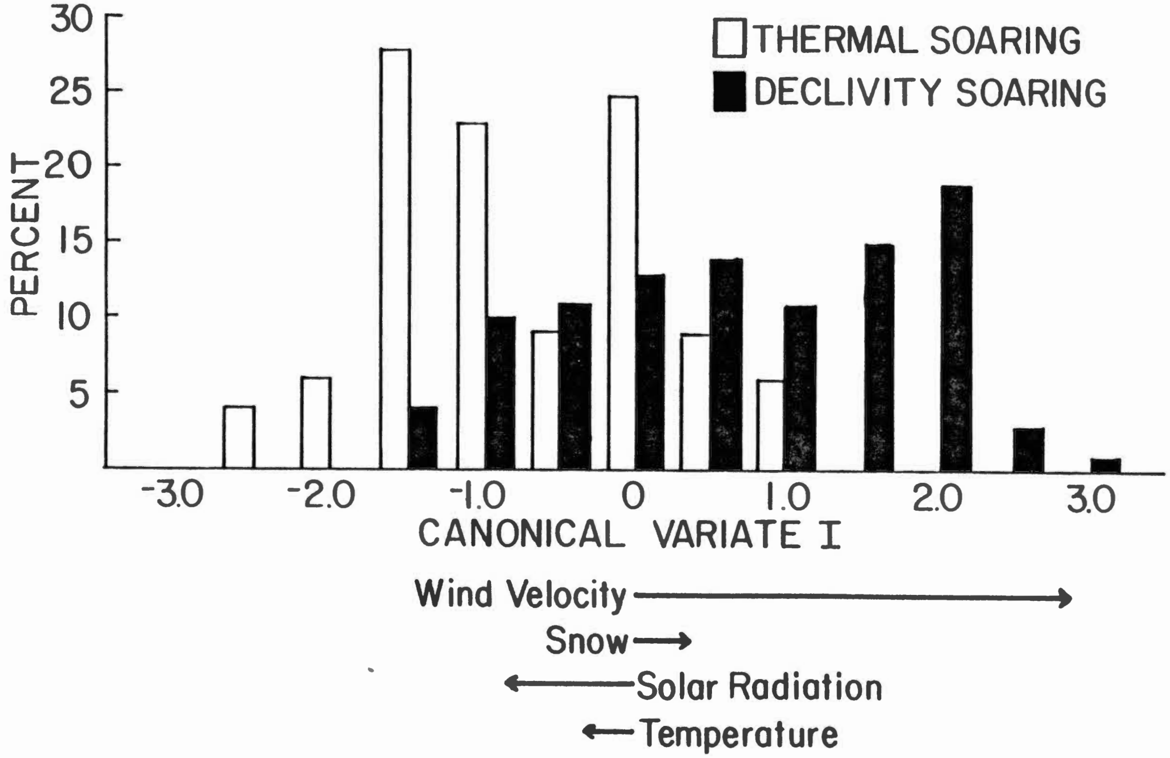
FIGURES

Figure 1: Red-tailed Hawk behavior centroids with 95% confidence circles. Weather vectors represent the "push" of each variable in canonical space.



CANONICAL VARIATE II
CANONICAL VARIATE I
0.5
0.0
-0.5
0.0
0.5
1.0
HOVERING
PERCHING ON GROUND
DECLIVITY SOARING
Wind Velocity
PERCHED
DIRECTIONAL
Temperature
Solar Radiation
PREY
THERMAL SOARING

Figure 2: Percent occurence of Red-tailed Hawk declivity and thermal soaring over the single canonical variate from discriminant analysis.



THERMAL SOARING
DECLIVITY SOARING
PERCENT
30
25
20
15
10
5
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
CANONICAL VARIATE I
Wind Velocity
Snow
Solar Radiation
Temperature

Figure 3: Northern Harrier behavior centroids plotted with 95% confidence circles. Vectors represent each weather variables "push" in canonical space.

