BEHAVIORAL AND MORHPHOLOGICAL RESPONSES IN AVIAN GRANIVORES TO DIETS IN NORTHEAST KANSAS

BY

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OVERALL INTRODUCTION

It is hypothesized that competition, operating through natural selection affects how sets of species allocate their time and energy leading to an outcome which segregates species along resource-utilization axes (Cody and Diamond 1975), and that interspecific competition plays a major role in the structuring of natural communities, and in particular, in limiting the number of species present (Thompson and Lawton 1983). Wiens (1977) states that competition theory has assumed an increasingly dominant position in ecology and population biology primarily through developments in mathematical representation of the competition process (e.g. Wiegert 1974, Schoener 1974a, Shorrocks and Begon 1975, Vandermeer 1975, Levins 1975, Gilpin and Case 1976, Armstrong and Gilpin 1977). Wiens (1977), however, warns that the current emphasis upon competition theory in ecology and population biology has led to an overinterpretation of species differences and a neglect of important features of populations and their environments. Thompson and Lawton (1983) observed that of the many studies on interspecific competition, most have simply looked at differences between close relatives which might permit coexistence (e.g. Lack 1971, MacArthur 1972, Cody 1974) and very few have been experimental in nature.

One of the main purposes of this research was to look at the role of competition in an experiment using confined flocks of three species of emberizids wintering in Kansas, northern cardinal (*Cardinalis cardinalis*), Harris' sparrow (*Zonotrichia querula*) and American tree sparrow (*Spizella arborea*). In the first year birds were kept in outdoor flight pens on the Konza Prairie Research Natural Area (KPRNA), 25 km south of Manhattan, Kansas. Birds were kept in various flock combinations, ranging from single species flocks to flocks containing all three species and variations were made both in numbers of birds present and in feeder site availability.

Data were collected using the time-budget method. Orians (1961) was the first to use the time-energy budget and the method has been used quite frequently since (e.g. Verbeek 1964, Schartz and Zimmerman 1971, Utter and LeFebvre 1971, Wolf and Hainsworth 1971, Wolf 1975, Tarboten 1978, Ashkenazie and Safriel 1979, Barnard 1980a, Ettinger and King 1980, Biedenweg 1983, Shuman 1984, Weathers et al. 1984, Tacha et al. 1987, Paulus 1988, Sullivan 1988). A time-budget method should not only be able to evaluate and quantify an organism's interaction with its environment, but should also be able to provide insight into the evolution of the allocation patterns (King 1974, Ashkenazie and Safriel 1979, Biedenweg 1983).

The second year's research also studied time budgets, but in this case used only two species, northern cardinals and Harris' sparrow, and studied unconfined birds rather than confined birds. There has been a great deal of work done on the relationships between flocking behavior and feeding efficiency in wild birds. When examining the effects of flocking on individual time budgets, the amount of time a bird allocates to different behaviors may be influenced by the size and composition of the flock (Pulliam 1973, 1975, Pulliam et al. 1974, and Caraco 1979 a,b). This research attempted to not only look at the winter behavior of these unconfined birds, but also to draw some comparisons with the previous year's confined birds.

During both years ongoing research also investigated morphological changes in the digestive systems of the three species of birds previously discussed. Interest in an animal's ability to alter its own physiology in response to its current diet has been documented for years, but is only recently being investigated in passerines (Davis 1961, Pulliainen and Tunkkari 1981, Klem et al. 1984, Robel et al.

pers. comm.). Reasons for these changes have been attributed to several factors, including dietary fiber content (Thomas 1984, Moss 1982, Miller 1975), quality and quantity of food consumed (Drobney 1984) and the metabolic requirement of wintering migratory birds to improve energy absorption from foods of variable quality (Paulus 1982).

Two years of data were taken in the morphological research: in the first year confined birds on a diet of white proso millet (*Panicum miliaceum*) were compared to wild birds eating a more nutritious, diverse diet, while the second year compared wild birds found on two experimental sites which varied greatly in the nutritional value of food plants found.

LITERATURE REVIEW

Study 1. Time budgets of captive passerine birds while varying flock sizes, flock compositions and feeder availability.

Study 2. Time budgets of unconfined passerine birds in habitats of high and low metabolizable energy food sources.

Since David Lack's classic study of Darwin's finches (1947), it has become widely accepted that interspecific competition plays a major role in the structuring of natural communities, and in particular, in limiting the number of species present (Thompson and Lawton 1983). Consideration of competition, resource utilization, niche differentiation, and coexistence among ecologically similar species has been a central focus in ecology for the last 40 years, stimulating flurries of activity in field studies, laboratory experimentation, and theory development (Wiens 1977). However, the basic premises of competition appear to be so fully accepted by ecologists that the theory is in danger of becoming a firmly entrenched dogma (Peters 1976). Theorists have warned that competition may be less pervasive in its effects than is usually assumed and that what we witness in nature may at times represent merely a coarse fit to the optimal states predicted by theory (Wiens 1977).

Competition theory has become widely held largely due to developments in mathematical representation of the competition process (e.g. Wiegert 1974, Schoener 1974a, Shorrocks and Begon 1975, Vandemeer 1975, Levins 1975, Gilpin and Case 1976, Armstrong and Gilpin, 1977) and through studies of resource utilization and partitioning among coexisting species. MacArthur and Levins (1964) and Cody (1974), discuss the hypothesis that related or similar sized coexisting species must differ in habitat or feeding methods in order to peacefully coexist. This hypothesis predicts outcomes in which natural selection always weeds out all but the optimal phenotypes and that these are the forces that guide community structures. Cody and Diamond (1975:5) state, "It is natural selection, operating through competition, that makes the strategic decisions on how sets of species allocate their time and energy; the outcome of this process is the segregation of species along resource-utilization axes" or "the evolution of optimal strategies comes about through natural selection, via competition for the resources that two or more phenotypes or species attempt to use". The development of this view of nature has involved an interplay of theory and observational studies found satisfactory by Hutchinson (1975). Support for the theory, however, seems largely based upon intuition and indirect evidence. Most often a set of closely related or ecologically similar species is selected for study.

Theory predicts that we may expect competition among such species over some set of resources, and the species must differ in order to coexist (Wiens 1977). Differences are of course found, and these are then labelled the mechanisms that permit coexistence (e.g. Fraser 1976). Direct documentations of competition are disappointingly few (Connell 1975), given the supposed theoretical importance of the process in organizing communities. The ubiquitous role of competition in nature has been questioned by some (e.g. Birch and Ehrlich 1967, Paine 1971, Dayton 1971, 1973, Connell 1975, Culver 1975, Menge and Sutherland 1976).

Competition theories on optimal foraging (e.g. Schoener 1971, MacArthur and Pianka 1966, Emlen 1973) predict that as resources become more abundant relative to demands, individuals should progressively restrict their diets, specializing on the optimal (most profitable) prey types or most productive habitat patches. "The basic procedure for determining optimal utilization of time or energy budgets is very simple: an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss. When any further enlargement would entail a greater loss than gain no such enlargement should take place. The problem is to find which components of a time or energy budget increase and which decrease as certain activities are enlarged" (MacArthur and Pianka 1966:603). In Pratt's study (1984) on frugivores, he found that when an aggressive frugivore is faced with competition from subordinate individuals, it may be reluctant to forfeit its claim to part or all of a fruiting plant. It is more beneficial for the dominant frugivore to stand and fight than to expend the energy to leave the source of abundant food in search of a new source.

Theory also predicts that coexisting species must differ to circumvent competition, and the degree of ecological overlap or divergence among coexisting species is often used as a measure of competitive intensity (Wiens 1977). Measures of body sizes or relative bird bill sizes have been investigated (Wilson 1975) and Pulliam (1975) observed that the probable importance of food competition among granivorous sparrows was indicated by the amazingly constant average ratio of bill sizes of adjacent pairs when the species are ranked by size. Brown (1975) proposed that body size differences were critical to the coexistence of desert rodents. Quantitative measures of the overlap in trophic morphology or feeding behaviors have been used as direct estimates of the intensity of competition among species (Cody 1974, 1975, Hespenheide 1975, Wiens and Rotenberry 1978).

It would seem that while studying competition primarily for food and status in a limited environment, it should be of the utmost importance to balance all the years of competitive theory with real life situations. One cannot discard years of carefully calculated theory, but these theories cannot always be applied to each situation occurring in nature. Even the most vigorous proponents of competition theory have noted that natural environments may indeed vary and that, if resources are superabundant, then the predictions of theory may not hold (Schoener 1974a, 1974b, Pianka 1974, 1976, Cody 1974, Colwell and Futuyma 1971, Vandermeer 1975), but they believe such situations to be rare (Wiens 1977). Wiens (1977), however, suggests that these conditions may be commonplace in many environments.

Competition is undoubtedly important in natural systems and may well play a critical role in determining the resource-utilization functions of populations (Wiens 1977). But in many cases it is likely to be an intermittent process (Grant 1972, Jaeger 1974, Conley 1976), and thus we should not always expect to find it in evidence. Ingeniously designed manipulative experiments (e.g. Grant 1972, 1975, DeBenedictis 1974, Schroder and Rosenzweig 1975) should be central to studies of competition. Rather than looking solely at the patterns of nature and inferring which mechanisms have produced them, attention must be directed to exploring the influences of various alternative and complementary processes upon the observed patterns (Wiens 1977).

ON TIME BUDGETS

Optimum fitness and survival and reproductive success demand that organisms can balance activities necessary to survive with the time and energy it takes to perform those same activities. Natural selection requires that all organisms be able to optimally allocate their time to these activities and a time budget study should reflect just that. Verner (1965) found that many factors influence the optimal allocation of time spent in certain activities, such as habitat, season, individual and a myriad of environmental factors. Quantification of habitat selection can delineate resources important to wildlife (Iverson et al. 1985 a,b), while time budgets reveal how available habitats are used (Frederick and Klaas, 1982). Natural selection should therefore favor the adaptable species, the species that maximize energy uptake while minimizing time spent, and science would favor an adaptable time budget methods as well. A time budget method should not only be able to evaluate and quantify an organism's interactions with is environment, but should also be able to provide insight into the evolution of the adaptive allocation patterns (King 1974, Ashkenazie and Safriel 1979, Biedenweg 1983). King (1974) has extensively studied the physical, morphological and ecological processes which influence avian energetics.

Orians (1961) was the first to use the time-energy budget as he studied the ecology of blackbirds (Agelaius) and the method has been used frequently since (e.g. Verbeek 1964, Schartz and Zimmerman 1971, Utter and LeFebvre 1971, Wolf and Hainsworth 1971, Wolf 1975, Tarboten 1978, Ashkenazie and Safriel 1979, Ettinger and King 1980, Biedenweg 1983, Shuman 1984, Weathers et al. 1984, Sullivan 1988). Despite its widespread use, contradictions did occur. There seemed to be no consistency in some energy cost rates for certain basic activities. While Tucker (1966) estimated bird flight as 6.25 x BMR (basal metabolic rate), Schartz and Zimmerman (1971) used 6.0 x EE (existence energy) for dickcissels (Spiza americana) and Wakely (1978) used 11.55 x SMR (standard metabolic rate) in raptors. While these rates could be expected to differ for the vastly different species involved, Utter (1971) and Biedenweg (1983), both studied mockingbirds (Mimus polyglottus) but arrived at rates of 12.0 x BMR and 9.4 x BMR, respectively, for the energetic costs of flight. Weathers et al. (1984) warn that the same time-budget data can give rise to widely different daily energy expenditures depending on the time budget analysis model used. Weathers et al. (1984) utilized a sophisticated battery of microcomputers and elaborate environmental measurements in attempt to accurately predict daily energy expenditures for loggerhead shrikes (*Lanius ludovicianus*), then analyzed their data by methods described by Pearson (1954), Kendeigh (1949) and Koplin et al. (1980). Ashkenazie and Safriel (1979) state that, while accuracy of the final energy budget may be affected by measuring energy cost rather indirectly in the time-energy budgets used by Pearson (1954), Orians (1961), Schartz and Zimmerman (1971), Stiles (1971), Wolf and Hainsworth (1971), Custer and Pitelka (1972), Wiens and Innis (1973) and Custer (1974), the direct method using the $D_2{}^{18}O$ techniques described by Gessaman (1973) does not produce a time-activity budget and does not provide insight into the adaptive significance of activity patterns.

ON UNCONFINED BIRDS

In recent years there has been a great deal of work done on the relationships between flocking behavior and feeding efficiency in wild birds, with many examining the effects of flocking on individual time budgets (e.g. Krebs 1974, Pulliam, et al. 1974, Powell 1974, Lazarus 1979, Caraco 1979a,b, Barnard 1980a, Schults et al. 1988). Pulliam (1973,1975), Pulliam et al. (1974) and Caraco (1979 a,b) all came to similar conclusions; in flock-feeding birds the amount of time a bird allocates to different behaviors may be influenced by the size and composition of the flock. Barnard

(1980a) examined this theory as it applied to House sparrows (*Passer domesticus*) and found that the organization of both flocking and the time budgeting of feeding behavior reflected the selective pressures of the habitat in which the birds were feeding. The "early warning function of flocking" as described by Lazarus (1979:855) emphasized the importance of early detection of predators and was supported by similar findings by Powell (1974) for starlings (*Sturnus vulgaris*) and Siegfried and Underhill (1975) for laughing gulls (*Larus atricilla*). Barnard (1980a) and Powell (1974) also found that birds in flocks were able to spend less time scanning for predators and more time feeding than individual birds. There is much information in the literature concerning interspecific interactions in mixed flocks (e.g. Morse 1970, 1978, Krebs 1973, Rubenstein, et.al. 1977, Kushlan 1977, 1978, Balph and Balph 1979, Caldwell 1981), ranging from the hypothesis held by Rubenstein et al. (1977) that observational learning and utilization of social cues tends to increase feeding efficiency and dietary overlap to the foraging commensalism found by Balph and Balph (1979) in pine siskins (*Carduelis pinus*) and Evening Grosbeaks (*Hesperiphona vespertina*). However, little attention has been paid to the effects of species composition within flocks on time budgeting and flocking dynamics of component species (Barnard, et.al. 1982). Many of these studies, however, concentrate on the breeding season and fail to recognize any seasonal changes in behavior. Several papers have illustrated seasonal contrasts, (e.g. Baker and Baker 1973, Ulfstrand 1977, Crome 1978, Herrera 1978, Smith, et al. 1978, Alatalo 1980). Rohwer's 1977 paper on status signalling in Harris' sparrows (Zonotrichia querula) emphasized winter feeding behavior and the mechanics of competition. Wagner (1981:973) asks some very important questions directed at seasonal shifts in behavior, such as, "Do niche breadths and overlaps between species shift seasonally? How are seasonal shifts in niche breadths and overlaps related to shifts in resource abundance?" and "Is there evidence that interspecific competition influences guild structure and its seasonal changes?" These seasonal changes and shifts in behavior are important and do demand to be investigated, as the ability of a species to mobilize energy under different environmental conditions may greatly affect its responses and behavior.This is shown by the limits it can extend its distribution, the size and fluctuations in its population in any area, whether or not it is a permanent resident, the time of year at which it initiates migration, nesting, and molt, the length of single migratory flights, the size of egg clutches, etc. (Kendeigh 1969). It has been documented that seasonal temperature changes demand physiological modification. Energy balance is the relation between energy intake and outgo, the latter being the existence and productive levels. If the total energy metabolized is less than the intake, the bird draws upon its reserves, loses weight, and dies (Kendeigh 1969). On the other hand, when intake is greater than outgo there is deposition of energy, partly carbohydrates but mostly fats, and the bird gains weight. When a drop in ambient temperature persists over one or more days, the gain in weight with feeding during the daytime becomes greater than the loss at night, so that an increase in weight occurs until a new balance is attained. In permanent resident species, bird weights during the winter average higher than during the summer (Kontogiannis 1968, Kendeigh 1969). Many other winter fattening experiments have supported this hypothesis (e.g. Baldwin and Kendeigh 1938, Dolnik and Blyumental 1964, Hagen 1942, Hayward 1965, Helms and Drury 1960, Inozemtzev 1964, Newton and Evans 1966). It would seem to follow that seasonal behavior changes would be expected to accompany the higher energy demands of winter.

This experiment was designed to examine the interactions of mixed species flocks of birds competing for food and shelter in "good habitats", areas with food plants high in caloric value and abundant shelter, and "poor habitats", areas with food plants low in caloric value and minimal shelter. The shelter values were drawn from the lay out of the experimental areas themselves and previous studies on plant usage by birds

(Robel and Browning 1981). The food values of the plant species present, their importance in bird diets, and seed preferences by birds were gleaned from the works of Kendeigh and West 1965, Willson 1971, Johnson and Robel 1968, Robel et al. 1974, Robel et al. 1979, and Robel and Slade 1965.

METHODS STUDY 1

Flight pen studies-- Time budgets of captive passerine birds while varying flock sizes, flock compositions and feeder availability.

During the winter of 1983-84 time budget studies were conducted on three species of passerine birds on the Konza Prairie Research Natural Area (KPRNA) in northeast Kansas. The experiment was designed to study the influence of both interspecific and intraspecific competition for food, water and cover on time budgets. This was accomplished by varying flock compositions, flock sizes and feeder availability within nine large flight pens located on the prairie.

KPRNA is a typical native tallgrass prairie located in northeast Kansas in Riley county, near Manhattan. This particular section of Kansas is located in what is known as the Flint Hills, a 48-80 km wide strip of land extending from Nebraska to Oklahoma consisting of rolling hills and valleys, quite uncharacteristic from the rest of the state. The rockiness of this part of the state contributed much to the preservation of the native prairies, which lend themselves much more to ranching than to farming (Hulbert, 1985).

Time budget data for the three species of birds were collected using a 6 x 6 Latin Square design blocking observers and pens (treatments) (Figure 1). A Latin Square is designed to provide randomness while cancelling consistent differences between subjects or orders when the differences between treatment means are taken (Snedecor and Cochran 1980). As figure 1 shows, I used pens as my treatment and the order was the order of observations conducted by research assistants on pens. The numbers along the top of the Latin Square each correspond to one of six observers. The individual birds themselves were randomly observed by one of the six observers once they had been randomly assigned their pen.

Test birds for the three species of birds [12 test northern cardinals plus 3 reserve birds; 12 test tree sparrows plus 3 reserve birds; and 6 test Harris' sparrows plus 3 reserve birds] were captured in the Manhattan, Kansas area using 1.9-cm2 mesh mist nets during December 1983 and January 1984. Cardinals and Harris' sparrows were considered to be medium sized birds, with mean weights of 37.9g and 33.5g, respectively, from a sample of 14 birds of each species kept in pens for the duration of the experiment. Tree sparrows were considered to be small birds with a mean

OBSERVERS

Order of observation of pens	1	2	3	4	5	6
1	D	B	C	F	A	E
2	B	F	A	D	E	C
3	E	C	D	A	B	F
4	C	A	B	E	F	D
5	A	E	F	C	D	B
6	F	D	E	B	C	A

Figure 1. Latin square design showing order of observations by observers, using pens as treatments. Each letter, A-F, corresponded to one of six pens. Each observer, 1-6, was assigned a bird to observe in one of the six pens for each data sheet. Pens were observed by each observer in the order shown in the column corresponding to the observer.

weight from a sample captive population of 13 birds of 20.4g. The birds were banded with numbered aluminum and colored plastic bands so that individual birds could be identified. The birds were confined in six 9.0 x 4.7 x 2.3-m flight pens constructed of 1.3 cm mesh hardware cloth over a wooden frame built of 5cm x 5cm boards. Throughout the study the birds were provided an _ad libitum_ diet of white proso millet (_Panicum miliaceum_) and fresh water. A dense cone of red cedar (_Juniperus virgiana_) boughs was constructed in the center of the pen for cover and protection of the birds from the weather (Figure 2).

When the desired number of birds was captured, they were randomly assigned to their respective pens. Pen assignments in the first half of this experiment included: three single species pens, one for each species with three individuals in each pen; two 6-bird, 2-species pens, one with 3 cardinals and 3 tree sparrows (medium birds vs. small birds) and one with 3 cardinals and 3 Harris' sparrows (medium birds vs. medium birds); and one 9-bird, 3-species pen with three individuals from each species (Figure 3). Reserve birds of all three species to be used as replacements for mortalities or accidental escapes were also banded and kept in holding pens of similar construction, but approximately half the size of the experimental pens, on the site at a

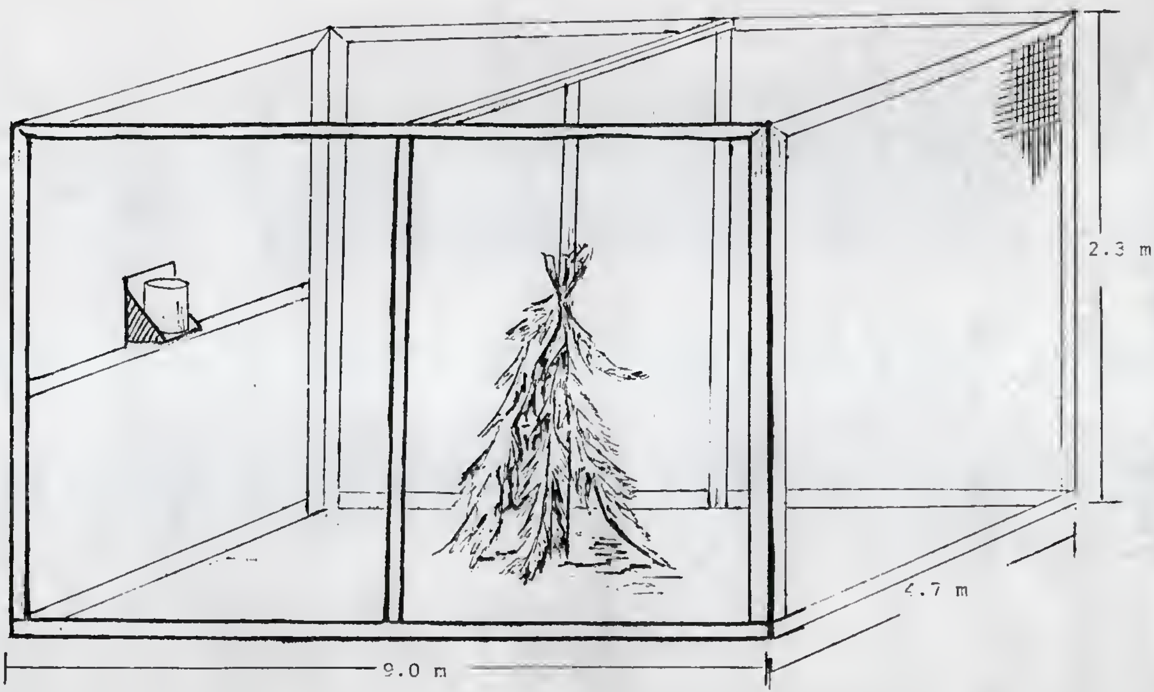


Figure 2. Sketch of flight pen with cedar boughs for protection of birds from the weather. A feeder is shown on the left wall. Feeders were present in the ratio required in the experiments. Feeders were placed in random lo-

6 Bird pen 3 Cardinals 3 Harris' sparrows Pen F	3 Bird pen 3 Tree sparrows Pen E
6 Bird pen 3 Cardinals 3 Tree sparrows Pen D	9 Bird pen 3 Cardinals 3 Harris'sparrows 3 Tree sparrows Pen C
3 Bird pen 3 Cardinals Pen B	3 Bird pen 3 Harris'sparrows Pen A

Figure 3. Pen assignments for the first half of the 1983-1984 experiment on KPRNA. The first half of this experiment utilized low numbers of birds in single species flocks and a feeder ratio of one feeder per bird.

distance to prevent interaction with the test birds. These birds were fed and watered the same way as the experimental birds. Experimental birds were re-randomized midway through the first half of the experiment. The first half of the experiment was conducted between 29 January and 3 March, 1984.

The diet of white proso millet remained the same throughout the experiment--only the ratio of feeding stations to birds varied. This diet was selected on the basis of its characteristically low gross energy content and low handling time (Shuman, 1984). Due to the nature of this food source, the birds had ample access to a highly desirable diet, yet that diet required high consumption rates in order to meet energy demands.

In the second half of the experiment (conducted between 18 March and 21 April, 1984) pen arrangement included: three single species pens, this time with 9 individuals in each pen; two 6-bird, 2-species pens, one with 3 cardinals and 3 tree sparrows and one with 3 cardinals and 3 Harris' sparrows; and one 9-bird, 3-species pen with 3 individuals from each species (Figure 4). Birds were randomized to pens to begin the experiment but not re-randomized during the second half of the experiment.

6 Bird pen 3 Cardinal 3 Harris' sparrows Pen F	9 Bird pen 9 Tree sparrows Pen E
6 Bird pen 3 Cardinals 3 Tree sparrows Pen D	9 Bird pen 3 Cardinals 3 Harris'sparrows 3 Tree sparrows Pen C
9 Bird pen 9 Cardinals Pen B	9 Bird pen 9 Harris'sparrows Pen A

Figure 4. Pen assignments for the second half of the 1983-1984 experiment on KPRNA. The second half of this experiment utilized greater numbers of birds in single species flocks than in the first half and a feeder ratio of 1 feeder per three birds.

In the first half of the 1983-84 experiment feeders made of covered 1-pound coffee cans (volume 1030 ml) inverted on a wooden platform and mounted on the walls of the pens were kept filled with millet. Feeders were available at a ratio of one per bird. In the second half of the experiment the same feeders filled with the same type of food source were provided at a ratio of one per every three birds. Water was provided ad libitum throughout the experiment in plastic tubs equipped with perches. Warm water was added daily in periods of freezing temperatures when snow was not available.

Six Kansas State University undergraduate students were hired to collect data through observations and were trained by me personally in an attempt to insure consistency in observational techniques. They were all made familiar with the site, the birds and the proper techniques before the experiment began. I used the same six research assistants throughout the entire 1983-84 experiment. All observations were made from inside one of the 91 x 183 x 91 cm blinds adjacent to the flight pens (Figure 5). The four blinds consisted of plywood sides with corrugated plastic roofing, hinged observation windows, and benches for the comfort of the research assistants. The observation windows were kept closed until the research assistant was in position and

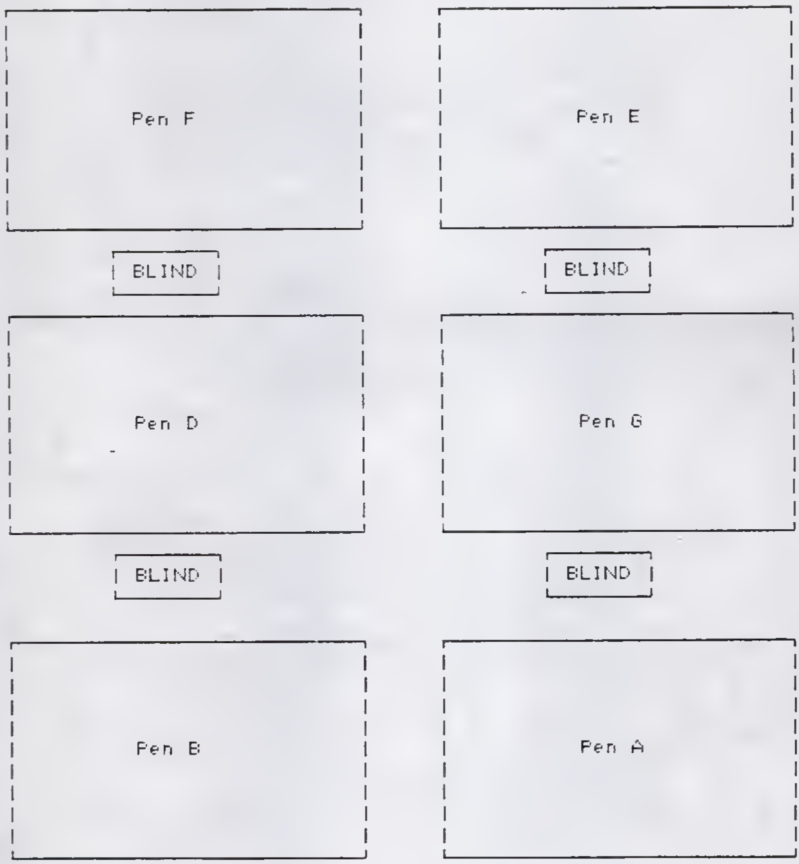


Figure 5. Location of observation blinds in relation to pens on KPRNA.

ready to begin collecting behavioral data. Data were collected at 10-second intervals signalled by portable metronomes, using the methods described by Wiens et al. (1970), and recorded on data sheets which had been pre-labelled to show each research assistant which bird to observe and the order in which to observe. Each day was divided into four quarters (early morning, late morning, early afternoon and late afternoon). Scheduling problems prohibited equal observations in all quarters, so I attempted to schedule as evenly as possible.

Behavioral activities recorded included: feeding at the feeders (FF), flying (FLY), drinking (DR), sitting (SIT), feeding on the ground (FG), miscellaneous activities (MSC), submission (SUB), attacking with contact (AC), attacking by visual threat (AV1), attack with a vocal threat (AV0), attack with both visual and vocal threats but no contact (AV2), and standing on the ground (SG). For a full description of the definition of the activities listed above, see the glossary in Appendix 1. Each behavioral activity had a corresponding abbreviation which was used in compiling the data sheets. An example of a data sheet is shown in Appendix 2.

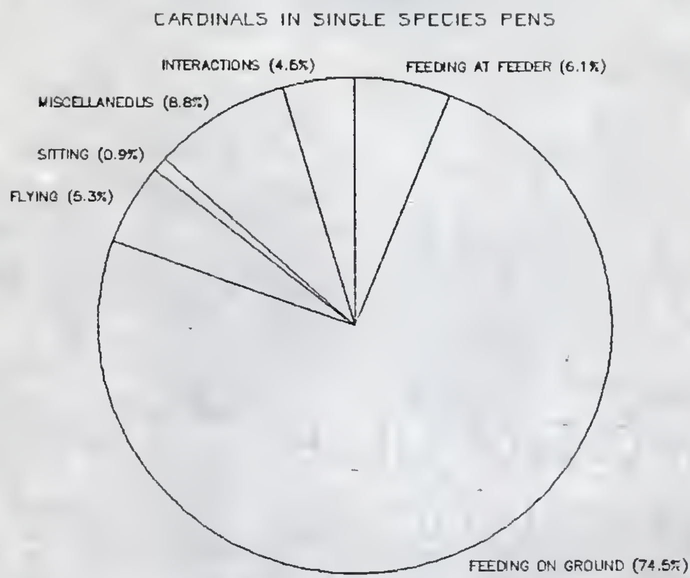
RESULTS STUDY 1

Single species flocks-some general characteristics

When all the main effects [experiment (the effect of the two halves of this experiment which illustrated the flock compositions and feeder ratios), quarter and observer] were combined and single species pens were observed for some general species-related tendencies, it was observed that all three species spent the largest percentage of time in the activity the observers interpreted as feeding on the ground, ranging from 74.5% for cardinals to 73.2% for Harris' sparrows. The next highest category varied with species, with interactions being next highest for tree sparrows and Harris' sparrows with values of 11.5% and 11.7%, respectively, while cardinals spent only 4.5% of their time interacting with one another. Of all the interaction categories, submission was highest for all three species, with values of 11.5% for Harris' sparrows, 11.3% for tree sparrows and 4.3% for cardinals. The lowest of the interactions was the attack with visual and vocal threat with no contact, with no interactions recorded for the three species in the single species pens. Cardinals spent their next highest percentage of time in the miscellaneous category with a value of 8.8% while Harris' sparrows had a value just slightly lower at 8.5% followed by tree sparrows at 8.0% (Figures 6-8).

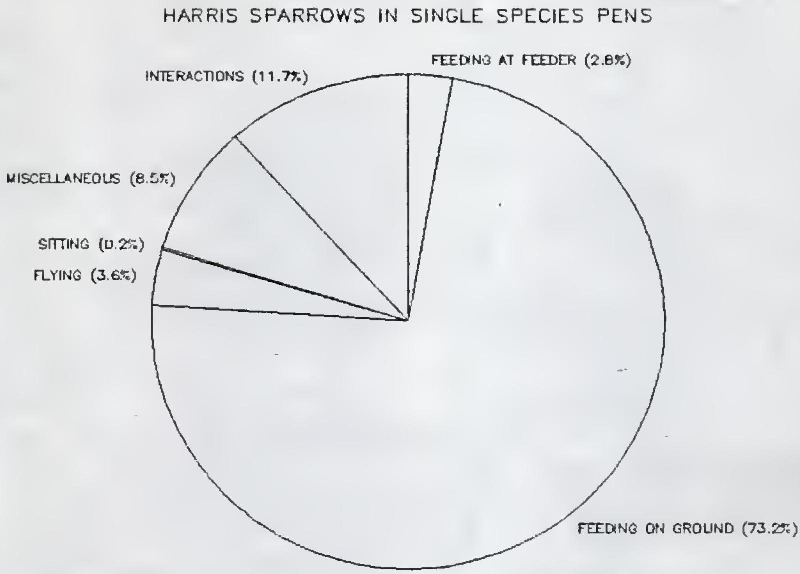
Flock composition

The effect of flock composition was analyzed by comparing the combinations of birds in pens: single species pens vs. two species pens vs. three species pens. (Tables 1 and 2). There were 3 single species pens, one for each species, 2 six bird two species pens, one with 3 cardinals and 3 Harris' sparrows and one with 3 cardinals and 3 tree sparrows, and 1 nine bird three species pen with 3 cardinals, 3 Harris' sparrows and 3 tree sparrows. In experiment 1, the largest percentage of time again was spent feeding on the ground, with values highest in the single species pens at 76.7%, next highest at 69.3% for the three species pens and lowest at 63.8% for the two species pens. While single species pens and 3 species pens exhibited considerably less feeding on the ground activity, (single species pens decreasing from 76.7% to 61.2%, 3 species pens decreasing from 63.8% to 53.9%) the 2 species pens increased feeding on the ground slightly, from 63.8% to 66.7%. Feeding at the feeder decreased for all three combinations from the first half of the experiment to the second half from a high for single species pens of 8.8% to a low of 1.8%. When interactions were grouped together, they, as a category, also decreased for all



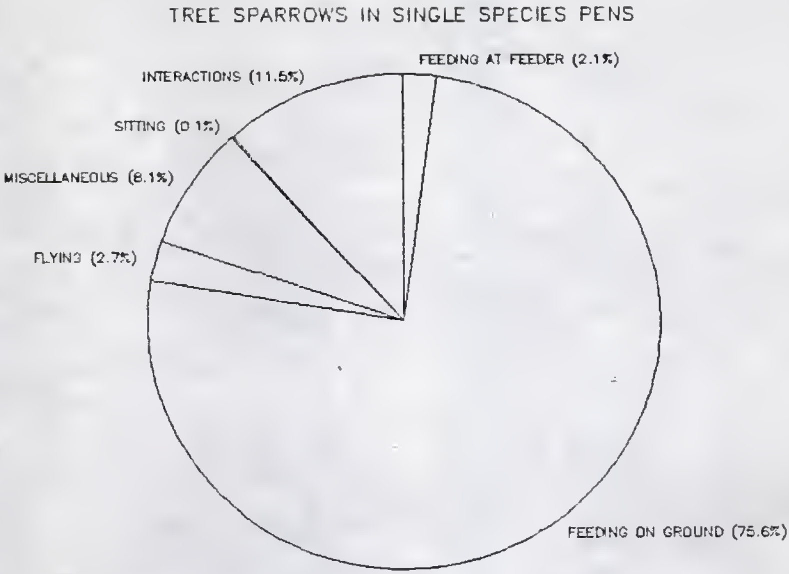
BEHAVIOR	PERCENT OF TIME
STANDING ON GROUND	0.00 ±0.01
FEEDING AT FEEDER	6.06 ±1.04
FEEDING ON GROUND	74.51 ±3.68
FLYING	5.25 ±0.70
SITTING	0.93 ±0.22
MISCELLANEOUS	8.79 ±1.39
INTERACTIONS:	
SUBMISSION	4.27 ±2.19
ATTACK WITH CONTACT	0.13 ±0.06
ATTACK WITH VISUAL THREAT	0.02 ±0.01
ATTACK WITH VOCAL THREAT	0.04 ±0.03
ATTACK WITH VISUAL & VOCAL	0.00 ±0.01

Figure 6. Pie chart for Cardinals in single species Cardinal pens. This activity breakdown combines all the variable main effects: time of day, feeder ratio, flock size and observer.



BEHAVIOR	PERCENT OF TIME
STANDING ON GROUND	0.01 ±0.01
FEEDING AT FEEDER	2.82 ±0.94
FEEDING ON GROUND	73.19 ±3.31
FLYING	3.62 ±0.63
MISCELLANEOUS	8.48 ±1.25
SITTING	0.20 ±0.20
INTERACTIONS:	
SUBMISSION	11.46 ±1.97
ATTACK WITH CONTACT	0.14 ±0.06
ATTACK WITH VISUAL THREAT	0.01 ±0.01
ATTACK WITH VOCAL THREAT	0.07 ±0.03
ATTACK WITH VISUAL & VOCAL	0.00 ±0.01

Figure 7: Pie chart for Harris' sparrows in single species Harris' sparrow pens. This activity breakdown combines all the variable main effects: time of day, feeder ratio, flock size and observer.



BEHAVIOR	PERCENT OF TIME
STANDING ON GROUND	0.00 ±0.01
FEEDING AT FEEDER	2.08 ±1.04
FEEDING ON GROUND	75.62 ±3.67
FLYING	2.66 ±0.69
MISCELLANEOUS	8.05 ±1.39
SITTING	0.11 ±0.22
INTERACTIONS:	
SUBMISSION	11.34 ±2.18
ATTACK WITH CONTACT	0.05 ±0.06
ATTACK WITH VISUAL THREAT	0.01 ±0.01
ATTACK WITH VOCAL THREAT	0.08 ±0.03
ATTACK WITH VISUAL & VOCAL	0.00 ±0.01

Figure 8. Pie chart for Tree sparrows in single species Tree sparrow pens. This activity breakdown combines all the variable main effects: time of day, feeder ratio, flock size and observer.

three combinations from the first half of the experiment to the second, with single species pens decreasing from 4.1% to 3.1%, 2 species pens decreasing from 14.1% to 4.6%, and 3 species pens decreasing from 10.8% to 8.1%.

Table 1. Means and standard errors of proportions of daily activity spent in differenct behavioral activities for all bird species combined in all three types of flock compositons, (single-species, two-species, three species) during the winter of 1983-1984. These are the results from experiment 1, the first half of the first year's research. Flock sizes ranged from 3 birds in the single-species pens to 6 birds in the two-species pens to 9 birds in the three-species pens. Feeder ratios were 1 per bird. Common superscripts across a row indicate values that do not differ. (P=0.05)

	Pen compositions (all species combined)			
Behaviors	Single-species pens	Two species-pens	Three-species pens	SE
Feeding at feeder	8.78^{A}	5.64^{A}	5.55^{A}	±4.15
Flying	5.95^{A}	2.67^{B}	5.40^{A}	±1.76
Sitting	0.84^{A}	0.36^{A}	0.34^{A}	±0.28
Feeding on ground	76.72^{A}	63.80^{B}	$69.35^{A,B}$	±6.48
Miscellaneous	2.23^{A}	6.69^{B}	$5.28^{A,B}$	±2.28
Submission	3.86^{A}	13.91^{B}	$10.48^{A,B}$	±5.11
Attack/contact	0.19^{A}	0.18^{A}	0.19^{A}	±0.01
Attack/visual threat	0.03^{A}	$0.01^{A,B}$	0.00^{B}	±0.01
Attack/vocal threat	0.06^{A}	0.02^{A}	0.08^{A}	±0.03
Attack/visual & vocal	0.00^{A}	0.00^{A}	0.01^{A}	±0.01
Standing on ground	0.00^{A}	0.01^{A}	0.01^{A}	±0.01

Table 2. Means and standard errors of proportions of daily activity spent in different behavioral activities for all bird species combined in all three types of flock compositions, (single-species, two-species, three-species) during the winter of 1983-1984. These are the results for experiment 2, the second half of the first year's research. Flock sizes ranged from 9 birds in the single-species pens to 6 birds in the two-species pens to 9 birds in the three-species pens. Feeder ratios were 1 per every 3 birds. Common superscripts across a row indicate values that do not differ. ($P=0.05$)

	Pen compositions (all species combined)			
Behaviors	Single-species pens	Two-species pens	Three-species pens	SE
Feeding at feeder	1.85^{A}	3.62^{A}	1.92^{A}	±1.00
Flying	4.10^{A}	4.11^{A}	4.35^{A}	±0.14
Sitting	0.85^{A}	0.12^{A}	0.44^{A}	±0.36
Feeding on ground	$61.18^{A,B}$	$66.71^{A,B}$	53.86^{A}	±6.45
Miscellaneous	13.69^{A}	6.57^{B}	12.53^{A}	±3.82
Submission	3.07^{A}	4.42^{A}	7.97^{B}	±2.53
Attack/contact	0.03^{A}	0.12^{A}	0.09^{A}	±0.01
Attack/visual threat	0.02^{A}	0.00^{A}	0.02^{A}	±0.01
Attack/vocal threat	0.02^{A}	0.09^{A}	0.03^{A}	±0.04
Attack/visual & vocal	0.00^{A}	0.01^{A}	0.00^{A}	±0.01
Standing on ground	0.00^{A}	0.01^{A}	0.00^{A}	±0.01

Species combinations

This particular analysis is a general comparison and is designed to show general trends. These same combinations of birds are analyzed more specifically later in the interspecific interactions section.