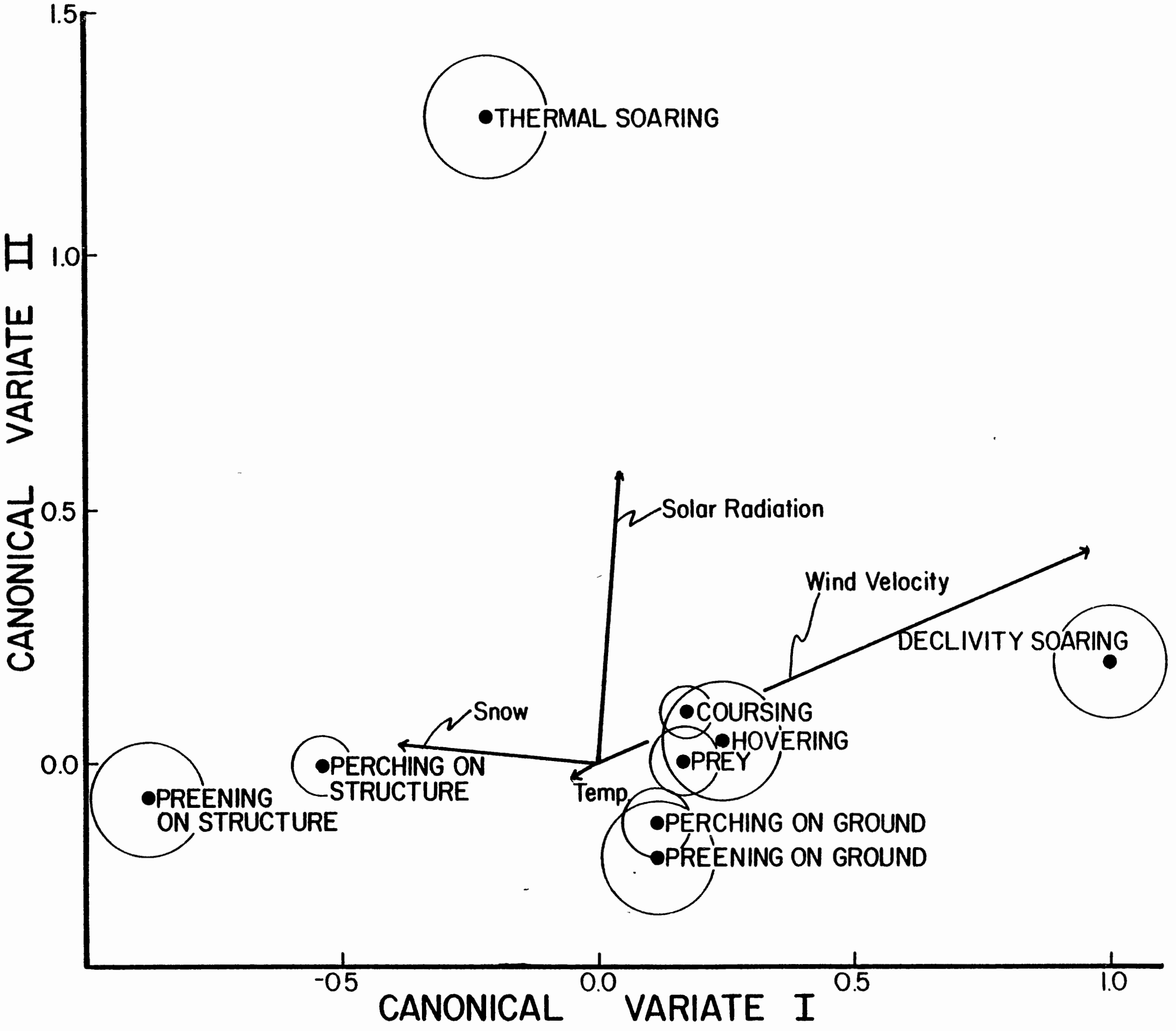
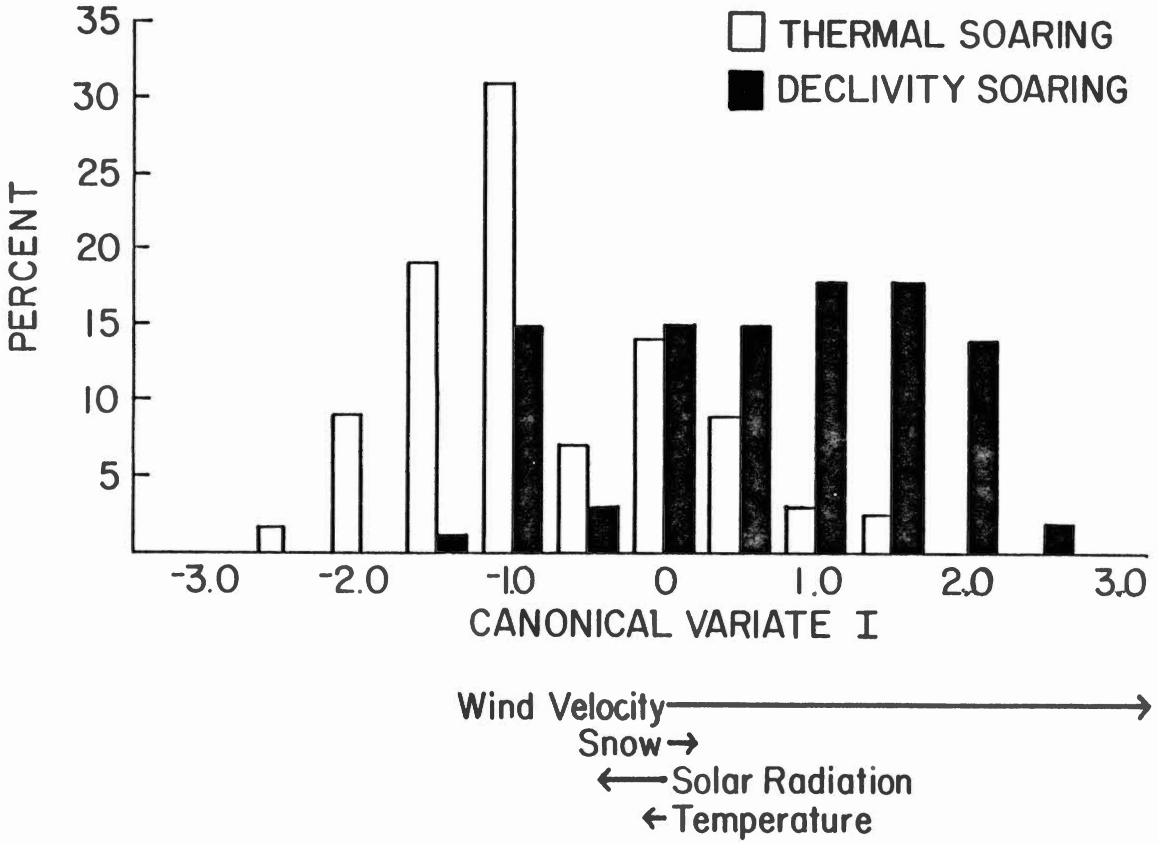