Feeding on the ground was consistently the category in which all combinations of birds spent the most time. The most time spent in this category was 68.7% for cardinals alone and the least time spent was 55.1% for tree sparrows alone. The interactive category of submission the next highest for Harris' sparrows alone who spent 10.4% of their time submitting while cardinals alone had the lowest value of 3.6%. Miscellaneous activities were the next highest, with the cardinal-tree sparrow combination spending 8.6% of their time in these activities, while the birds in the tree sparrow single-species pen only spent 5.9% of their time in this category. The aggressive interactions were all low and saw no general trends from single species to multiple species pens (Table 3).

Experiment

The category of experiment was analyzed first by comparing the first half of the experiment to the second half while combining all other factors (quarter, bird species) to observe the general trends between single species and multiple species pens (Tables 4 and 5). By comparing between halves of the experiment, the effect of increased numbers of birds in the single species pens and decreased available feeders per bird was seen.

Table 3. Means and standard deviations of proportions of daily activity spent in different behavioral activities for all flock combinations in outdoor pens during the winter of 1983-1984. Each species was represented in a single-species pen, two pens contained two-species flocks with cardinals in combination with the two sparrow species, and a sixth pen contained all three species. This table represents results combined for both experiment 1 and 2. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2.

	Flock compositions					
Behaviors	Cardinal	Harris' sparrow	Tree sparrow	Cardinal-Harris'	Cardinal-Tree	Cardinal-Harris'-Tree
Feeding at feeder	5.59 ±1.04	2.56 ±0.94	1.52 ±1.04	5.03 ±0.97	3.72 ±1.10	3.55 ±0.75
Flying	4.84 ±0.70	3.29 ±0.63	1.94 ±0.69	4.29 ±0.65	3.69 ±0.73	4.91 ±0.50
Sitting	0.86 ±0.22	0.16 ±0.20	0.06 ±0.22	0.21 ±0.20	0.33 ±0.23	0.42 ±0.16
Feeding on ground	68.71 ±3.68	66.48 ±3.31	55.12 ±3.67	67.09 ±3.42	61.04 ±3.87	63.48 ±2.64
Miscellaneous	6.11 ±1.39	7.70 ±1.25	5.87 ±1.39	6.12 ±1.30	8.63 ±1.47	7.88 ±1.06
Submission	3.62 ±2.19	10.41 ±1.97	8.27 ±2.18	9.49 ±2.04	8.99 ±2.31	7.83 ±1.57
Attack/contact	0.11 ±0.06	0.13 ±0.06	0.04 ±0.06	0.13 ±0.06	0.20 ±0.07	0.10 ±0.05
Attack/visual	0.02 ±0.01	0.01 ±0.01	0.01 ±0.01	0.00 ±0.01	0.00 ±0.01	0.01 ±0.01
Attack/vocal	0.04 ±0.03	0.06 ±0.03	0.06 ±0.03	0.00 ±0.03	0.13 ±0.03	0.04 ±0.02
Attack/visual & vocal	0.00 ±0.01	0.00 ±0.01	0.00 ±0.01	0.00 ±0.01	0.03 ±0.01	0.01 ±0.01
Standing on ground	0.00 ±0.01	0.01 ±0.01	0.00 ±0.01	0.02 ±0.01	0.00 ±0.01	0.00 ±0.01

Table 4. Means and standard deviations of proportions of daily activity spent in different behavioral activities for all flock combinations in outdoor pens during the winter of 1983-1984. Each species was represented in a single-species pen, two pens contained two-species flocks with cardinals in combination with the two sparrow species, and a sixth pen contained all three species. This table represents results from experiment 1. Experiment 1 and 2 designate the irst and secon half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2.

	Flock compositions					
Behaviors	Cardinals	Harris'sparrows	Tree sparrows	Cardinal-Harris'	Cardinal-Tree	Cardinal-Harris'-Tree
Feeding at feeder	8.92 ±1.75	2.85 ±1.49	0.74 ±1.74	6.95 ±1.16	3.97 ±1.11	5.43 ±0.78
Flying	5.56 ±1.17	2.54 ±0.99	2.21 ±1.16	2.93 ±0.77	3.60 ±0.74	5.33 ±0.52
Sitting	0.90 ±0.37	0.27 ±0.31	0.09 ±0.36	0.34 ±0.24	0.35 ±0.23	0.37 ±0.16
Feeding on ground	76.10 ±6.17	66.01 ±5.26	57.14 ±6.13	63.24 ±4.08	65.83 ±3.90	69.41 ±2.73
Miscellaneous	2.75 ±2.34	6.81 ±1.99	5.19 ±2.32	7.43 ±1.54	5.07 ±1.48	5.17 ±1.03
Submission	3.98 ±3.67	12.77 ±3.14	10.69 ±3.65	15.20 ±2.43	11.51 ±2.32	10.43 ±1.63
Attack/contact	0.19 ±0.11	0.05 ±0.91	0.00 ±0.11	0.15 ±0.71	0.19 ±0.07	0.20 ±0.05
Attack/visual threat	0.03 ±0.02	0.00 ±0.02	0.01 ±0.02	0.01 ±0.01	0.00 ±0.01	0.00 ±0.01
Attack/vocal threat	0.06 ±0.06	0.04 ±0.05	0.00 ±0.06	0.01 ±0.04	0.05 ±0.03	0.08 ±0.02
Attack/visual & vocal	0.00 ±0.01	0.00 ±0.01	0.00 ±0.01	0.00 ±0.01	0.02 ±0.01	0.01 ±0.01
Standing on ground	0.00 ±0.02	0.01 ±0.02	0.00 ±0.02	0.01 ±0.01	0.00 ±0.01	0.00 ±0.01

Table 5. Means and standard deviations of proportions of daily activity spent in different behavioral activities for all flock combinations in outdoor pens during the winter of 1983-1984. Each species was represented in a single-species pen, two pens contained two-species flocks with cardinals in combination with the two sparrow species, and a sixth pen contained all three species. This table represents results from experiment 2. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2.

	Flock compositions					
Behavior categories	Cardinals	Harris' sparrows	Tree sparrows	Cardinal-Harris'	Cardinal-Tree	Cardinal-Harris'-Tree
Feeding at feeder	2.26 ±1.14	2.26 ±1.14	2.31 ±1.14	3.11 ±1.57	3.47 ±1.90	1.67 ±1.30
Flying	4.12 ±0.76	4.03 ±0.76	1.66 ±0.76	5.66 ±1.04	3.78 ±1.27	4.49 ±0.87
Sitting	0.83 ±0.24	0.09 ±0.24	0.08 ±0.24	0.75 ±0.33	0.30 ±0.40	0.47 ±0.27
Feeding on ground	61.31 ±4.02	66.95 ±4.03	53.09 ±4.03	70.94 ±5.52	56.25 ±6.70	57.55 ±4.60
Miscellaneous	13.47 ±1.52	8.59 ±1.52	6.54 ±1.52	4.81 ±2.09	12.20 ±2.54	10.58 ±1.74
Submission	3.25 ±2.40	8.05 ±2.40	5.84 ±2.40	3.78 ±3.29	6.46 ±3.99	5.24 ±2.74
Attack/contact	0.03 ±0.07	0.21 ±0.07	0.07 ±0.07	0.10 ±0.10	0.20 ±0.12	0.00 ±0.08
Attack/visual threat	0.02 ±0.01	0.02 ±0.01	0.03 ±0.01	0.00 ±0.02	0.00 ±0.02	0.01 ±0.01
Attack/vocal threat	0.02 ±0.04	0.07 ±0.04	0.12 ±0.04	0.00 ±0.05	0.22 ±0.06	0.01 ±0.04
Attack/visual & vocal	0.00 ±0.01	0.01 ±0.01	0.00 ±0.01	0.00 ±0.01	0.04 ±0.01	0.01 ±0.01
Standing on ground	0.00 ±0.01	0.05 ±0.01	0.00 ±0.01	0.00 ±0.01	0.00 ±0.02	0.00 ±0.01

These two factors seemed to have the greatest impact upon the proportion of time the birds spent feeding at the feeder. The percent of time spent feeding at the feeders decreased for all combinations of birds except the single species tree sparrow pen from the first half to the second half. The larger numbers of birds and fewer available feeder sites seemed to affect the birds in the single species cardinal pen the most, with time spent feeding at the feeder significantly declining 6.6 percentage points from 8.9% in the first half to 2.3% in the second half. The cardinals did not compensate for their lost feeding time by increasing the amount of time they spent feeding on the ground, but instead also significantly reduced the amount of time spent in that activity from 76.1% to 61.3%. The cardinals in the first half spent 10.7% more time in miscellaneous activities (hopping, preening, etc.) than in the second half, with this category compensating for much of the lost feeding time and representing the only other significantly different activity from the first half to the second (Table 6).

Tree sparrows, however, increased the amount of time they spent feeding at the feeder 1.6 percentage points from 0.7% in the first half to 2.3% in the second half, although this was not a significant difference.

These birds did spend slightly less time feeding on the ground (57.1% to 53.1%) and divided the time they had spent in submitting behavior in half, going from 10.7% in the first half to 5.8% in the second half, although, again, these differences were not significant. Tree sparrows exhibited no significant differences between halves of the experiment in the single species pen (Table 8).

The single species Harris' sparrow pen seemed relatively unaffected by the addition of birds or subtraction of feeders. The only significantly different activity was the standing on the ground category which increased from the near negligible value of 0.01% in the first half to 0.05% in the second half. Time spent feeding at the feeders decreased only 0.6 percentage points from 2.9% to 2.3% from the first half to the second and time spent feeding on the ground only increased 0.9 percentage points from 66.0% to 66.9% between the two halves. The greatest difference for single species Harris' sparrows (although it was not significantly different) came in the submission category, with a decline from 12.8% to 8.1% between the two halves (Table 7).

The birds in the cardinal-Harris' sparrow pen decreased the amount of time they spent feeding at the feeder from 6.9% in the first half to 3.1% in the second and increased the amount of time they spent feeding on the ground from 63.2% to 70.9% from the first half to the second, although neither of these differences were significant. These birds did show significant differences in the category of flying, increasing the proportion of time they spent flying from 2.9% in the first half to 5.7% in the second half, and in the category of submission, with the decrease in the number of available feeder locations causing the proportion of time spent submitting to another bird to drop from 15.2% in the first half to 3.8% in the second half (Table 9).

The birds in the cardinal-tree sparrow combination did not show significant differences in the feeding on the ground or feeding at the feeder categories, although both categories exhibited decreases in the proportion of time spent in the first half of the experiment versus the second half (feeding at the feeder decreasing from 4.0% to 3.5% and feeding on the ground decreasing from 65.8% to 56.2%). These birds did show significant differences due to the fewer available feeders in the miscellaneous activities, with birds spending 5.1% of their time in this category in the first half and 12.2% in the second half. The time spent in the attack with visual threat also increased slightly but significantly from the first half to the second from 0.1% to 0.2% (Table 10).

The 3 species pen containing the combination of cardinals, Harris' sparrows and tree sparrows seemed to be the most affected by the limited feeder availability in experiment 2, as 4 of the 11 behavior activities exhibited significant differences. Both feeding categories decreased in the proportions of time spent from experiment 1 to experiment 2, with the percent of time spent feeding at the feeder decreasing from 5.4% to 1.7% and the percent of time spent feeding on the ground decreasing from 69.4% to 57.5%. The proportion of time spent in miscellaneous activities increased from experiment 1 to experiment 2 with values of 5.2% and 10.6%, respectively. The only interactive category to display any significant differences due to the limited feeding opportunities was the attack with contact category which decreased from 0.2% in experiment 1 to 0.0% in experiment 2 (Table 11).

When experiment was analyzed by grouping all birds in all combinations together significant differences were seen in the feeding at the feeder activity, which decreased from 4.8% in experiment 1 to 2.5% in experiment 2, the miscellaneous activity, which increased from 5.4% in experiment 1 to 9.4% in experiment 2, and the submission category, which decreased from 10.8% in experiment 1 to 5.4% in experiment 2 (Table 12).

Table 6. Means and standard deviations of proportions of daily activity spent in different behavioral activities for the single-species cardinal pen during the winter of 1983-1984. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicated no significant differences (P=0.05).

	Effect of flock composition, flock size and feeder ratios	
Behaviors	Experiment 1	Experiment 2
Feeding at feeder	8.92 ±1.75[A]	2.26 ±1.14[B]
Flying	5.56 ±1.17[A]	4.12 ±0.76[A]
Sitting	0.90 ±0.37[A]	0.83 ±0.24[A]
Feeding on ground	76.10 ±6.17[A]	61.31 ±4.02[B]
Miscellaneous	2.75 ±2.34[A]	13.47 ±1.52[B]
Submission	3.98 ±3.67[A]	3.25 ±2.40[A]
Attack/contact	0.19 ±0.11[A]	0.03 ±0.07[A]
Attack/visual threat	0.03 ±0.02[A]	0.02 ±0.01[A]
Attack/vocal threat	0.06 ±0.06[A]	0.02 ±0.04[A]
Attack/visual & vocal	0.00 ±0.01[A]	0.00 ±0.01[A]
Standing on ground	0.00 ±0.02[A]	0.00 ±0.01[A]

Table 7. Means and standard deviations of proportions of daily activity spent in different behavioral activities for the single-species Harris' sparrow pen during the winter of 1983-1984. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05)

	Effect of flock composition, flock size and feeder ratios	
Behaviors	Experiment 1	Experiment 2
Feeding at feeder	2.85 ±1.49^{A}	2.26 ±1.14^{A}
Flying	2.54 ±0.99^{A}	4.03 ±0.76^{A}
Sitting	0.27 ±0.31^{A}	0.09 ±0.24^{A}
Feeding on ground	66.01 ±5.26^{A}	66.95 ±4.03^{A}
Miscellaneous	6.81 ±1.99^{A}	6.59 ±1.52^{A}
Submission	12.77 ±3.14^{A}	8.05 ±2.40^{A}
Attack/contact	0.05 ±0.91^{A}	0.21 ±0.07^{A}
Attack/visual threat	0.00 ±0.02^{A}	0.02 ±0.01^{A}
Attack/vocal threat	0.04 ±0.05^{A}	0.07 ±0.04^{A}
Attack/visual & vocal	0.00 ±0.01^{A}	0.01 ±0.01^{A}
Standing on ground	0.01 ±0.02^{A}	0.05 ±0.01^{B}

Table 8. Means and standard deviations of proportions of daily activity spent in different behavioral activities by tree sparrows in single-species pens during the winter of 193-1984. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05).

	Effect of flock composition, flock size and feeder ratios	
Behavior categories	Experiment 1	Experiment 2
Feeding at feeder	0.74 ±1.74[A]	2.31 ±1.14[A]
Flying	2.21 ±1.16[A]	1.66 ±0.76[A]
Sitting	0.09 ±0.36[A]	0.08 ±0.24[A]
Feeding on ground	57.14 ±6.13[A]	53.09 ±4.03[A]
Miscellaneous	5.19 ±2.32[A]	6.54 ±1.52[A]
Submission	10.69 ±3.65[A]	5.84 ±2.40[A]
Attack/contact	0.05 ±0.11[A]	0.07 ±0.07[A]
Attack/visual threat	0.01 ±0.02[A]	0.03 ±0.01[A]
Attack/vocal threat	0.00 ±0.06[A]	0.12 ±0.04[A]
Attack/visual & vocal	0.00 ±0.01[A]	0.00 ±0.01[A]
Standing on ground	0.00 ±0.02[A]	0.00 ±0.01[A]

Table 9. Means and standard deviations of proportions of daily activity spent in different behavioral activities by the birds in the 6 bird cardinal-Harris' sparrow pen during the winter of 1983-1984. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05).

	Effect of flock composition, flock size and feeder ratio	
Behaviors	Experiment 1	Experiment 2
Feeding at feeder	6.95 ±1.16[A]	3.11 ±1.57[A]
Flying	2.93 ±0.77[A]	5.66 ±1.04[B]
Sitting	0.34 ±0.24[A]	0.75 ±0.33[A]
Feeding on ground	63.24 ±4.08[A]	70.94 ±5.52[A]
Miscellaneous	7.43 ±1.54[A]	4.81 ±2.09[A]
Submission	15.20 ±2.43[A]	3.78 ±3.29[B]
Attack/contact	0.15 ±0.71[A]	0.10 ±0.10[A]
Attack/visual threat	0.01 ±0.01[A]	0.00 ±0.02[A]
Attack/vocal threat	0.01 ±0.04[A]	0.00 ±0.05[A]
Attack/visual & vocal threat	0.00 ±0.01[A]	0.00 ±0.01[A]
Standing on ground	0.01 ±0.01[A]	0.00 ±0.01[A]

Table 10. Means and standard deviations of daily activity spent in different behavioral activities by the birds in the 6 bird cardinal-tree sparrow pen during the winter of 1983-1984. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05).

	Effect of flock composition, flock size and feeder ratio	
Behaviors	Experiment 1	Experiment 2
Feeding at feeder	3.97 ±1.11[A]	3.47 ±1.90[A]
Flying	3.60 ±0.74[A]	3.78 ±1.27[A]
Sitting	0.35 ±0.23[A]	0.30 ±0.40[A]
Feeding on ground	65.83 ±3.90[A]	56.25 ±6.70[A]
Miscellaneous	5.07 ±1.48[A]	12.20 ±2.54[B]
Submission	11.51 ±2.32[A]	6.46 ±3.99[A]
Attack/contact	0.19 ±0.07[A]	0.20 ±0.12[A]
Attack/visual threat	0.00 ±0.01[A]	0.00 ±0.02[A]
Attack/vocal threat	0.05 ±0.03[A]	0.22 ±0.06[B]
Attack/visual & vocal threat	0.02 ±0.01[A]	0.04 ±0.01[A]
Standing on ground	0.00 ±0.01[A]	0.00 ±0.02[A]

Table 11. Means and standard deviations of proportions of daily activity spent in different behavioral activities by the birds in the 9 bird cardinal-Harris' sparrow-tree sparrow pen during the winter of 1983-1984. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences ($P=0.05$).

	Effect of flock composition, flock size and feeder ratio	
Behaviors	Experiment 1	Experiment 2
Feeding at feeder	5.43 ±0.78^{A}	1.67 ±1.30^{B}
Flying	5.33 ±0.52^{A}	4.49 ±0.87^{A}
Sitting	0.37 ±0.16^{A}	0.47 ±0.27^{A}
Feeding on ground	69.41 ±2.73^{A}	57.55 ±4.60^{B}
Miscellaneous	5.17 ±1.03^{A}	10.58 ±1.74^{B}
Submission	10.43 ±1.63^{A}	5.24 ±2.74^{A}
Attack/contact	0.20 ±0.05^{A}	0.00 ±0.08^{B}
Attack/visual threat	0.00 ±0.01^{A}	0.01 ±0.01^{A}
Attack/vocal threat	0.08 ±0.02^{A}	0.01 ±0.04^{A}
Attack/visual & vocal threat	0.01 ±0.01^{A}	0.01 ±0.01^{A}
Standing on ground	0.00 ±0.01^{A}	0.00 ±0.01^{A}

Table 12. Means and standard deviations of proportions of daily activity spent in different behavioral activities for all birds combined from all pen combinations during the winter of 1983-1984. Pen combinations included 3 single-species pens containing flocks of each individual species (cardinals, Harris' sparrows and tree sparrows), 2 two-species flocks containing cardinals in combination with both sparrow species, and 1 three-species pen containing birds from all three species. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences ($P=0.05$).

	Effect of flock composition, flock size and feeder ratios	
Behaviors	Experiment 1	Experiment 2
Feeding at feeder	4.81 ± 0.56^{A}	2.51 ± 0.57^{B}
Flying	3.70 ± 0.38^{A}	3.96 ± 0.38^{A}
Sitting	0.39 ± 0.12^{A}	0.31 ± 0.12^{A}
Feeding on ground	66.29 ± 1.99^{A}	61.02 ± 1.99^{A}
Miscellaneous	5.40 ± 0.75^{A}	9.36 ± 0.75^{B}
Submission	10.76 ± 1.18^{A}	5.44 ± 1.19^{B}
Attack/contact	0.13 ± 0.03^{A}	0.10 ± 0.03^{A}
Attack/visual threat	0.00 ± 0.01^{A}	0.02 ± 0.01^{A}
Attack/vocal threat	0.04 ± 0.02^{A}	0.07 ± 0.02^{A}
Attack/visual & vocal	0.00 ± 0.00^{A}	0.01 ± 0.00^{A}
Standing on ground	0.00 ± 0.01^{A}	0.01 ± 0.01^{A}

Dirunal patterns

In order to obtain some general characteristics for quarters, all main effects (bird species, experiment, observer) were combined. This analysis displayed significant differences in 3 of the 11 behavior activities. Feeding on the ground exhibited a significant peak in quarter 2 (late morning) with 66.85 of the birds' time spent in this activity and a significantly low amount of time spent in quarter 4 (late afternoon) with 61.5% of the birds' time spent in this activity. Birds spent approximately the same proportion of time in the miscellaneous activities for quarters 1, 2 and 4 (with respective amounts of 8.7%, 7.6% and 8.4%), but experienced a significantly lower amount of time spent in this category in quarter 3 with a percentage of 4.9%. The submission category also displayed a significantly high and low proportion of time spent. The peak occurred in quarter 3 with 9.3% of total time spent in submission and the low occurred in quarter 2 with 6.2% of total time spent in submission (Table 13).

Table 13. Means and standard deviations of proportions of daily activity spent indifferent behavioral activities by all birds in all pen combinations by quarter of the day during the winter of 1983-1984. Pen combinations included 3 single-species pens containing flocks of each species (cardinals, Harris' sparrow, tree sparrows), 2 two-species pens containing cardinals in combination with both sparrow species and 1 three-species pen containing the combination of all three species. This table represents results combined for both halves of the first year's research. Flock sizes changed from the first half of the experiment to the second only in the single species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in the first half to 1 per every 3 birds in the second half. Common superscripts across a row indicate no significant differences (P=0.05).

	Time of day			
Behavior categories	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	2.86 $\pm$0.58^{A}	3.97 $\pm$0.61^{A}	3.37 $\pm$0.58^{A}	4.43 $\pm$0.62^{A}
Flying	4.26 $\pm$0.36^{A}	4.06 $\pm$0.38^{A}	3.54 $\pm$0.36^{A}	3.44 $\pm$0.39^{A}
Sitting	0.51 $\pm$0.15^{A}	0.26 $\pm$0.16^{A}	0.26 $\pm$0.15^{A}	0.33 $\pm$0.16^{A}
Feeding on ground	64.50 $\pm$1.82^{A,B}	66.78 $\pm$ 1.92^{A}	61.81 $\pm$1.80^{A,B}	61.51 $\pm$1.94^{A}
Miscellaneous	8.68 $\pm$0.76^{A}	7.60 $\pm$0.80^{A}	4.90 $\pm$0.76^{B}	8.36 $\pm$0.82^{A,C}
Submission	8.48 $\pm$0.84^{A}	6.16 $\pm$0.89^{A,B}	9.30 $\pm$0.83^{A,C}	8.48 $\pm$0.90^{A}
Attack/contact	0.10 $\pm$0.04^{A}	0.11 $\pm$0.04^{A}	0.15 $\pm$0.04^{A}	0.11 $\pm$0.04^{A}
Attack/visual threat	0.00 $\pm$0.01^{A}	0.02 $\pm$0.01^{A}	0.01 $\pm$0.01^{A}	0.00 $\pm$0.01^{A}
Attack/vocal threat	0.03 $\pm$0.03^{A}	0.10 $\pm$0.03^{A}	0.06 $\pm$0.02^{A}	0.03 $\pm$0.03^{A}
Attack/visual & vocal	0.01 $\pm$0.01^{A}	0.01 $\pm$0.01^{A}	0.00 $\pm$0.01^{A}	0.01 $\pm$0.01^{A}.
Standing on ground	0.00 $\pm$0.01^{A}	0.00 $\pm$0.01^{A}	0.02 $\pm$0.01^{A}	0.00 $\pm$0.01^{A}

When experiment was also taken into account (Tables 14-15), time spent feeding at the feeder was significantly greater in the first half for quarters 2 and 4 (6.2% and 5.8%, respectively) than quarters 1 and

3 (3.2% and 4.0%, respectively), while in the second half there was no statistically significant difference between quarters for the same category. In the fist half, time spent flying decreased by quarter, from 4.7% in quarter 1 to 2.9% in quarter 4, while flying did not vary significantly in the second half. More time was spent in miscellaneous activities in the second half but no consistent trends existed between the quarters or experiments. The amount of time spent in submission was lower in the second half than in the first half and was highest in both halves in quarter 3 and lowest in quarter 2. There were no differences attributable to quarters in either halves for sitting, feeding on the ground, attack with contact, attack with visual threat, attack with vocal threat, attack with both visual and vocal threats or standing on the ground.

When combining for experiments while analyzing for individual pen combinations, the single species cardinal pen exhibited no statistical differences for feeding at the feeder but did have a smaller amount of time in this category for quarter 1 (60.1%). The other three quarters were not statistically different from each other. The birds in this flock combination spent less time (1.9%) flying in quarter 4 than in any other quarter. The birds also spent statistically more time sitting in quarter 1 (2.5%) than in any other quarter and the other quarters were not different from one another. The amount of time spent in miscellaneous activities was lower in quarter 3 (4.2%) than in any other quarter and all other quarters were not different from one another. There were also differences in the attack with visual threat category, with no encounters at all in quarters 1 and 3, and 0.08% and 0.02% of time spent in quarters 2 and 4, respectively (Table 16).

The single species Harris' sparrow pen displayed much less reaction to the differences in time of day. The birds in this pen experienced a flying peak in quarter 4 (4.9%) that was statistically higher than all other quarters. These birds also experienced statistically more aggressive encounters in the attack with vocal threat at 0.14% in quarter 2 than in any of the other quarters (Table 17).

The single species tree sparrow pen spent much more time feeding on the ground in quarters 1 and 2 (65.0% and 69.0%, respectively) than in quarters 3 and 4 (45.4% and 41.0%, respectively). The birds spent more time in the miscellaneous activities in quarters 1 (5.1%) and 4 (10.5%) than in quarters 2 (3.9%) and 3 (4.0%). The tree sparrows displayed significant differences in three interaction categories: the submission category experienced a peak at 12.9% in quarter 4 while all other quarters were statistically similar, the attack with visual threat category was higher in quarter 2 (0.08%) than in any other quarter, and the attack with vocal threat category was also higher in quarter 2 (0.12%) than in any other quarter (Table 18).

The cardinal-tree sparrow combination flock experienced a feeding on the ground peak in quarter 3, spending 69.9% of their time in this activity and experienced the lowest value in this category in quarter 4, spending only 51.2% of their total time. These birds spent more time in the submission category in quarter 4 (13.7%) than in any other quarter. This flock experienced peaks and valleys in three of the four attack categories, but with no consistent trend between quarters. While the amount of time spent in the attack with contact category peaked in quarter 4 (0.36%) and experienced its low in quarter 3 (0.01%), the amount of time spent in attack with vocal threat peaked in quarter 2 (0.28%) and experienced its low in quarter 1 (0.02%). The attack with both visual and vocal threat category saw no activity in quarters 1 and 3, 0.07% in quarter 2, and 0.04% in quarter 4 (Table 19).

The cardinal-Harris' sparrow combination flock exhibited differences in all four quarters for feeding at the feeder, with the largest amount of time spent in this category in quarter 4 with a value of 7.8% and the lowest in quarter 3 with a value of 3.4%. This combination of birds saw no statistical differences in the feeding on the ground category. The other activity which saw large differences was the submission category with the largest amount of time spent in quarter 3 at 12.2% and the smallest amount of time in quarter 4 with 6.4% (Table 20).

The cardinal-Harris' sparrow-tree sparrow combination pen did not have any significantly different values for either feeding category. These birds had a low value of 3.6% for flying in quarter 4 but all other quarters were statistically similar. The most time was spent in the miscellaneous category in quarter 1 with 10.1% of time spent and the least time was spent in quarter 3 with 4.1% of time spent. The category of submission experienced a peak of 13.9% in quarter 3 and while all other quarters were statistically similar. The attack with contact category had the highest value of 0.39% in quarter 3 and the lowest value of 0.03% in quarter 4. The category of attack with vocal threat had a peak in quarter 3 of 0.18% but all the other values were statistically similar. The category of attack with both visual and vocal threat experienced a high value of 0.03% in quarter 2 (Table 21).

Table 14. Means and standard deviations of proportions of daily activity spent in different behavioral activities for all birds in all pen combinations during the winter of 1983-1984. Pen combinations included 3 single-species pens for each species in the study, 2 two-species pens containing cardinals-Harris' sparrows and cardinals-tree sparrows, and 1 three-species pen containing all species. This table combines both halves of the first year's research. Flock sizes changed from the first half to the second half only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05).

	Time of day			
Behaviors	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	3.19 ±0.83^{A}	6.18 ±0.90^{B}	4.03 ±0.80^{A,B}	5.85 ±0.85^{B}
Flying	4.67 ±0.52^{A}	3.74 ±0.56^{A,B}	3.44 ±0.49^{A,B}	2.93 ±0.53^{B}
Sitting	0.44 ±0.21^{A}	0.45 ±0.23^{A}	0.31 ±0.21^{A}	0.34 ±0.22^{A}
Feeding on ground	68.47 ±2.60^{A}	69.45 ±2.82^{A}	62.50 ±2.49^{A}	64.73 ±2.66^{A}
Miscellaneous	7.31 ±1.09^{A}	3.32 ±1.18^{B}	4.61 ±1.05^{A,B}	6.38 ±1.12^{A,B}
Submission	11.81 ±1.20^{A,B}	8.40 ±1.30^{A,B}	12.22 ±1.15^{A}	10.62 ±1.23^{A,B}
Attack/contact	0.16 ±0.06^{A}	0.13 ±0.07^{A}	0.17 ±0.06^{A}	0.07 ±0.06^{A}
Attack/visual threat	0.00 ±0.01^{A}	0.01 ±0.01^{A}	0.01 ±0.01^{A}	0.00 ±0.01^{A}
Attack/vocal threat	0.03 ±0.04^{A}	0.06 ±0.04^{A}	0.06 ±0.03^{A}	0.01 ±0.04^{A}
Attack/visual & vocal	0.00 ±0.01^{A}	0.01 ±0.01^{A}	0.00 ±0.01^{A}	0.00 ±0.01^{A}
Standing on ground	0.01 ±0.01^{A}	0.01 ±0.01^{A}	0.00 ±0.01^{A}	0.00 ±0.01^{A}

Table 15. Means and standard deviations of proportions of daily activity spent in different behavioral activities by all birds in all pen combinations during the winter of 1983-1984. Pen combinations included 1 single-species pen for each species, 2 two-species pens for the combinations of Harris' sparrow-cardinal and tree sparrow-cardinal, and 1 three-species pen containing all species. These results are combined for both halves of the first year's research. Flock sizes changed from the first half to the second half only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05).

	Time of day			
Behaviors	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	2.56 ±0.83^{A}	1.77 ±0.86^{A}	2.71 ±0.88^{A}	3.01 ±0.97^{A}
Flying	3.88 ±0.52^{A}	4.37 ±0.53^{A}	3.65 ±0.55^{A}	3.94 ±0.60^{A}
Sitting	0.57 ±0.22^{A}	0.13 ±0.22^{A}	0.22 ±0.23^{A}	0.31 ±0.25^{A}
Feeding on ground	60.53 ±2.61^{A}	64.12 ±2.69^{A}	61.12 ±2.76^{A}	58.30 ±3.03^{A}
Miscellaneous	10.04 ±1.10^{A}	11.87 ±1.13^{A}	5.20 ±1.16^{B}	10.34 ±1.27^{A}
Submission	5.14 ±1.21^{A}	3.91 ±1.24^{A}	6.37 ±1.28^{A}	6.33 ±1.40^{A}
Attack/contact	0.04 ±0.06^{A}	0.05 ±0.06^{A}	0.12 ±0.06^{A}	0.16 ±0.07^{A}
Attack/visual threat	0.01 ±0.01^{A}	0.03 ±0.01^{A}	0.02 ±0.01^{A}	0.00 ±0.01^{A}
Attack/ vocal threat	0.04 ±0.04^{A}	0.14 ±0.04^{A}	0.07 ±0.04^{A}	0.04 ±0.04^{A}
Attack/visual & vocal	0.01 ±0.01^{A}	0.02 ±0.01^{A}	0.00 ±0.01^{A}	0.01 ±0.01^{A}
Standing on ground	0.00 ±0.01^{A}	0.00 ±0.01^{A}	0.04 ±0.01^{A}	0.00 ±0.02^{A}

Table 16. Means and standard deviations of proportions of daily activity spent in different behavioral activities by cardinals in a single-species outdoor pen during the winter of 1983-1984. This table combines both halves of the first year's research. Flock sizes changed from the first half to the second half only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05).

	Time of day			
Behaviors	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	4.02 ±1.73^{A}	5.08 ±1.53^{A}	7.54 ±1.47^{A}	5.72 ±1.67^{A}
Flying	6.53 ±1.07^{A}	6.13 ±0.95^{A}	4.77 ±0.91^{A}	1.93 ±1.03^{B}
Sitting	2.49 ±0.45^{A}	0.38 ±0.40^{B}	0.28 ±0.38^{B}	0.30 ±0.43^{B}
Feeding on ground	60.12 ±5.42^{A}	74.34 ±4.77^{B}	67.99 ±4.60^{A,B}	72.36 ±5.21^{A,B}
Miscellaneous	11.12 ±2.27^{A}	8.12 ±2.00^{A}	4.19 ±1.93^{B}	9.00 ±2.19^{A}
Submission	4.50 ±2.51^{A}	2.33 ±2.21^{A}	4.98 ±2.12^{A}	2.67 ±2.41^{A}
Attack/contact	0.09 ±0.13^{A}	0.24 ±0.11^{A}	0.07 ±0.11^{A}	0.04 ±0.12^{A}
Attack/visual threat	0.00 ±0.03^{A}	0.08 ±0.02^{B}	0.00 ±0.02^{A}	0.02 ±0.03^{A,B}
Attack/vocal threat	0.02 ±0.08^{A}	0.03 ±0.07^{A}	0.06 ±0.06^{A}	0.04 ±0.07^{A}
Attack/visual & vocal	0.00 ±0.02^{A}	0.00 ±0.01^{A}	0.00 ±0.01^{A}	0.00 ±0.02^{A}
Standing on ground	0.00 ±0.03^{A}	0.00 ±0.03^{A}	0.00 ±0.02^{A}	0.00 ±0.03^{A}

Table 17. Means and standard deviations of daily activity spent in different behavioral activities by Harris' sparrows in a single-species outdoor pen during the winter of 1983-1984. These results combine both halves of the first year's research. Flock sizes changed from the first half to the second half only the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences ($P=0.05$).

Behaviors	Time of day			
	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	2.37 ± 1.35^{A}	3.89 ± 1.74^{A}	0.99 ± 1.35^{A}	2.98 ± 1.49^{A}
Flying	$3.85 \pm 0.84^{A,B}$	$2.40 \pm 1.08^{A,B}$	$1.99 \pm 0.84^{A,B}$	4.92 ± 0.92^{A}
Sitting	0.05 ± 0.35^{A}	0.29 ± 0.45^{A}	0.15 ± 0.35^{A}	0.23 ± 0.39^{A}
Feeding on ground	65.32 ± 4.21^{A}	66.06 ± 5.44^{A}	65.68 ± 4.21^{A}	68.87 ± 4.65^{A}
Miscellaneous	10.36 ± 1.77^{A}	7.74 ± 2.28^{A}	5.66 ± 1.77^{A}	7.04 ± 1.95^{A}
Submission	11.65 ± 1.95^{A}	9.59 ± 2.51^{A}	10.39 ± 1.95^{A}	9.80 ± 2.15^{A}
Attack/contact	0.19 ± 0.10^{A}	0.04 ± 0.13^{A}	0.21 ± 0.10^{A}	0.18 ± 0.11^{A}
Attack/visual threat	0.01 ± 0.02^{A}	0.01 ± 0.03^{A}	0.05 ± 0.02^{A}	0.00 ± 0.02^{A}
Attack/vocal threat	0.10 ± 0.06^{A}	0.14 ± 0.08^{B}	0.00 ± 0.06^{A}	0.01 ± 0.07^{A}
Attack/visual & vocal threat	0.02 ± 0.01^{A}	0.01 ± 0.02^{A}	0.00 ± 0.01^{A}	0.00 ± 0.01^{A}
Standing on ground	0.00 ± 0.02^{A}	0.01 ± 0.03^{A}	0.09 ± 0.02^{B}	0.01 ± 0.02^{A}

Table 18. Means and standard deviations of proportions of daily activity spent in different behavioral activities by tree sparrows in a single-species outdoor pen during the winter of 1983-1984. These results represent the combination of both halves of the first year's research. Flock sizes changed from the first half to the second half only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts across a row indicate no significant differences (P=0.05).

	Time of day			
Behaviors	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	1.14 ±1.57^{A}	3.09 ±1.44^{A}	0.78 ±1.57^{A}	1.09 ±1.57^{A}
Flying	1.73 ±0.98^{A}	3.19 ±0.90^{A}	1.78 ±0.98^{A}	1.04 ±0.98^{A}
Sitting	0.05 ±0.41^{A}	0.21 ±0.37^{A}	0.12 ±0.41^{A}	0.06 ±0.41^{A}
Feeding on ground	65.05 ±4.92^{A}	68.98 ±4.52^{A}	45.40 ±4.93^{B}	41.05 ±4.93^{B}
Miscellaneous	5.09 ±2.07^{A,B}	3.87 ±1.90^{A}	4.04 ±2.07^{A}	10.46 ±2.07^{A,B}
Submission	8.88 ±2.28^{A,B}	4.11 ±2.09^{A,B}	7.22 ±2.28^{A,B}	12.86 ±2.28^{A}
Attack/contact	0.01 ±0.11^{A}	0.13 ±0.11^{A}	0.02 ±0.11^{A}	0.01 ±0.11^{A}
Attack/visual threat	0.01 ±0.02^{A}	0.08 ±0.02^{B}	0.01 ±0.02^{A}	0.01 ±0.02^{A}
Attack/vocal threat	0.10 ±0.07^{A}	0.12 ±0.06^{B}	0.02 ±0.07^{A}	0.01 ±0.07^{A}
Attack/visual & vocal	0.00 ±0.02^{A}	0.00 ±0.01^{A}	0.00 ±0.01^{A}	0.00 ±0.01^{A}
Standing on ground	0.00 ±0.03^{A}	0.01 ±0.02^{A}	0.01 ±0.03^{A}	0.00 ±0.03^{A}

Table 19. Means and standard deviations of proportions of daily activities by all 6 birds combined in the cardinal-tree sparrow pen during the winter of 1983-1984. These results combine both halves of the first year's research. Flock sizes changed from the first half of the experiment to the second only in single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in the first half to 1 per every 3 birds in the second half. Common superscripts across a row indicate no significant differences (P=0.05).

	Time of day			
Behaviors	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	2.58 ± 1.23^{A}	2.69 ± 1.23^{A}	4.86 ± 1.40^{A}	4.35 ± 1.98^{A}
Flying	2.89 ± 0.76^{A}	4.09 ± 1.09^{A}	2.92 ± 0.87^{A}	4.84 ± 1.23^{A}
Sitting	0.21 ± 0.32^{A}	0.10 ± 0.46^{A}	0.11 ± 0.36^{A}	0.89 ± 0.51^{A}
Feeding on ground	64.11 ± 3.85^{A}	58.93 ± 5.51^{A}	$69.88 \pm 4.39^{A,B}$	$51.24 \pm 6.21^{A,B}$
Miscellaneous	8.35 ± 1.62^{A}	9.07 ± 2.31^{A}	5.68 ± 1.84^{A}	11.44 ± 2.61^{A}
Submission	8.34 ± 1.78^{A}	6.89 ± 2.55^{A}	7.03 ± 2.03^{A}	$13.68 \pm 2.87^{A,B}$
Attack/contact	0.11 ± 0.09^{A}	0.31 ± 0.13^{A}	$0.01 \pm 0.10^{A,B}$	$0.36 \pm 0.14^{A,C}$
Attack/visual threat	0.00 ± 0.02^{A}	0.00 ± 0.03^{A}	0.00 ± 0.02^{A}	0.01 ± 0.03^{A}
Attack/vocal threat	0.02 ± 0.05^{A}	0.28 ± 0.08^{B}	$0.09 \pm 0.06^{A,B}$	$0.14 \pm 0.09^{A,B}$
Attack/visual & vocal	0.00 ± 0.01^{A}	0.07 ± 0.02^{B}	0.00 ± 0.01^{A}	$0.04 \pm 0.02^{A,B}$
Standing on ground	0.00 ± 0.02^{A}	0.00 ± 0.03^{A}	0.01 ± 0.02^{A}	0.00 ± 0.03^{A}

Table 20. Means and standard deviations of proportions of daily activity spent in different behavioral activities by all 6 birds in the cardinal-Harris' sparrow outdoor pen during the winter of 1983-1984. These results combine both halves of the first year's research. Flock sizes changed from the first half to the second half only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in the first half to 1 per every 3 birds in the second half. Common superscripts across a row indicate no significant differences ($P=0.05$).