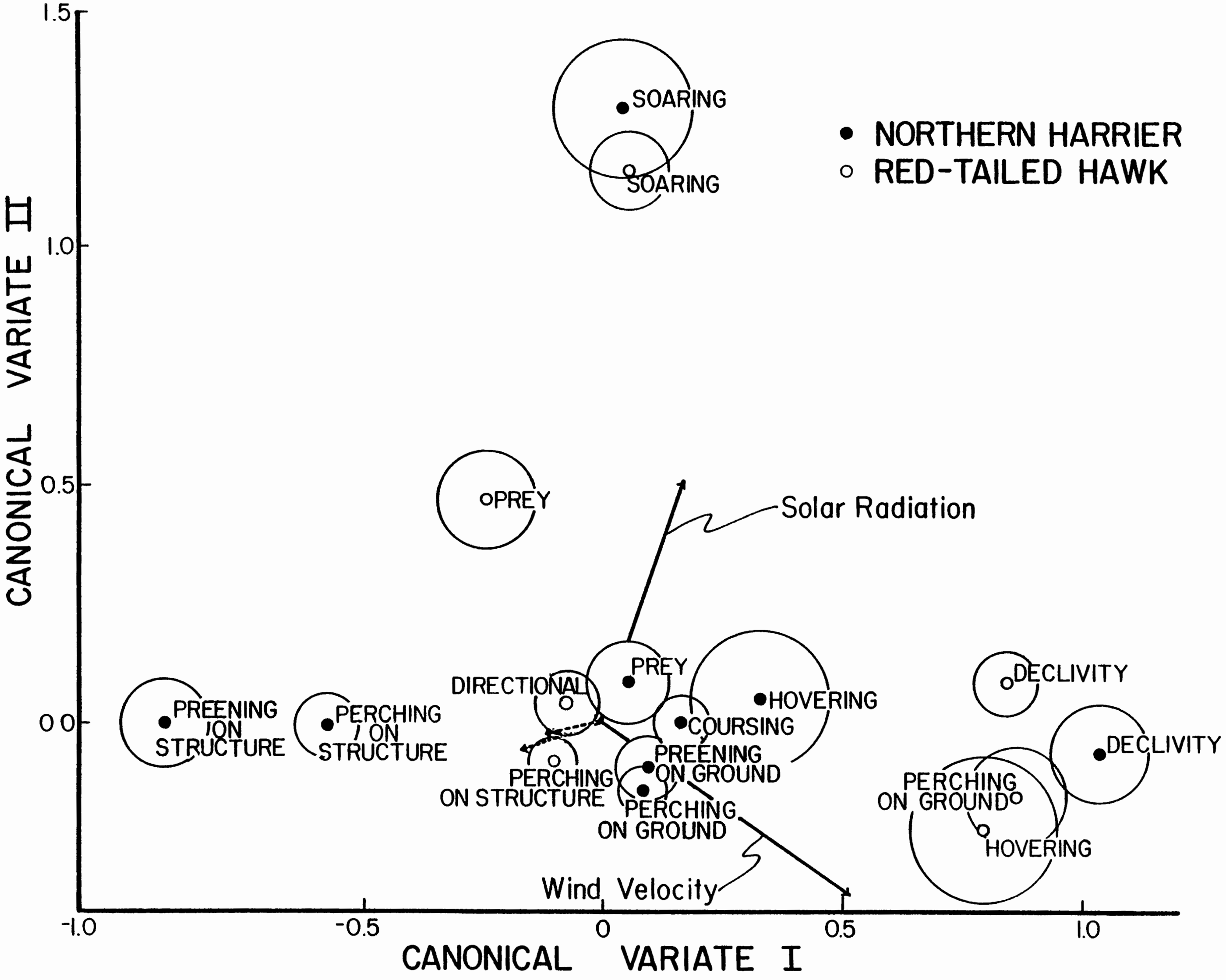

THERMAL SOARING
Solar Radiation
Wind Velocity
DECLIVITY SOARING
Snow
COURSING
HOVERING
PREY
PERCHING ON STRUCTURE
PREENING ON STRUCTURE
Temp
PERCHING ON GROUND
PREENING ON GROUND
1.5
1.0
0.5
0.0
-0.5
0.0
0.5
1.0
CANONICAL VARIATE II
CANONICAL VARIATE I

Figure 4: Percent occurrence of Northern Harrier declivity and thermal soaring over the single canonical variate from discriminant analysis.



☐ THERMAL SOARING
■ DECLIVITY SOARING
PERCENT
35
30
25
20
15
10
5
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
CANONICAL VARIATE I
Wind Velocity→
Snow→
←Solar Radiation
←Temperature

Figure 5: Both species behavior centroids plotted with 95% confidence circles. Vectors represent each weather variables "push" in canonical space.


SOARING
SOARING
● NORTHERN HARRIER
○ RED-TAILED HAWK
PREY
Solar Radiation
PREY
DIRECTIONAL
HOVERING
DECLIVITY
PREENING ON STRUCTURE
PERCHING ON STRUCTURE
COURSING
DECLIVITY
PREENING ON GROUND
PERCHING ON STRUCTURE
PERCHING ON GROUND
PERCHING ON GROUND
HOVERING
Wind Velocity
CANONICAL VARIATE II
1.5
1.0
0.5
0.0
-1.0
-0.5
0
0.5
1.0
CANONICAL VARIATE I

VITA^{2}

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