	Time of day			
Behaviors	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	$3.54 \pm 1.46^{A,C}$	$5.42 \pm 1.36^{A,B,C}$	$3.40 \pm 1.42^{A,C}$	7.76 ± 1.41^{B}
Flying	5.20 ± 0.91^{A}	4.07 ± 0.85^{A}	3.62 ± 0.88^{A}	4.28 ± 0.88^{A}
Sitting	0.13 ± 0.38^{A}	0.08 ± 0.35^{A}	0.37 ± 0.37^{A}	0.25 ± 0.37^{A}
Feeding on ground	67.30 ± 4.57^{A}	70.73 ± 4.26^{A}	61.13 ± 4.43^{A}	69.21 ± 4.43^{A}
Miscellaneous	7.03 ± 1.9^{A}	7.61 ± 1.79^{A}	5.77 ± 1.66^{A}	4.07 ± 1.86^{A}
Submission	$11.89 \pm 2.11^{A,B,C}$	$7.48 \pm 1.97^{A,B,C}$	$12.23 \pm 2.05^{A,B,C}$	$6.38 \pm 2.05^{B,D}$
Attack/contact	0.11 ± 0.11^{A}	0.13 ± 0.10^{A}	0.19 ± 0.10^{A}	0.08 ± 0.10^{A}
Attack/visual threat	0.00 ± 0.02^{A}	0.00 ± 0.02^{A}	0.03 ± 0.02^{A}	0.00 ± 0.02^{A}
Attack/vocal threat	0.01 ± 0.06^{A}	0.00 ± 0.06^{A}	0.03 ± 0.06^{A}	0.01 ± 0.06^{A}
Attack/visual & vocal	0.00 ± 0.01^{A}	0.00 ± 0.01^{A}	0.00 ± 0.01^{A}	0.00 ± 0.01^{A}
Standing on ground	0.03 ± 0.02^{A}	0.00 ± 0.02^{A}	0.00 ± 0.02^{A}	0.00 ± 0.02^{A}

Table 21. Means and standard deviations of proportions of daily activity spent in different behavioral activities by all 9 birds in the three-species cardinal-Harris' sparrow-tree sparrow pen during the winter of 1983-1984. These results combine the halves of the first year's research. Flock sizes changed from the first half to the second half only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in the first half to 1 per every 3 birds in the second half. Common superscripts across a row indicate no significant differences (P=0.05).

	Time of day			
Behaviors	Quarter 1	Quarter 2	Quarter 3	Quarter 4
Feeding at feeder	3.20 ±1.20^{A}	3.66 ±1.20^{A}	2.64 ±1.28^{A}	4.69 ±1.03^{A}
Flying	5.39 ±0.75^{A}	4.46 ±0.74^{A}	6.18 ±0.80^{A,B}	3.62 ±0.64^{B}
Sitting	0.25 ±0.37^{A}	0.23 ±0.31^{A}	0.70 ±0.31^{A}	0.54 ±0.33^{A}
Feeding on ground	65.11 ±3.75^{A}	61.67 ±3.75^{A}	60.80 ±4.01^{A}	66.34 ±3.24^{A}
Miscellaneous	10.09 ±1.57^{A,B}	9.16±1.57^{A,B}	4.09 ±1.68^{C}	6.16 ±1.36^{A,B,C}
Submission	5.39 ±1.74^{A}	6.56 ±1.74^{A}	13.92 ±1.85^{B}	5.46 ±1.50^{A}
Attack/contact	0.10 ±0.09^{A}	0.12 ±0.09^{B}	0.39 ±0.09^{C}	0.03 ±0.07^{A,B}
Attack/visual threat	0.02 ±0.02^{A}	0.00 ±0.02^{A}	0.01 ±0.02^{A}	0.01 ±0.02^{A}
Attack/vocal threat	0.03 ±0.05^{A,B}	0.02 ±0.05^{A,B,C}	0.18 ±0.06^{B,C}	0.01 ±0.05^{A,B}
Attack/visual & vocal	0.00 ±0.01^{A,B}	0.03 ±0.01^{A,B}	0.01 ±0.01^{A}	0.00 ±0.01^{A,B}
Standing on ground	0.01 ±0.02^{A}	0.01 ±0.02^{A}	0.01 ±0.02^{A}	0.00 ±0.02^{A}

Interspecific interactions

This section of the results analyzes each species with regard to its interaction with the other birds in all the pen combinations in which it is present.

Cardinals in single species pens reduced the time they spent at the feeder from the first half to the second half from 8.92% to 2.25%, but in the multiple species pens only adjusted their feeding at the feeder time in the cardinal-Harris' sparrow pen, where the proportion of time spent feeding also decreased, from 7.85% to 3.08%. Cardinals did not significantly alter their time spent feeding at the feeder when only other cardinals and tree sparrows were present, or when all three species were present. Time spent flying increased from the first half to the second only in the cardinal-Harris' sparrow pen, where it increased from 2.03% to 7.32%. All other pens had statistically similar flying times. Time spent feeding on the ground did not change significantly in the cardinal-Harris' sparrow pen, but decreased significantly in all the other combinations from experiment 1 to 2. The cardinals in the presence of all three species displayed the largest drop in time spent, decreasing from 74.33% to 49.70%. Cardinals with tree sparrows decreased from 77.57% to 50.65% and cardinals alone decreased from 76.14% to 61.32%. The cardinals in the presence of Harris' sparrows also did not statistically alter the amount of time they spent in miscellaneous activities, although, once again, cardinals in all other combinations were statistically different. Cardinals in the three species pens spent 15.96% of their time in miscellaneous activities in the second half, increasing from their percent of time (0.36%) spent in those activities in the first half. Cardinals with tree sparrows increased from 1.73% in the first half to 16.99% in the second half and cardinals alone increased from 2.74% to 13.47%. The attack with vocal threat exhibited a difference only in the three species pen, where cardinals decreased the amount of time spent in this activity from 0.15% in the first half to 0.03% in the second half. Cardinals experienced no significant differences in time spent from the first half to the second half for the categories of submission, attack with contact, attack with visual threat, attack with both visual and vocal (Table 22).

Harris' sparrows only modified their behavior in one flock combination for one behavior category. These birds decreased the amount of time they spent submitting in the Harris' sparrow-cardinal pen from 16.25% of their time in the first half to 3.49% of their time in the second half (Table 23).

Tree sparrows also seemed to modify their behavior very little. These birds decreased the amount of time they spent submitting in the three species pen from 17.59% in experiment 1 to 6.64% in experiment 2. They displayed no other significant differences in the time they spent submitting in any of the other pens. The tree sparrows significantly increased the amount of time they spent in two of the aggressive categories in the tree sparrow-cardinal pen. The amount of time spent in the category of attack with vocal threat increased in this pen from 0.05% in the first half to 0.36% in the second half. Tree sparrows also increased the amount of time spent in the category of attack with visual and vocal threat in the tree sparrow-cardinal pen from 0.03% to 0.08%. These birds exhibited no significant differences for any of the categories in the tree sparrow single species pen (Table 24).

Table 22. Means and standard deviations of proportions of daily activity spent in different behavioral activities by cardinals in all pens containing cardinals during the winter of 1983-1984. Cardinals were present in 1 single-species pen, 2 two-species pens (cardinal-tree sparrow and cardinal-Harris' sparrow), and in 1 three-species pen containing all three species. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts on paired mean values indicate no significant differences (P=0.05).

	Effect of flock composition, flock size, and feeder ratios							
	Cardinal-Harris'		Cardinal-Harris'-Tree		Cardinal-Tree		Cardinals alone	
Behaviors	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Feeding at feeder	7.81±1.20^{A}	3.08±1.78^{B}	10.07±0.97^{A}	6.37±1.69^{A}	6.56±1.18^{A}	6.12±2.01^{A}	8.92±1.33^{A}	2.25±0.87^{B}
Flying	2.03±0.99^{A}	7.32±1.46^{B}	6.31±0.80^{A}	3.63±1.39^{A}	4.86±0.97^{A}	2.19±1.65^{A}	5.55±1.09^{A}	4.12±0.71^{A}
Sitting	0.44±0.34^{A}	0.09±0.50^{A}	0.45±0.27^{A}	0.46±0.47^{A}	0.21±0.33^{A}	0.13±0.56^{A}	0.89±0.37^{A}	0.83±0.24^{A}
Feeding on the ground	64.88±5.18^{A}	73.91±7.67^{A}	74.33±4.19^{A}	49.70±7.31^{B}	77.57±5.11^{A}	50.65±8.69^{B}	76.14±5.76^{A}	61.32±3.75^{B}
Miscellaneous	5.67±1.89^{A}	3.84±2.79^{A}	0.36±1.52^{A}	15.96±2.66^{B}	1.73±1.86^{A}	16.99±3.17^{B}	2.74±2.10^{A}	13.47±1.37^{B}
Submission	15.09±3.15^{A}	5.01±4.66^{A}	6.16±2.54^{A}	3.67±4.44^{A}	4.76±3.10^{A}	5.79±5.28^{A}	3.97±3.50^{A}	3.25±2.28^{A}
Attack/contact	0.23±0.10^{A}	0.00±0.15^{A}	0.21±0.08^{A}	0.10±0.14^{A}	0.07±0.10^{A}	0.12±0.17^{A}	0.19±0.11^{A}	0.03±0.07^{A}
Attack/visual threat	0.02±0.02^{A}	0.00±0.03^{A}	0.00±0.01^{A}	0.05±0.02^{A}	0.00±0.02^{A}	0.00±0.03^{A}	0.03±0.02^{A}	0.02±0.01^{A}
Attack/vocal threat	0.03±0.05^{A}	0.00±0.07^{A}	0.15±0.04^{A}	0.03±0.07^{B}	0.03±0.05^{A}	0.08±0.08^{A}	0.06±0.05^{A}	0.02±0.04^{A}
Attack/visual & vocal	0.00±0.01^{A}	0.00±0.02^{A}	0.00±0.01^{A}	0.00±0.02^{A}	0.00±0.01^{A}	0.00±0.02^{A}	0.00±0.01^{A}	0.00±0.01^{A}
Standing on ground	0.02±0.02^{A}	0.01±0.03^{A}	0.00±0.01^{A}	0.01±0.03^{A}	0.00±0.02^{A}	0.00±0.03^{A}	0.00±0.02^{A}	0.00±0.01^{A}

Table 23. Means and standard deviations of proportions of daily activity spent in different behavioral activities by Harris' sparrows in all pens containing Harris' sparrows during the winter of 1983-1984. Harris' sparrows were present in 1 single-species pen, 1 two-species pen containing Harris' sparrows and cardinals, and one three species pen containing all three species. Experiment 1 and 2 designate the first and second half, respectively, of the first year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts on paired mean values indicate no significant differences (P=0.05).

	Effect of flock composition, flock size and feeder ratio					
	Harris' sparrow-Cardinal		Harris' sparrow-Cardinal-Tree sparrow		Harris' sparrow alone	
Behaviors	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Feeding at feeder	5.45±1.33^{A}	2.78±1.51^{A}	3.44±0.97^{A}	0.07±1.68^{A}	2.84±1.14^{A}	2.26±0.87^{A}
Flying	3.84±1.10^{A}	3.55±1.24^{A}	5.36±0.80^{A}	6.14±1.38^{A}	2.55±0.93^{A}	4.03±0.71^{A}
Sitting	0.24±0.37^{A}	0.12±0.42^{A}	0.21±0.27^{A}	0.17±0.47^{A}	0.27±0.32^{A}	0.09±0.24^{A}
Feeding on ground	62.06±5.76^{A}	66.72±6.51^{A}	69.08±4.20^{A}	70.61±7.24^{A}	66.05±4.91^{A}	66.95±3.76^{A}
Miscellaneous	9.07±2.10^{A}	6.10±2.37^{A}	9.00±1.53^{A}	7.83±2.64^{A}	6.80±1.79^{A}	8.59±1.37^{A}
Submission	16.25±3.50^{A}	3.49±3.96^{B}	10.12±2.55^{A}	5.47±4.40^{A}	12.77±2.98^{A}	8.05±2.28^{A}
Attack/contact	0.06±0.11^{A}	0.20±0.12^{A}	0.14±0.08^{A}	0.00±0.14^{A}	0.05±0.09^{A}	0.21±0.07^{A}
Attack/visual threat	0.00±0.02^{A}	0.00±0.02^{A}	0.00±0.01^{A}	0.00±0.02^{A}	0.00±0.02^{A}	0.02±0.01^{A}
Attack/vocal threat	0.00±0.05^{A}	0.00±0.06^{A}	0.03±0.04^{A}	0.01±0.07^{A}	0.04±0.05^{A}	0.07±0.04^{A}
Attack/visual & vocal threat	0.00±0.01^{A}	0.00±0.01^{A}	0.00±0.01^{A}	0.00±0.01^{A}	0.00±0.01^{A}	0.01±0.01^{A}
Standing on ground	0.00±0.02^{A}	0.00±0.02^{A}	0.00±0.01^{A}	0.01±0.03^{A}	0.01±0.02^{A}	0.05±0.01^{B}

Table 24. Means and standard deviations of proportions of daily activity spent in different behavioral activities by tree sparrows during the winter of 1983-1984. Tree sparrows were present in 1 single-species pen, 2 two-species pens containing tree sparrows and cardinals, and in 1 three-species pen containing all three species. Experiment 1 and 2 designate the first and second half, respectively, of the firt year's research. Flock sizes changed from experiment 1 to 2 only in the single-species pens as the flock increased from 3 birds to 9 birds and feeder ratios changed from 1 per bird in experiment 1 to 1 per every 3 birds in experiment 2. Common superscripts on paired mean values indicate no significant differences ($P=0.05$).

	Effect of flock composition, flock size and feeder ratios					
	Tree sparrow-Cardinal-Harris' sparrow		Tree sparrow-Cardinal		Tree sparrow alone	
Behavior characteristics	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Feeding at feeder	0.40 ± 1.17^{A}	0.16 ± 1.70^{A}	1.03 ± 1.20^{A}	0.88 ± 2.02^{A}	0.74 ± 1.33^{A}	2.31 ± 0.87^{A}
Flying	3.74 ± 0.96^{A}	3.65 ± 1.40^{A}	2.05 ± 0.98^{A}	5.36 ± 1.65^{A}	2.21 ± 1.09^{A}	1.66 ± 0.71^{A}
Sitting	0.52 ± 0.33^{A}	1.07 ± 0.4	0.51 ± 0.34^{A}	0.48 ± 0.57^{A}	0.09 ± 0.37^{A}	0.08 ± 0.24^{A}
Feeding on ground	63.17 ± 5.04^{A}	48.22 ± 7.34^{A}	52.23 ± 5.17^{A}	61.53 ± 8.70^{A}	57.14 ± 5.73^{A}	53.09 ± 3.76^{A}
Miscellaneous	6.41 ± 1.84^{A}	8.93 ± 2.67^{A}	8.68 ± 1.88^{A}	7.50 ± 3.17^{A}	5.19 ± 2.08^{A}	6.54 ± 1.37^{A}
Submission	17.59 ± 3.06^{A}	6.64 ± 4.46^{B}	19.40 ± 3.14^{A}	7.18 ± 5.29^{A}	10.69 ± 3.48^{A}	5.84 ± 2.28^{A}
Attack/contact	0.25 ± 0.10^{A}	0.09 ± 0.14^{A}	0.32 ± 0.10^{A}	0.27 ± 0.17^{A}	0.00 ± 0.11^{A}	0.07 ± 0.07^{A}
Attack/visual threat	0.00 ± 0.02^{A}	0.00 ± 0.02^{A}	0.00 ± 0.02^{A}	0.00 ± 0.02^{A}	0.01 ± 0.02^{A}	0.03 ± 0.01^{A}
Attack/vocal threat	0.08 ± 0.05^{A}	0.08 ± 0.07^{A}	0.05 ± 0.05^{A}	0.36 ± 0.08^{B}	0.00 ± 0.05^{A}	0.12 ± 0.04^{A}
Attack visual & vocal	0.04 ± 0.01^{A}	0.02 ± 0.02^{A}	0.03 ± 0.01^{A}	0.08 ± 0.02^{B}	0.00 ± 0.01^{A}	0.00 ± 0.01^{A}
Standing on ground	0.03 ± 0.02^{A}	0.01 ± 0.03^{A}	0.00 ± 0.02^{A}	0.00 ± 0.03^{A}	0.00 ± 0.02^{A}	0.00 ± 0.01^{A}

DISCUSSION STUDY 1

Small passerines typically have limited energy storage capacity and high existence energy requirements (Walsberg 1983). When available food is of low quality, efforts to acquire adequate energy should be reflected in the time budget. The category of feeding on the ground was consistently the category in which birds spent the largest amount of time and was independent of all other variables. This rate (74.4% averaged for all three species) seems abnormally high for the bird species involved. Although feeding rates near this have been recorded [70.5% for wintering gadwalls (*Anas strepera*), Paulus 1982], Benkman and Pulliam (1988) offer guidelines for sparrow feeding at one seed consumed, on average, every 1-5 seconds. Birds wintering in Kansas have approximately 10 hours of daylight available to feed. Extrapolating this guideline for the upper average of one seed every five seconds would mean that the test birds in this experiment should have spent approximately 20% of their time in feeding activity. Shuman (1984) studied cardinals at this same location on the same diet and found that the birds spent the most significant amount of time perching (70%), with only 19% of total time spent feeding at feeders or foraging on the ground.

Barnard (1980a) describes a feeding bout as consisting of several different behaviors. In addition to actually picking up and handling prey, a bird moves about the feeding site, scans for food, other birds or predators, and interacts with other foragers. Barnard (1980a) condenses these activities even further into three mutually exclusive behaviors: feeding, scanning for predators and aggression. Pulliam (1975) lists the hierarchical organization of behaviors in this model as such: scanning for predators takes priority over feeding and feeding takes priority over initiating fights. This model suggests that birds join flocks in order to be able to reduce their commitment to scanning for predators and devote more time to feeding. This model was devised mainly with respect to species exploiting food supplies which are virtually unlimited and predictable in time and space (1980a), as was the case in this study. While research assistants were instructed that the category of feeding on the ground was to only include observations that actually involved consuming a seed, undoubtedly the research assistants attributed more than actual seed consumption to the data in this category. Predator scanning would have been included (as per instruction) in the miscellaneous category, and total proportions of time in this category averaged only 8.4% for all activities considered to be miscellaneous (preening, hopping, walking, bathing, predator scanning). Barnard (1980a: p. 297) describes predator scanning as "side-to-side head movement about the vertical axis. . . usually associated with a sleek, erect posture". This activity was carried out as the birds foraged and was probably included as feeding on the ground behavior by the research assistants in this study. The category of standing on the ground was only seen 0.003% of the time (averaged for all three species) and undoubtedly this is where the error lies. As this overestimation is carried on throughout the data and seems to be consistent, all feeding on the ground results can be considered to be relative.

Cardinals spent more time feeding at the feeders than the two sparrow species which can be attributed to the nature of the species' feeding strategies. Sparrows in general tend to be ground feeders (Benkman and Pulliam 1988) while Cardinals prefer to feed off the ground and will usually seize the opportunity to feed at a feeder (Bent 1968).

The amounts of time spent in the aggressive categories were consistently low for all variables and would reflect MacArthur and Pianka's (1966) theory that an activity should only be enlarged as long as the resulting gain in time spent per unit food exceeds the loss. Time spent interacting with the other birds would be costly in a situation such as this when energy is at a premium. Rohwer (1977) described how winter flocking behavior in many cases overrides territoriality and Lazarus (1979) described the benefits of flocking as opposed to operating as an individual.

Flock composition seemed to have some influence on behavior. Single species flocks spent the most time feeding at the feeder in the first half and the least time at the feeder in the second half. Single species flocks changed in number from the first half to the second half while the numbers remained constant in the other pens. Single species pens reduced their feeding on the ground time 15.5 percentage points while three species pens decreased only 9.9 percentage points. The single species pens demonstrate the effect of both increased size of flock and reduced feeder availability while the three species pen demonstrates only the effect of reduced feeder availability. From these results it would be difficult to decipher which variable had the most effect, and Barnard (1980a) found it difficult to explain the relationship between flock size and feeding activity. He found flock size to be correlated to seed density and all of his studies involved birds in open habitats. Rubenstein et al. (1974) found that in mixed species flocks feeding with neighbors, especially if some are of other species, significantly increased the duration of the feeding episode. It would seem, bearing all this in mind, that the limited feeder space would have more of an impact on feeding time than the increased numbers of birds.

Interaction categories also decreased from the first half to the second, suggesting that the birds behaved more as flocks, which derive benefits from the inherent nature of the flock, such as early predator detection (Lazarus 1979) and observational learning (Rubenstein et al. 1977), than as individuals competing for limited resources. Caraco (1979a) found that increased seed density reduces search time and should affect group size, since the birds can allocate time released from foraging to increasing aggression. Because the seed density in this case was decreased, it would follow that aggression would also decrease. Although birds spent less time in all of the interactive categories in the first half than the second, the most interesting aspect of this is the submission category. This category experienced a reduction of time spent from the first half to the second which could possibly be attributed to the bird's increased motivation to defend its feeding site in the second half, whereas in the first half there was always another feeding site to which the bird could move. Pratt's study on frugivores (1983) suggested that aggressive individuals would be less likely to forfeit their claims to their feeding site when faced with competition from a subordinate individual.

Experiment, the effect responsible for increasing numbers of birds and decreasing available feeders, was analyzed by pen combination and it was there that some of the individual characteristics of the birds were shown. The pen containing tree sparrows experienced no significant differences from the first half to the second half and the pen containing Harris' sparrows only increased the proportion of time spent standing on the ground a slight, yet significant, amount. In personal observations of the species, Harris' sparrows seemed to be particularly docile birds and were very tolerant, not only of each other, but also of other birds. Rohwer (1976) described the strict, winter social hierarchy of Harris' sparrows according to plumage and describes the most vicious interactions as active displacements, which consist of one bird flying at another and taking over the other bird's perch or foraging position. Passive avoidance is another tactic of the Harris' sparrow described by Rohwer (1976). Normally tree sparrows seemed a bit more aggressive, but not to be compared with the cardinals. Bent (1968) describes the cardinal as amiable at times, but generally mildly dominant at feeding stations and sometimes decidedly belligerent.

From the first half to the second, cardinals decreased both the amount of time they spent feeding at the feeders and on the ground, seeming to tolerate the increased flock size and limited feeder availability much less than the two smaller sparrow species. Much of this lost feeding time was channelled into increased miscellaneous activity which, as a category, increased in proportion of time spent from 2.75% in the first half to 13.47% in the second half.

The birds in the cardinal-Harris' sparrow 6 bird pen experienced significant differences in only two categories due to the decreased feeder availability (in this case numbers of birds did not increase). Time spent flying increased from 2.93% to 5.66%. This particular section did not break these results down into species, so it is not known if one species experienced an increase in activity over the other, or if both increased the amount of time in this activity. In the single species pens containing these two species, Harris' sparrows increased the amount of time spent flying from the first half to the second while cardinals decreased the amount of time in that activity, although neither change was significant. It would seem from knowledge of the species and the previous results that the Harris' sparrows probably experience the increase in flying activity in an effort to eliminate some of the stress accompanying the reduction of feeder availability.

The birds in the cardinal-tree sparrow 6 bird pen also did not experience any significant differences in feeding behavior due to the reduced feeder availability. These birds did, however, significantly increase the amount of time spent in the miscellaneous activities and in the attack with visual threat category (significantly yet very slightly). As it was not recorded who was the aggressor in the interactions it is unknown which species increased in this activity, but once again I would suspect the cardinals due to their nature.

Rubenstein's findings (1977) of increased feeding time when in mixed species flocks was not substantiated in the three species cardinal-Harris' sparrow-tree sparrow flock. Rubenstein (1977), however, was working with wild flocks without spatial constraints. Birds in three species pens spent significantly less time in both feeding categories when the feeder availability was reduced in the second half. The amount of time spent in the miscellaneous activities increased from the first half to the second half, probably to compensate for the lost feeding time. The only interactive category to experience a significant difference was the attack with contact category which decreased. Again, as the identity of the aggressor was not recorded, it is unknown which species was accountable for this difference.

When quarter of the day was analyzed in the individual pens, the single species cardinal pen experienced no significant differences in time spent at the feeder but did see a feeding peak for feeding on the ground in quarter 2 and a low in quarter 1. In the less energetically stressful seasons of the year, most birds will feed early in the morning and late in the afternoon (Robel et al. in press). However, during the winter many birds are forced to feed almost continually throughout the day. Although the results did show significant differences for the feeding on the ground category, overall birds did seem to feed throughout the day. Cardinals experienced a significantly lower value for flying in quarter 4 than in the other three quarters (which were not significantly different from each other). Shuman (1984) found the same results for cardinals, with her birds flying much less in quarter 4 than in the other 3 quarters. Shuman (1984) found no significant differences in feeding by quarter for cardinals. Shuman (1984) found no significant differences in sitting by quarter, whereas these birds sat much more in quarter 1 than in any other quarter. However, Shuman's research had a category for both perching and sitting, while this research only used sitting to describe this behavior. Shuman did find significant differences in perching, with a peak in quarter 3 and a low in quarter 1 (this research had a high value for sitting in quarter 1). Shuman also found a peak in interactions in quarter 3 which was reflected in this research.

Harris' sparrows in the single species pen had little reaction to the differences in quarter. The one very interesting effect in this pen was a significant peak in flying in quarter 4 which is in direct conflict with the low flying value for quarter 4 for cardinals both in this research and in Shuman's (1984).

There was no significant flying peak for tree sparrows in the single species pen. The tree sparrows also had a different feeding strategy than the other two single species pens as they fed on the ground significantly more in quarters 1 and 2 than in quarters 3 and 4. These birds also spent significantly more time in the miscellaneous activities in quarters 1 and 4 than in 2 and 3. Both resting categories (sitting, standing on the ground) increased, although not significantly, during the middle two quarters of the day, which, in concert with the lower miscellaneous activities at these times, would seem to indicate these birds followed the more accepted bird activity pattern by resting more in the middle of the day. These birds also experienced interesting interactive results for quarter 2. The proportion of time spent submitting significantly decreased in quarter 2 while the amount of time attacking with visual threat and attacking with vocal threat both significantly increased in quarter 2.

The birds in the 6 bird cardinal-tree sparrow pen experienced a feeding peak in quarter 3 and a low in quarter 4. This once again, seems to be more attributable to the fact that wintering birds need to eat continuously to stay alive, as none of the flock compositions seem to be following any particular pattern in feeding by quarter of the day. This combination of birds also experienced several significant differences in the interactive categories. The birds spent a larger amount of time submitting in quarter 4 than in any other quarter and none of the other quarters were significantly different from each other. These birds had encounters involving attacks with contact in all four quarters, but had a low value of 0.01% for quarter 3 and a high in the next quarter of 0.36%. There were also attacks with vocal threats in all four quarters, but in this case, the low value was 0.02% in quarter 1 and the high was 0.28% in quarter 2. There were also significant differences in the attack with both visual and vocal threats, with no interactions in quarters 1 and 3 and statistically similar, low values for quarters 2 and 4. None of these interactive categories seem to follow any pattern whatsoever. However, when compared to the quarterly results from the single species pens, it is observed that cardinals did not vary significantly in amount of time spent submitting for any quarter, while the tree sparrows experienced a peak in submitting time in the same quarter experiencing a peak in this pen, quarter 4. It would seem that the tree sparrows are carrying this behavior through in the presence of the cardinals, but did change dramatically in the total amount of time spent in that activity. The tree sparrows may also have been responsible for the peak in time spent attacking with vocal threat, which peaked in the same quarter for both pens.

The 6 bird cardinal-Harris' sparrow pen exhibited significant differences in all quarters for feeding at the feeder while neither single species pen (for cardinals or Harris' sparrows) saw any differences in this category. The birds in this pen spent the most time feeding at the feeder in quarter 4, followed closely by quarter 2, with the lowest value in quarter 3. The birds in this pen also saw quite a bit of variance in the amount of time spent in the submission category, spending the most time submitting in quarter 3 and the least in quarter 4. Neither of these species saw any significant differences in time spent submitting in their respective single species pens.

In the 9 bird, three species pen, there were no significant differences due to quarter in either of the feeding categories, while both the single species cardinal and tree sparrow pens exhibited differences in the feeding on the ground category. Again, I would have to dispute Rubenstein et al. (1977) in their theory that mixed species flocks cause increases or more efficient feeding. The benefits of flocking are numerous (Powell 1973, Lazarus 1979, Caraco 1979a,b, Barnard 1980a) but would seem to benefit wild populations in their food finding and predator detecting much more than they would benefit this small, captive population.

The interspecific interactions compared by experiments held information about the behavior of the individual species. Neither tree sparrows nor Harris' sparrows changed their feeding behavior due to the presence of either increased numbers of their conspecifics or increased numbers of species. Instead, these birds decreased the amount of time spent submitting to another bird when resources became scarce. None of the other species in their pens had correspondingly increased the amount of time being aggressive; rather, the sparrows instead stood their ground in the face of limited resources, as did Pratt's frugivores (1983). Morse (1970) found that individual birds modify their areas of foraging in the presence of socially dominant species, but that a reciprocal effect is not well developed or is absent. In the wild, the presence of socially dominant species would make subordinate species modify their foraging in a direction that facilitated increased use of their special foraging adaptations. In this case, modified foraging was not an option as only two feeding strategies were possible. In order to survive the subordinate sparrow species would have to submit less, both to the cardinals and to the other sparrows. When feeders were present in a ratio of one per bird in the first half, there was always another site to move to and submitting was not a costly behavior. When feeders decreased in the second half to a ratio of one per every three birds, it became more beneficial to stay at the resource and tolerate the other birds. Tree sparrows even went so far as to increase in two aggressive categories, attack with vocal threat and attack with both visual and vocal threat, to maintain their right to share the resource. Unfortunately, the identity of the target of this aggressive action is unknown. However, Morse (1970) found that in mixed species flocks the majority of all aggressive interactions occur among individuals of the same species. I feel that this was probably also the case here.

Cardinals seemed to be the species most sensitive to change. When cardinals were housed in a single species flock, they experienced significant differences as flock size increased and feeder ratios decreased from the first half to the second. However, none of these differences were in any of the interactive categories. Proportions of time spent feeding at the feeder and feeding on the ground decreased as flock size increased and feeding sites were reduced. The cardinals seemed to compensate for this by increasing the amount of time spent in miscellaneous activities. This behavior neither follows the theory of increased feeding time in flocks (Caraco 1979a,b) nor the theory of increased aggression within a species (Morse 1970).

When cardinals were housed with Harris' sparrows in the 6 bird flock in which only feeder ratios were altered, the birds only experienced a significant difference in feeding at the feeder, which decreased as feeders became less abundant and in flying, which increased. Harris' sparrows are not that much smaller than cardinals (mean weights of 37.9 g and 33.5 g, respectively) and perhaps seemed too formidable to oppose. The cardinals in this pen did increase the amount of time they spent feeding on the ground, however the amount was not significant.

Cardinals in the 6 bird cardinal-tree sparrow pen did not significantly alter the amount of time they spent feeding at the feeder but did significantly reduce the amount of time spent feeding on the ground. Interestingly, the tree sparrows in the same pen did not significantly alter either feeding category, although the proportions of time spent feeding at the feeder are much smaller than the amounts for the cardinals. The cardinals in this pen experienced a large increase in the amount of time spent in miscellaneous activities and no differences in any of the interactive categories. This might suggest that the cardinals are not as dominant as Bent (1968) suggests as the tree sparrows are much smaller than the cardinals with a mean weight of 20.4 g.

In the 9 bird three species pen, cardinals once again experienced a large decrease in time spent feeding on the ground and an increase in time spent in miscellaneous activities. The only difference in any of the interactive categories occurred in the attack with vocal threat which decreased in amount of time spent for cardinals as feeder ratios decreased. Again, this would suggest that cardinals are perhaps not the dominant species, at least not in this winter research. Most of the literature that discusses the benefits of flocking in relation to feeding state that it is the benefit derived from predator detection that increases the amount of time the flocking birds spends feeding (Powell 1974, Lazarus 1979). Shuman (1984) found that cardinals did not seem to benefit from any predator detection as the birds were exposed visually to predators as they perched on side supports of the pens and may have developed an artificial sense of security as she saw reductions in the amount of time the birds spent scanning for predators as the experiment continued. The birds in this research did not follow this pattern and perhaps these theories can only be attributed to birds in the wild.

METHODS STUDY 2

Unconfined studies-- Time budgets of unconfined passerine birds in habitats of high and low metabolizable energy food sources.

The unconfined time budget study was divided into early season and late season. Early season extended from 5 November to 20 December 1984 and late season extended from 29 January to 30 March 1985. Time budget data were collected in these two periods on unconfined birds on high quality and low quality sites in the Manhattan area. Each site was selected based on the energy content of the seeds produced there that would be consumed by cardinals and Harris' sparrows, the isolation of the site from the general public, and the presence of cardinal and Harris' sparrow populations.

The high quality site had dominant plant species that produced seeds relatively high in energy, that were preferred by the birds (Kendeigh and West 1965, Willson 1971, Browning and Robel 1981). The site chosen was an old field dominated by wild sunflower (*Helianthus* spp.) and Lamb's quarter (*Chenopodium* spp.) located in a limited access area controlled by the Kansas State University Forestry Department. The field was 8 km northeast of Manhattan. The 1.3-ha field was bordered on the west edge by groves of trees maintained by the Forestry Department and on the south edge by a wooded area. The other two sides were surrounded by uncultivated fields. The site appeared suitable habitat for birds wintering in the area to remain on it for relatively long periods of time. Foods available for Cardinals and Harris' sparrows on the site consisted primarily of sunflower, lamb's quarter, and ragweed (Ambrosia spp.) seeds. These seeds have a mean gross energy content of 5.4 kcal/g and a mean metabolic energy value of 3.5 kcal/g (Robel et al. 1974, Shuman et al. 1989).

The low quality site was a grain sorghum field 13 km southwest of Manhattan on the edge of the Fort Riley Military Reservation. The majority of the plant species in this area produced seeds low in energy content. The grain sorghum and seeds of native grasses and sumac (Rhus spp.) present on the site had a mean gross energy content of 4.7 kcal/g and a metabolic energy content of 2.4 kcal/g (Robel et al. 1974). This 3.9-ha site was bordered on the east side by a paved road, on the west side by sparse woods and extended as the sorghum field to the north and south of the experimental area. While this habitat did not provide a food source as high in energy as the high quality environment, its low energy food resources were sufficiently abundant to support wintering birds for extended periods.

Three undergraduate research assistants were hired and trained in the field techniques established in the previous year's field work. Observational data were collected on Cardinals and Harris' sparrows by the three research assistants and myself. Observation time was divided equally between the low quality and high quality sites. Days were divided into four quarters (early morning, late morning, early afternoon, and late afternoon) and an effort was made to spend equal time observing in each quarter. In the early portion of this phase of the study, the research assistants and I dispersed ourselves throughout the experimental sites and observed birds from benches through binoculars mounted on photography tripods. As birds became more scarce later in the winter, it became necessary for us to seek birds rather than wait for the birds to come to us. Observational data were recorded on preprinted observation sheets (Appendix 3) using the abbreviations (found in Appendix 4) for the following behavioral activities: feeding, flying, singing, drinking, sitting, miscellaneous activities, submission, attack with contact, attack with visual threat, attack with vocal threat and attack with both vocal and visual threat.

Behavioral activities of individual Cardinals and Harris' sparrows were recorded. Because it was impossible to distinguish one individual from another, composite birds were created. This was accomplished by observing an individual bird and recording its activities until it left the observer's field of vision. Observations were discontinued until another individual of either of the desired species entered the area, at which time observations were resumed and activities recorded on data sheets specific only to species, rather than to individuals. No special preference was given to one species over another, so individuals of each species were observed in the order in which they appeared.

Field data from all observers were pooled by species and analyzed for effects of time of day (quarter), food quality site and time of year (season). Data were analyzed by analysis of variance (ANOVA) which enabled the effects (if any) of the environment on the species to be shown. Means were also derived from the data on proportion of time spent in each activity which illustrated where any differences in behavior occurred.

RESULTS STUDY 2

The technique of data gathering necessary in this study essentially left the research to the mercy of the birds. Because rigid study areas were required in the experiment, research assistants were very limited in their observational opportunities. If birds were not present on the experimental site, research came to a halt until birds once again became available. Due to this rather inconvenient fact, my efforts to divide observation time equally between species, observers, quarters of the day, season (early vs. late) and sites became futile. Therefore, the results show tremendous imbalances in observations on all of the above factors except season. The number of observations on quarter of the day were greatest in quarter 4 with 38.0% and least in quarter 2 with 10.8%. 79.8% of all observations were made on the low quality food plot while only 20.2% of the observations were made on the high quality food plot. 63.6% of all observations were made on Harris' sparrows and only 36.4% were made on cardinals. The observations in seasons were nearly equally distributed with 48.5% in the early winter and 51.5% in the late winter. The number of observations made by observer was also imbalanced as observer 4 saw 43.8% of all birds seen while observer 3 saw only 15.5% of all birds (Table 25).

Table 25. Comparative analysis of disparity in total observations on all main experimental variables in the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985. Results are given as frequencies of observations and percentages of total observations for each variable.

	Quarter				Site		Species		Season		Observer			
	1	2	3	4	High	Low	Cardinal	Harris' sparrow	Early	Late	1	2	3	4
Frequency	61	32	91	113	60	237	108	189	144	153	53	68	46	130
Percent	20.5	10.8	30.6	38.0	20.2	79.8	36.4	63.6	48.5	51.5	17.8	22.9	15.5	43.8

The analysis of variance (ANOVA) on the main effects x site x species showed nothing that was consistently statistically significant throughout but did illuminate some interesting smaller effects. The analysis for quarter yielded significantly different amounts of time spent only in the feeding category, in which the birds fed 13.5% in quarter 2 but only 1.2% in quarter 3 (ranking of feeding activity gives: quarter 2>quarter 1>quarter 4>quarter 3). No other behavior activity exhibited significant differences for quarter (Table 26).

Table 26. Means of proportions of daily activity spent in different behavioral activities by all birds in the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985. Quarter 1-4 designate the four quarters of each experimental day: quarter 1 = early morning, quarter 2 = late morning, quarter 3 = early afternoon, quarter 4 = late afternoon.

	Categories**									
Quarter	F*	FLY	SIT	SING	MSC	SUB	AC	AVI	AVO	AV2
1	9.39	16.81	65.38	4.66	3.21	0.04	0.01	0.49	0.00	0.00
2	13.53	17.36	58.84	8.85	0.99	0.02	0.01	0.42	0.00	0.00
3	1.19	17.09	73.95	4.48	2.86	0.07	0.02	0.14	0.00	0.00
4	6.02	15.28	66.88	6.18	5.76	0.01	0.00	0.03	0.60	0.00

*Denotes category in which significant differences were found (P=0.05)

**F=feeding, FLY=flying, SIT=sitting, SING=singing. MSC=miscellaneous, SUB=submission, AC=attack with contact, AVI=attack with visual threat, AVO=attack with vocal threat, AV2=attack,both visual and vocal.

The analysis for site discovered significant differences in both the sitting and singing categories. The birds spent significantly more time singing in the high quality food plot (10.53%) than in the low quality food plot (1.56%). The birds spent significantly more time sitting in the low quality food plot (74.11%) than in the high quality food plot (58.41%). No other significant differences were found for this effect (Table 27).

Table 27. Mean values of proportions of daily activity spent in different behavioral activities by all birds in the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985. Site designates the quality of the experimental food plot on which the research was conducted. High = a high quality food plot and low = a low quality food plot.

	Categories**									
Site	F	FLY	SIT*	SING*	MSC	SUB	AC	AV1	AVO	AV2
High	8.78	19.01	58.41	10.53	3.06	0.02	0.01	0.23	0.00	0.00
Low	6.29	14.27	74.11	1.56	3.35	0.05	0.02	0.31	0.00	0.00

*Denotes category in which significant differences were found (P=0.05)
**F=feeding, FLY=flying, SIT=sitting, SING=singing, MSC=miscellaneous, SUB=submission, AC=attack with contact, AV1=attack with visual threat, AVO=attack with vocal threat, AV2=attack,both visual and vocal.

Species analysis only found the behavior activity of flying to be significantly different between the two species. Cardinals spent significantly more time flying (20.06%) then the Harris' sparrows (13.22%). None of the other activities displayed any significant differences (Table 28).

Table 28. Mean values of proportions of daily activity spent in different behavioral activities by all birds in the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985.

Species	F	FLY*	SIT	SING	MSC	SUB	AC	AVI	AVO	AV2
					Categories**					
Cardinal	8.85	20.06	63.06	5.33	2.37	0.06	0.02	0.19	0.01	0.00
Harris'	6.22	13.22	69.47	6.75	4.03	0.01	0.00	0.35	0.00	0.00

*Denotes category in which significant differences were found (P=0.05)
**F=feeding, FLY=flying, SIT=sitting, SING=singing, MSC=miscellaneous, SUB=submission, AC=attack with contact, AVI=attack with visual threat, AVO=attack with vocal threat, AV2=attack,both visual and vocal.

The analysis for season found only one behavior activity in which the birds spent significantly more time in one season than the other. The birds spent significantly more time feeding late in the winter (10.62%) than early in the winter (4.44%) (Table 29).

Table 29. Mean values of proportions of daily activity spent in different behavioral activities by all birds in the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985. Season designates the time of year. Early = early winter, late = late winter.

Season	F*	FLY	SIT	SING	MSC	SUB	AC	AVI	AVO	AV2
					Categories**					
Early	4.44	16.83	67.18	6.63	4.57	0.05	0.02	0.15	0.00	0.00
Late	10.62	16.45	65.34	5.45	1.83	0.02	0.01	0.39	0.00	0.00

*Denotes category in which significant differences were found (P=0.05)
**F=feeding, FLY=flying, SIT=sitting. SING=singing, MSC=miscellaneous, SUB=submission. AC=attack with contact. AVI=attack with visual threat, AVO=attack with vocal threat, AV2=attack,both visual and vocal.

The observer effect displayed the most significantly different values for time spent in behavior activities. Feeding activity was significantly different for observers, with observer 3 recording the birds as feeding 11.88% while observers 1, 2, and 4 saw the birds feeding 7.22%, 5.32% and 5.71%, respectively. The category of flying also exhibited significant differences in amount of time spent according to observer. Observer 4 saw the birds flying 21.22% of the time while observers 1, 2 and 3 saw them flying 14.12%, 14.67% and 16.54%, respectively. The miscellaneous category also displayed a large disparity in results, with observer 1 recording 11.53% of all activity as miscellaneous while observer 2 only recorded 0.12% of all time spent as miscellaneous. The amount of time spent in the two interactive categories was relatively low but significantly different as to observer. Observer 3 saw the most submitting activities at 0.14% while observer 4 saw none. Observer 2 saw the most attack with visual threats with 0.51%, but observer 3 was right behind with 0.30% (Table 30).

Table 30. Mean values of proportions of daily activity spent in different behavioral activities by all birds in the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985. Observer designates the proportion of time each observer, 1-4, saw birds in each behavioral activity.

					Categories**					
Observer	F*	FLY*	SIT	SING	MSC*	SUB*	AC	AV1*	AVO	AV2
1	7.22	14.12	61.60	5.41	11.53	0.01	0.00	0.05	0.00	0.01
2	5.32	14.67	72.17	7.21	0.12	0.01	0.00	0.51	0.00	0.00
3	11.88	16.54	66.25	3.92	0.67	0.14	0.04	0.30	0.00	0.00
4	5.71	21.22	65.02	7.63	0.49	0.00	0.00	0.01	0.00	0.00

*Denotes category in which significant differences were found (P=0.05)

**F=feeding, FLY=flying, SIT=sitting, SING=singing, MSC=miscellaneous, SUB=submission, AC=attack with contact, AV1=attack with visual threat, AVO=attack with vocal threat, AV2=attack,both visual and vocal.

When observers were analyzed for frequency of observations by species, inconsistencies turned up. While observers 2 and 3 were relatively equal for both species, observers 1 and 4 saw Harris' sparrows for over 70% of their total observations on birds (Appendix 5)

Observers were not the only effect in which inconsistencies were evident. Some could not be helped. In analyzing for site by quarters, there were always more observations taken on the low quality site (60 total observations on the low quality site versus 237 total observations on the high quality site) (Table 31) But while analyzing for site by both season and quarter, this was not always the case. In quarter 1 there were no late season observations on the low quality site, while in quarters 3 and 4 there were no late season observations on the high quality site (Tables 32 and 33). The general trend, however, tends to suggest that there was simply a larger population of birds on the low quality site.

Table 31. Frequency results for the number of observations included in the analysis of site X quarter for the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985. [Values are frequencies followed by (percent)].

	Site		
Quarter	High	Low	Total
1	19 (31.15)	42 (68.85)	61
2	6 (18.75)	26 (81.25)	32
3	14 (15.38)	77 (84.62)	91
4	21 (18.58)	92 (81.42)	113
TOTAL	60	237	297

Table 32. Frequency results for the number of observations included in the analysis of season on the high quality food plot by quarter of the day during the second year's unconfined research on cardinals and Harris' sparrows during the winter of 199984-1985. Values are frequencies followed by (percent).

	Quarter				
Season	1	2	3	4	Total
Early	9 (17.65)	5 (16.67)	14 (87.50)	21 (44.68)	49
Late	10 (100.00)	1 (50.00)	0 (0)	0 (0)	11
Total	19	[illegible]	14	21	60

Table 33. Frequency results for the number of observations included in the analysis of season on the low quality food plot by quarter of the day during the second year's unconfined research on cardinals and Harris' sparrows during the winter of 1984-1985. Values are frequencies followed by (percents).

	Quarter				
Season	1	2	3	4	Total
Early	42 (82.35)	25 (83.33)	2 (12.50)	26 (55.32)	95
Late	0 (0)	1 (50.00)	75 (100.00)	66 (100.00)	142
Total	42	26	77	92	237

DISCUSSION STUDY 2

Quantification of habitat selection can delineate resources important to wildlife, whereas the time-activity budgets reveal how available habitats are used (Tacha 1987). The results from this time-budget study hopefully give some beneficial information on the habitat usage and behavior of cardinals and Harris' sparrows.

As always, field studies on wild bird populations are difficult. When attempting to be sure all results of observations on and between species are equal and random, many imbalances in observations on species and site seemed unavoidable in this experiment. However, even imbalanced observations should produce valid results.

The analysis for quarter produced significantly different results only in the feeding category. These birds spent the most time feeding in quarter 2, the designation given to represent the late morning. Free feeding birds normally feed the most in what were known in this experiment as quarters 1 and 4 (early morning and late afternoon). Tacha (1987) found that Sandhill cranes (*Grus* canadensis) follow this "normal" pattern, feeding most in the first and last two hours of the day.

Paulus (1988) also found the early morning and late afternoon to be the peak feeding hours in his work on mottled ducks (*Anas fulvigula*). Tacha's (1987) study was conducted in the spring, however, and his birds did not express the temperature stress associated with winter behavior. Paulus' work was conducted in the winter but took place in southwestern Louisiana along the Gulf of Mexico, removing winter temperature stress in his case, also. During the winter many non-migratory birds in temperate zones are forced to consume food continuously to meet energy needs (Robel et al. in press) which would account for the deviation in behavior from "normal" free feeding birds.

The results from the analysis for site yielded relatively expected results, as the birds in the high quality site, where significantly more singing occurred than the low quality site, would be expected to have more time and energy available for a "luxury'" behavior, such as singing. However, the birds in the low quality site spent significantly more time sitting in view than the birds in the high quality site, which does deviate from expected behavior. The high quality site contained an abundance of sunflower seeds and Shuman (1984) found that cardinals fed sunflower seeds spent significantly more time perching than the birds fed millet, which is a low energy content seed. There was no significant increase in the amount of time spent feeding, as one would expect. Perhaps the diversity of available seeds on both sites muddied the categories of "high quality" and "low quality". Shuman (1984) also suspected the sunflower seeds of being an incomplete (nutritionally) diet, as the birds eating millet, which is lower in energy than sunflower, fed at the feeders more than the birds eating sunflower, yet foraged away from the feeder less than the birds eating sunflower. This may be the case here, as birds, although preferring sunflower seeds (Willson 1971), may consume a more diverse diet in order to meet total nutritional requirements.

Significant differences between species were seen only in amount of time spent flying, with cardinals seen flying more than Harris' sparrows. This could possibly by explained by the physical characteristics of the species. The brightly colored cardinal would probably be more easily identified and observed flying by the observer than the dull, brown Harris' sparrow.

The time of year was found to affect the birds only in the amount of time they spent feeding. In the early winter birds spent significantly less time feeding than in the late winter. In the winter, seeds are a non-renewable resource and as such, would become less available as the winter progresses. It would follow that as seeds became less abundant the birds would have to spend more time seeking them.

The observer effect displayed the most significant differences, with variability found in the categories of feeding, flying, miscellaneous activity, submission and attack with visual threat. Human error seems inevitable and it is well documented that multiple observers can confound results (Enemar 1962, Dawsom et al. 1978, Robbins 1978, Ratkowsky and Ratkowsky 1979, Shields 1979, Cullen 1980, Kavanagh and Recher 1983). Observer variability has been attributed to many causes: differences in observer search patterns, differences in visual and hearing acuity, differences in motivation, differences in fatigue and differences in personality (Kavanagh and Recher 1983). The influence upon data of an observer's preconceived notions or wishes has been recognized and investigated at least since the beginning of the century (Balph and Balph 1983). Rosenthal (1969) speculated that in the experimental literature of the behavioral sciences, the effects of the experimental variable are not impressively larger than the effects of observer-expectancy bias. He also found that among observers of animal subjects, 100% of observers obtained results in the direction of their expectancy. With all these factors working in concert on observer variability, it would seem optimum to have a single observer collect all data. The only way to preclude observer-expectancy bias would seem to be to keep the observer completely ignorant of expected or desired results, although this would most probably make for an unmotivated observer, which would lead to even more variability. When multiple observers are necessary, as in this case, it is essential that procedures be standardized and analysis should be designed to minimize the effects of observer variability (Kavanagh and Recher 1983). I believe the variability in this case was primarily due to observer-expectancy bias as the observers in this year's research were particularly conscientious and very motivated.

The fact that none of the attack or submission categories appeared as significant except in the observer effect seems in itself significant to me. Both species of birds are very territorial during the breeding season (Bent 1968), yet are seen in flocks during the winter. Rohwer (1977) found that winter flocking behavior in many cases overrides territoriality. Flocking influences the time allocated to feeding activity not only in actual time spent eating but also in time spent searching for food (Barnard 1980a). Flocks of birds are more efficient at finding food than individuals (Caraco 1979a,b). Flocking also serves as an early warning function (Lazarus 1979) enabling members of a flock to spend less time scanning for predators than individuals would have to spend and to detect predators earlier than individuals would (Barnard 1980 a, Powell 1974). While many of the birds in this study were observed occurring in flocks, it was unfortunately not included in the analysis. Based upon the literature, flock size would seem to have a more pronounced effect on time budgets than perhaps any of the variables included in this research. This would certainly provide more detailed insights into the behavior of these species in the wild. The benefits of flocking would certainly enable wintering birds to spend more time searching for the vital energy they need rather than expending energy in aggressive encounters seen at other times of the year. Perhaps the effect of flocking is disguised in these results as the absence of aggression.

METHODS STUDY 3

Laboratory studies-- Intestinal morphology of selected passerines on differential diets.

On 26 April 1984 all birds used in the flight pen study on KPRNA were killed in a CO_2 gas chamber located in the Veterinary Medicine College at Kansas State University. The flight pen bird sample consisted of fourteen captive cardinals, 14 captive Harris' sparrows and 13 captive tree sparrows. These birds were killed to study the effects of the proso millet diet on their digestive tracts. Twenty-two wild Harris' sparrows captured on KPRNA were killed for comparison of their digestive tracts with those of the confined birds on a simple diet. The wild birds had access to many types of seeds produced by prairie and woodland grass and forbes on the KPRNA.

During the winter of 1984-85, while the unconfined time budget study was being conducted, birds also were being collected from each experimental site (from study 2) for intestinal morphology studies. Birds were collected in the early morning or late afternoon using either a 1.9-cm^2 mesh mist net or a shotgun loaded with #9 shot. All bird carcasses were carefully tagged with an identifying number and time of death in the field.

Birds captured alive were brought back to the laboratory and killed by cervical dislocation, taking care to record time captured and time killed. Sixteen cardinals and 26 Harris' sparrows were collected from the high quality site whereas 32 cardinals and 31 Harris' sparrows were collected from the low quality site.

In the laboratory all collected birds were weighed and dissected to obtain measurements of: body weight (g), large intestine length (cm), small intestine length (cm), gizzard dry weight (g) and liver dry weight (g). Birds were measured as quickly after death as possible, with most measurements taken within one hour of death. Intestines were cut at the base of the gizzard and laid flat. Measurements of the small intestine were taken by placing a ruler along the length of the intestine and measuring to the nearest 0.1 cm from the caeca forward to the cut end (Leopold 1953). Measurements of the large intestine were taken at the same time and by the same method, with the large intestine consisting of the area from the caeca to the cloaca (Farner and King 1953). Care was taken to be consistent in measurement techniques and to not stretch or break the intestine (Leopold 1953). Gizzards and livers were removed from the body, washed, and placed in labelled Petri dishes, then oven dried for at least 48 hours at 64 C. Oven dried samples were weighed on a Mettler Balance and recorded to 0.0001g. Wet weights were not recorded.

Study 3. LITERATURE REVIEW

Intestinal morphology of selected passerines based on differential diets.

Interest in an animal's ability to alter its own physiology in response to its current diet has been simmering for many years, but was limited for years to studies of gallinaceous birds and mammals important to the agricultural industry (Brownlee and Moss 1959). The study of this phenomena moved next to waterfowl (Drobney 1984, Paulus 1982, Kehoe and Ankney 1985, Miller 1975) and is only recently being investigated in passerines (Davis 1961, Pulliainen and Tunkkari 1981, and Klem et al. 1984).

Aldo Leopold's landmark 1953 paper on the intestinal morphology of gallinaceous birds seemed to break new ground for studies on the adaptability of the digestive system. Leopold questioned why some gallinaceous birds, such as various species of grouse, could survive on a winter diet that would not support a quail for a week. He began a comparative survey of galliforms with samples of most North American species included. In his survey, Leopold (1953) found a marked difference, particularly in the caecal length, between grouse, quail, partridges, pheasants and turkeys. A summary of his findings showed that the "average" grouse is found to exceed the "average" seed-eating galliform by 30% in length of large intestine and 28% in length of small intestine, and by 136% in caecal length.

Leopold went even farther by investigating two subspecies of California quail (Lophortyx californica brunnescens and L. c. californica) that existed in areas which would provide them with much different qualities of foods. He looked at L. c. brunnescens, which lived on the coast and therefore consumed much more green food than L. c. californica which existed in the more arid interior. Leopold theorized that, as livestock men had always found that the green forage of the coast was lower in nutritive value than the forbs and grasses of the interior, the quail on the coast would have to consume much larger quantities than the quail in the interior. He sampled the population and found that the birds living on the coast had 11% longer small intestines and 19% longer caeca.

Leopold's work began the trend for scientists to compare between birds the lengths of intestines and caeca to the amount and quality of their food. He compared his findings to already known facts; carnivorous fishes whose diets are high in protein have short intestines compared to fish surviving on plant materials, and that predatory mammals have short intestinal tracts when compared to the complex alimentary tracts of grazing ungulates (Leopold 1953). Leopold paved the way for years of new research when he suspected and his work supported the theory that differences could occur within a species if it existed on different diets.

Leopold's work led to more studies in the wild of seasonal changes in gut lengths in California quail (*Lophortyx californicus*) by Levin (1963), in ruffed grouse (*Bonasa umbellus*) by Pendergast (1969, 1973), in rock ptarmigan (*Lagopus mutus*) by Gardarsson (1970), and in willow grouse (*Lagopus lagopus*) by Pulliainen and Tunkkari (1983). While Brittas (1980) studied willow grouse (*L. l. lagopus*) from only September to May to show his seasonal variation in gut lengths, Pulliainen and Tunkkari (1983) studied the same species throughout the year. They found that the lengths of the combined caeca of the male willow grouse decreased from April-May to June-July and then increased to his maximum recorded length in the winter. The length of the small intestine increased from June-July to August-September and then decreased until the next winter with no changes taking place during winter, spring and early summer. In terms of absolute lengths, he found no differences in small intestine lengths between juveniles and adults or between sexes. He did, however, find age-sex differences in caecal lengths, with adults longer than juveniles and males longer than females.

Thomas (1984) studied willow grouse also, as well as sharp-tailed grouse (*Tympanuchus phasianellus*) and rock ptarmigan (*Lagopus mutus*) but his results concentrated on organ weights as opposed to organ lengths. He found much correlation between organ weights and body sizes, but when body weight was adjusted statistically, he found heavier weights in the willow ptarmigan which was the species consuming the most fibrous, least nutritious diet. Thomas (1984) did concede that it was more difficult to compare organ size between species than within species. All of these studies showed seasonal variations demonstrating that guts were longer and heavier in the winter when the food was relatively fibrous and indigestible than in the spring and summer when better food was available. Various other theories on factors affecting gut size were examined, such as hormones, gut microbes, rhythm of feeding, composition of diet and amount of food eaten (Levin 1969, Jayne-Williams and Coates 1969 and Fell 1969). Moss (1972) examined all the above factors as they affected his studies on red grouse (*Lagopus lagopus scoticus*) and he found that change in diet from spring-summer to winter rather than these other factors was responsible for the changes in gut lengths that he found.

In the 1960's Moss (1969) began to keep red grouse (*L.l. scoticus*) in captivity to examine the long term effects of a change in diet. He found that his captive birds had much shorter caeca and small intestines than wild birds, and that caecal lengths became increasingly shorter each year that he kept them in captivity, while small intestine lengths stabilized after becoming progressively shorter. Moss questioned what had caused the differences and, after investigating the previously mentioned possibilities, he concluded that it was definitely the change in diet. He even went so far as to say that the caecal length continued to decrease because of the inherent function of the caeca themselves. In birds eating a bulky, fibrous diet long caeca are necessary to store and ferment the food, breaking down the cellulose and extracting all possible nutrients available (Moss and Parkinson 1972, Gasaway 1976). As the captive birds were receiving a high quality, pelleted diet, they no longer required the long caeca. Moss's birds were continuing to decrease their caecal length in each successive generation. Moss (1969) felt that shorter guts were being selected for in his population, as larger guts had increased likelihood for adhesions, infections and lesions. Moss (1983) also developed a model designed to relate the digestibility of a food to its intake and the size of the gut digesting it. After many years of studying grouse morphology and the relationship of morphology to environment, Moss (1983) found that gut length is particularly useful for describing a bird's ecology because it is so labile, responding quickly to changes in food and environment. His work suggests that "digestibility" is as much a property of the eater as of the food being eaten. Moss's model (1983) gave him the ability to estimate the digestive abilities of tetraonids in winter as a function of gut length and body weight.

In the 1970's, work began on the relationship between intestinal length to diet in waterfowl. Miller (1975) attempted to illustrate the short term adaptive response of digestive organs to diet. He split captive mallards (*Anas platyrhynchos*) into three test groups and fed them three different diets. The test birds receiving the high fiber alfalfa (*Medicago* spp.) diet had statistically larger intestines than the ducks fed corn (*Zea* spp.) or turkey starter. Miller (1975) hypothesized that it would be necessary for waterfowl to have rapidly adjustable alimentary tracts due to their migratory nature. He called for more data so comparative studies on many species of waterfowl could be performed. He also questioned Moss's (1972) theory that gut lengths could be indices to food habits and ecology.

Paulus (1982) studied gadwalls (*Anas strepera*) wintering in Louisiana and intended to examine the adaptability of the gut to diets varying in quality and to determine if gut morphology measurements could serve as an index to food habits, as Miller (1975) had suggested that these measurements were not useful indices. Paulus' (1982) results showed that most gut morphology measurements increased from November through February and then declined in March, but he failed to find many differences in comparisons between months. Overall, he found that gadwall food habits reflected nutritive value and quantity with preference of foods and diets varying seasonally. He theorized that, "since the primary metabolic requirement of wintering gadwalls was to develop sufficient metabolic reserves for winter survival and spring migration, variability in intestinal morphology was probably an adaptation that improved energy absorption from foods of variable quality" (Paulus 1982: 488). From October through February, the birds fed primarily on spiked watermilfoil (*Myriophylllum spicatum*), which was the highest in fiber and lowest in gross energy content of all the foods he analyzed. In mid-February the birds switched to predominantly algae and time spent feeding rose from 44.3% in October to 70.5% in March. Algae was found to also be low in gross energy content but contained less crude fiber than the watermilfoil. The smaller gut size associated with the periods when the birds fed predominantly on algae probably indicated that crude fiber in the diet was more important than gross energy in modifying gut morphology. Paulus (1982) did, however, find variability in response between sexes and discouraged using gut morphology as an index to food habits for wintering gadwalls.

Drobney (1984) looked at the effects of diet quality on the morphology of breeding wood ducks (*Aix sponsa*), based on the findings of Korschgen (1976) for American eiders (*Somateria mollisima dresseri*) and Ankney (1977) for lesser snow geese (*Chen caerulescens caerulescens*) that the size of digestive organs declines during laying and incubation. But these authors attributed decreases in size to the reduced food intake during reproductive activity in these species rather than diet quality. Wood duck hens, however, feed throughout laying and incubation and exhibit marked changes in diet during the reproductive cycle (Drobney and Fredrickson 1979). Drobney (1984) found that intestine weights for hens peaked during fall courtship and laying and were lowest in prebreeding and incubating females. Intestine weights for fall males were significantly greater than those of breeding males. The decreased weight of the intestines between fall and spring in both sexes corresponded with a change from hard-seeded, high fiber plant foods during fall to soft, low-fiber plant foods in the spring. Drobney (1984) concluded, however, that morphological changes were primarily related to the quality and/or quantity of food ingested but found inconsistencies in the response of all organs. Gizzard weights were greatest in both sexes in the fall when the high-fiber foods dominated the diet and decreased in the spring as the dietary fiber also decreased. Drobney attributed these changes to dietary fiber alone. But, he thought that changes in the lower digestive tract, including the caeca, were influenced by quantity of food ingested. These weights were also higher in the fall as the birds had to consume more of the high fiber foods that were difficult to digest. But while the males decreased in size in the spring with the improved food quality, hens continued to have heavy intestine weights during laying that were attributed to hyperphagia.

But Kehoe and Ankney (1985) illustrated best how the theory could be applied to waterfowl when they did a comparative study of five diving ducks including: ring-neck (*Aythya collaris*), lesser scaup (*Aythya affinis*), greater scaup (*Aythya marila*), redhead (*Aythya americana*) and canvasback (*Aythya valisineria*). They studied these species as they are similar in gross morphology, macrohabitat use and feeding mode (Bellrose 1976, Smith 1979). Their objective was to describe differences in gut morphology among the five *Aythya* spp. to increase information on comparative gut sizes in waterfowl. They found interspecific differences in gut morphology among all five species. Some differences were attributed to differences in body weights, but once that was corrected for statistically, remaining interspecific differences in gut morophology were attributed to dietary differences. Kehoe and Ankney (1985) dispelled Miller's (1975) earlier doubts that waterfowl intestines and caeca could not be used as an index of food habits.

Once again, there is little in the literature on similar work in passerines. There are several works on differences between species based on life histories, such as the study by Pulliainen et al (1981) on the adaptive radiation of the digestive system, heart and wings of Turdus pilaris, Bombycilla garrulus, Sturnus vulgaris, Pyrrhula pyrrhula, Pinicola enucleator and Loxia pytyopsittacus, Davis' 1961 study on the seasonal changes in morphology of the rufous-sided towhee (Pipilo erythrophthalmum megalonyx), and the work by Klem, et.al. (1984) on the gross morphology and general histology of the alimentary tract of the American robin (Turdus migratorius), but none that I could find examining short term adaptation of intestines in response to a change in diet in passerines.

This study combined two years of gut data from birds on poor versus good habitats or captive birds fed poor diets versus wild birds on a better, more varied diet. The study attempts to detect differences in gut data, if any, in relationship to food quality in passerines, building on the years of information on this subject in waterfowl and gallinaceous birds.

Results Study 3

The work on intestinal morphology was divided into two sections: year 1 (1983-1984) consisted of a single sample of 41 captive birds from the confined study flight pens compared to 22 wild birds from the KPRNA, while year 2 (1984-1985) consisted of continuous sampling from the unconfined study research sites resulting in a total of 105 birds. In the first year the three species of birds from the flight pens were killed while only one species (Harris' sparrow) of wild birds were sampled. Therefore the only true comparison to be made was between the captive (sample size of 14) versus wild Harris' sparrows (sample size of 22). These two samples statistically differed on every measurement taken. Captive birds had statistically heavier mean body weights at 33.46 g than the wild birds at 31.51 g. Captive birds had shorter small and large intestines, 16.81 cm and 1.48 cm, respectively, versus 18.34 cm and 2.04 cm for the wild birds. Gizzard and liver weights of captive birds also differed significantly as they were heavier at 0.12 g and 0.13 g, respectively, as opposed to 0.08 g and 0.09 g for the wild birds (Table 34).

Table 34. Least square means and standard deviations of morphological characteristics of captive versus wild Harris' sparrows from the 1983-1984 season. Common superscripts across a row indicate values that do not differ. (P=0.05)

Morphological characteristic	Bird status	
	Captive	Wild
Body weight (g)	33.46 ± 0.73^{A}	31.51 ± 0.60^{B}
Small intestine(cm)	16.61 ± 0.29^{A}	18.34 ± 0.23^{B}
Large intestine(cm)	1.48 ± 0.05^{A}	2.04 ± 0.06^{B}
Gizzard(g)	0.12 ± 0.00^{A}	0.08 ± 0.00^{B}
Liver(g)	0.13 ± 0.01^{A}	0.09 ± 0.01^{B}

The second section of the morphology research studied the birds taken from the unconfined study sites and consisted of a total sample of 16 cardinals and 26 Harris' sparrows from the high quality site and 32 cardinals and 31 Harris' sparrows from the low quality site. The morphological variables were analyzed both for the quality of the food plot and early winter versus late winter.

When analyzed by site, neither species exhibited significantly different mean body weights or small intestine lengths. Both species displayed significant differences in large intestine lengths; however, as the cardinals had longer large intestines in the low quality food plot (2.32 cm) than in the high quality food plot (2.01 cm) for a difference of .31 cm, the Harris' sparrows had shorter large intestines in the low quality food plot (1.93 cm) than in the high quality food plot (2.26 cm) for a difference of .33 cm. The Harris' sparrows exhibited no significant differences in gizzard or liver weights. The cardinals had both heavier gizzards and livers in the low quality food plot than the high quality food plot. Gizzards had mean weights of 0.14 g in the high quality site and 0.16 g in the low quality site. Livers had mean weights of 0.12 g in the low quality site and 0.15 g in the high quality site (Table 35).

When analyzed by season, cardinals showed a significant difference only in gizzard weight, with heavier mean gizzards weights in the late winter (0.16 g) than in the early winter (0.14 g). Harris' sparrows showed a significant difference only in large intestine length, with shorter mean large intestine lengths in the late winter (1.92 cm) than in the early winter (2.26 cm) (Table 36).

Table 35. Least square means and standard deviations of morphological characteristics of Cardinals and Harris' sparrows on the high and low food plots. Common superscripts between a pair indicate values that do not differ. (P=0.05)

	Bird species and quality of food plot			
	Cardinal		Harris' sparrow	
Morphological characteristic	High	Low	High	Low
Body weight(g)	44.09 ± 1.00^{A}	46.20 ± 0.72^{A}	34.79 ± 0.83^{A}	35.95 ± 0.76^{A}
Small intestine(cm)	20.71 ± 0.60^{A}	21.47 ± 0.42^{A}	17.53 ± 0.30^{A}	17.74 ± 0.29^{A}
Large intestine(cm)	2.01 ± 0.11^{A}	2.32 ± 0.08^{B}	2.26 ± 0.08^{A}	1.93 ± 0.07^{B}
Gizzard(g)	0.14 ± 0.03^{A}	0.16 ± 0.00^{B}	0.13 ± 0.00^{A}	0.13 ± 0.00^{A}
Liver(g)	0.12 ± 0.01^{A}	0.15 ± 0.00^{B}	0.12 ± 0.00^{A}	0.13 ± 0.00^{A}

Table 36. Least square means and standard deviations of morphological characteristics of Cardinals and Harris' sparrows in the early and late season designations. Common superscripts between a pair indicate values that do not differ. (P=0.05)

	Bird species and time of year data recorded			
	Cardinal		Harris' sparrow	
Morphological characteristic	Early season	Late season	Early season	Late season
Body weight(g)	45.21 ± 0.86^{A}	45.08 ± 0.89^{A}	34.67 ± 0.82^{A}	35.87 ± 0.77^{A}
Small intestine(cm)	21.03 ± 0.50^{A}	21.4 ± 0.53^{A}	17.36 ± 0.31^{A}	17.91 ± 0.27^{A}
Large intestine(cm)	2.28 ± 0.09^{A}	2.06 ± 0.10^{A}	2.26 ± 0.08^{A}	1.92 ± 0.07^{B}
Gizzard(g)	0.14 ± 0.00^{A}	0.16 ± 0.00^{B}	0.13 ± 0.00^{A}	0.13 ± 0.00^{A}
Liver(g)	0.13 ± 0.01^{A}	0.14 ± 0.01^{A}	0.13 ± 0.00^{A}	0.13 ± 0.00^{A}

These results were examined further by analyzing for site x season, or the influence each variable had on the other. Cardinals showed no difference in measurements in the high quality site due to season, but in the low quality site had heavier gizzard and liver weights due to late winter, with values increasing from 0.15 g to 0.17 g from early winter to late winter for mean gizzard weights and 0.13 g to 0.17 g from early winter to late winter for mean liver weights. The birds showed no differences in the early winter due to site, but in the late winter had heavier mean gizzard and liver weights on the low quality site than on the high quality site, with values of 0.14 g for mean gizzard weight on the high quality site and 0.17 g on the low quality site. Mean liver weights in this case were 0.11 g on the high quality site and 0.17 g on the low quality site (Table 37).

Harris' sparrows, however, showed no difference due to season in the low quality site, but on the high quality site had shorter large intestines in the late winter (2.07 cm) than in the early winter (2.45 cm). When season was held constant, Harris' sparrows showed some variance in both seasons. In the early winter large intestines were significantly longer on the high quality site (2.45 cm) than on the low quality site (2.07 cm). In the late winter large intestine lengths again decreased from 2.07 cm on the high quality site to 1.78 cm on the low quality site. Liver weights also showed variance, increasing from 0.12 g on the high quality site to 0.13 g on the low quality site (Table 38).

Table 37. Least square means and standard deviations of morphological characteristics of Cardinals for the comparison of site x season. Common superscripts between a pair indicate values that do not differ. (P=0.05)

Morphological characteristics	Effects of season and food plot designation combined			
	High[a] Early	High Late	High Early	Low Early
Body weight(g)	44.01±1.42[A]	44.17±1.42[A]	44.01±1.42[A]	46.42±0.97[A]
Small intestine(cm)	20.71±0.81[A]	20.70±0.87[A]	20.71±0.8[A]	21.36±0.58[A]
Large intestine(cm)	2.15±0.15[A]	1.89±0.17[A]	2.15±0.15[A]	2.41±0.11[A]
Gizzard(g)	0.15±0.01[A]	0.14±0.01[A]	0.15±0.01[A]	0.15±0.00[A]
Liver(g)	0.13±0.01[A]	0.11±0.01[A]	0.13±0.01[A]	0.13±0.01[A]
	Low Early	Low Late	High Late	Low Late
Body weight (g)	46.42±0.97[A]	45.99±1.07[A]	44.17±0.97[A]	45.99±1.07[A]
Small intestine(cm)	21.36±0.58[A]	21.58±0.62[A]	20.70±0.87[A]	21.58±0.62[A]
Large intestine(cm)	2.41±0.11[A]	2.24±0.12[A]	1.89±0.17[A]	2.24±0.12[A]
Gizzard(g)	0.15±0.00[A]	0.17±0.00[B]	0.14±0.00[A]	0.17±0.00[B]
Liver(g)	0.13±0.01[A]	0.17±0.01[B]	0.11±0.01[A]	0.17±0.01[B]

[a] High = high quality food plot, Low = low quality food plot, Early = early winter, Late = late winter

Table 38. Least square means and standard deviations of morphological characteristics of Harris' sparrrows for the comparison of site x season. Common superscripts between a pair indicate values that do not differ. (P=0.05)

Morphological characteristics	Effect of season and food plot designations combined			
	High* Early	High Late	high Early	Low Early
Body weight(g)	34.51±1.30^A	35.07±1.03^A	34.51±1.30^A	35.22±1.00^A
Small intestine(cm)	17.23±0.46^A	17.84±0.38^A	17.23±0.46^A	17.50±0.42^A
Large intestine(cm)	2.45±0.12^A	2.07±0.10^B	2.45±0.12^A	2.07±0.11^B
Bizzard(g)	0.13±0.00^A	0.13±0.00^A	0.13±0.00^A	0.13±0.00^A
Liver(g)	0.13±0.01^A	0.12±0.00^A	0.13±0.01^A	0.13±0.00^A
	Low Early	Low Late	High Late	Low Late
Body weight(g)	35.22±1.00^A	36.68±1.14^A	35.07±1.03^A	36.68±1.14^A
Small intestine(cm)	17.50±0.42^A	17.98±0.39^A	17.84±0.38^A	17.98±0.39^A
Large intestine(cm)	2.07±0.11^A	1.78±0.10^A	2.07±0.10^A	1.78±0.10^B
Bizzard(g)	0.13±0.00^A	0.13±0.00^A	0.13±0.00^A	0.13±0.00^A
Liver(g)	0.13±0.00^A	0.13±0.00^A	0.12±0.00^A	0.13±0.00^B

* High = high quality food plot, Low = low quality food plot, Early = early winter, Late = late winter

DISCUSSION STUDY 3

The most obvious conclusion to be drawn from the results for this study is that my experimental design placed more emphasis on the caloric value of the food plant species involved than on the fiber content of those food plant species. While early studies, such as Leopold's work on gallinaceous birds (1953), theorized that birds consuming a diet low in nutritive value would have to consume more than birds on a diet high in nutritive value, therefore causing larger intestines due to the larger quantity of food ingested, later studies found the fiber content of the diet to be more influential in fluctuating intestinal morphology (Moss 1972, Miller 1975, Gasaway 1976, Paulus 1982, Drobney 1984, Thomas 1984, Kehoe and Ankney 1985).

The results from the first year of this study illustrate large statistical differences due to diet in captive Harris' sparrows on a diet of white proso millet versus wild Harris' sparrows consuming the more varied, native diet found on the KPRNA. My original hyphothesis had been that the wild prairie diet would be a "better" diet due to its diversity and that millet would be the poorest quality diet in the experiment. _Panicum_ spp. and native grass species both have mean gross energies of 4.7 kcal/g (Kendeigh and West 1965, Robel et al.

1974). Therefore, morphological differences in intestinal measurements would seem to indicate that the native, grassy winter diet would be lower in fiber but more diverse than the millet, based on the findings in the literature. Miller (1975) found that all the digestive organs of his mallards on the high-fiber diet were larger than those on the better quality, low fiber diet, but found the percentage increase in organ weight exceeded the magnitude of the increase in length for all organs. Moss (1974) suggested that a species should have the shortest possible gut for a given diet to reduce metabolic costs of maintenance. Moss (1974) found that ptarmigan (Lagopus spp.) with the most diverse diets had the longest intestines and suggested that this enabled them to digest whatever foods were available at a given time. Kehoe and Ankney (1985) confirmed both of these findings in their waterfowl study. Their birds on high fiber diets had heavier gizzards than the birds on low fiber diets and the birds with the most diverse diets had the longest intestines. The Harris' sparrows in this study seem to reflect these previous findings: the wild birds eating a low fiber, very diverse diet had longer intestines and lighter gizzards and livers than the captive birds eating a high fiber, single species diet.

The analysis by food quality site provided less conclusive results, as differences were seen only in the large intestine lengths and the large intestine is not the primary site of digestion in birds. As no significant differences were seen in small intestine lengths, it is difficult to interpret the relevance of the large intestine data. Kehoe and Ankney (1985) did not even include the large intestine lengths in their analysis. The only relevant findings from this analysis would seem to be the cardinal organ weights. Cardinals exhibited the heavier organ weights associated with a high fiber diet in the low quality food plot. The high quality sunflower field led to lighter organ weights as sunflower is both a preferred diet of cardinals (Willson 1971, Browning and Robel 1981, Shuman 1984) and is relatively low in fiber content (Robel et al. in press).

Cardinals were also the only species to exhibit significant differences due to season. Cardinal gizzard weights were heavier late in the winter and lighter early in the winter. As stated previously, heavy gizzard weights are associated with a diet higher in fiber. The increase in gizzard weights would most likely be attributed to the fact that the preferred seeds became less abundant as the winter wore on.

The site x season results again showed significant differences only for cardinals. The poorest conditions for both site and season illicited the significantly different gizzard mean weights. The low quality food plot in the late winter resulted in heavier gizzard weights due to the waning of the already limited resources found in the low quality site. Harris' sparrows appeared unaffected by season or site. Slight differences were found in the inconclusive categories of large intestine length and liver weight. The liver weight increases associated with the low quality site late in the winter may possibly be associated with the liver's function as a glycogen storage organ. The birds in this set of circumstances would probably be consuming more low quality foods than the birds early in the winter or on the high quality site when better food was more readily available.

OVERALL CONCLUSIONS

Studies 1 and 2 explored the time budget activity of several emberizid species in response to several variables presented in the winters of 1983-1984 and 1984-1985. The birds in both studies exhibited both expected and unexpected behaviors.

The birds in 1983-1984's confined study performed some of the activities associated with flocking (Lazarus 1979, Barnard 1980a), such as very low proportions of time spent in aggressive interactions despite the spatial limitations, reduced resource availability and increased flock size. Time spent submitting to overtures from another bird did decrease as the resources became limited, but hostile reactions did not concurrently increase.

Some flocking characteristics were not substantiated, as Rubenstein's (1977) findings that mixed species flocks led to increased time spent feeding were not seen in the three species flock which decreased feeding time when resources became limited.

The confined study also gave some insight into the characteristics of the bird species themselves. Cardinals are usually described as aggressive and dominant at feeders and, as the largest species present, would have been expected to display those behaviors here. Cardinals decreased the amount of time spent feeding even in the presence of tree sparrows, a much smaller species, while not spending any more time in aggressive interactions. Tree sparrows, on the other hand, displayed the most increases in hostile attacks in this experiment. The traditionally docile Harris' sparrows were the least affected by any combinations of species.

The second year's study on unconfined birds produced expected winter behaviors. This study would best be followed by work studying the same species but also analyzing their flocking behavior. Winter flocking behavior seems extremely advantageous and perhaps at times crucial to survival. The study of how flocking affects behavior in the face of abundant versus limited resources would be fascinating.

Study 3 investigated the response of visceral morphology due to differential diets. Much work has been done on this subject in gallinaceous birds and waterfowl (Leopold 1953, Levin 1963, Pendergast 1969, 1973, Gardarsson 1970, Pulliainen and Tunkkari 1983, Thomas 1984, Moss 1969, 1972, 1974, 1983, Miller 1975, Paulus 1982, Drobney 1984, Kehoe and Ankney 1985) and now passerines seem to following the same pattern of manipulating intestine lengths and organ weights in response to the nutritional and fiber content of their food. The fact that the results in this section that involved the experimental food plots were relatively inconclusive was probably due to questionable food plot assignment as opposed to nonresponsive passerines.

LITERATURE CITED

Alatalo, R.V. 1980. Seasonal dynamics of resource partitioning among foliage-gleaning passerines in northern Finland. Oecol. 45:190-196.

Ankney, C.D. 1977. Feeding and digestive organ size in breeding lesser snow geese. Auk, 94, 275-282.

Armstrong, R.A. and M.E. Gilpin. 1977. Evolution in a time-varying environment. Science 195:591-592.

Ashkenazie, S. and V.N. Safriel. 1979. Time-energy budget of the semi-palmated sandpiper (Calidris pusilla) at Barrow, Alaska. Ecol. 60:783-799.

Baker, M.C. and A.E.M. Baker. 1973. Niche relationships among six species of shore birds on their wintering and breeding ranges. Ecol. Monogr. 43:193-212.

Baldwin, S.P. and S.C. Kendeigh. 1939. Variations in the weight of birds. Auk 55:416-467.

Balph, D.F. and M.H. Balph. 1979. Behavioral flexibility of pine siskins in mixed species foraging groups. Condor 81:211-212.

__________________________. 1983. On the psychology of watching birds: the problem of observer-expectancy bias. Auk 100: 755-757.

Barnard, C.J., D.B.A. Thompson, and H. Stephens. 1982. Time-budgets, feeding efficiency, and flock dynamics in mixed species flocks of lapwings, golden plovers and gulls. Behav. 80:44-69.

Barnard, C.J. 1980. Flock feeding and time-budgets in the house sparrow (Passer domesticus L.). Anim. Behav. 28:295-305.

Bellrose, F.C. 1976. Ducks, geese and swans of North America. 3rd ed. Stackpole Books, Harrisburg, PA.

Benkman, C.W. 1988. The comparative feeding rates of North American sparrows and finches. Ecol 69(4): 1195-1199.

Bent, A.C. 1968. Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhes, Finches, Sparrows, and Allies. Dover Publicatons, Inc. New York, NY.

Biedenweg, D.W. 1983. Time and energy budgets of the mockingbird (Mimus polyglottis) during the breeding season. Auk 100:149-160.

Birch, L.C. and P.R. Ehrlich. 1967. Evolutionary history and population biology. Nature 214:349-352.

Brittas, R. 1980. Varfor har dalripan langre tarmar pa vintern an pa sommaren? Jaktjournalen 1980(10):32-33, 62.

Brockman, H.J. and C.J. Barnard. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487-514.

Brown, J.H. 1975. Geographical ecology of desert rodents. In Cody and Diamond, eds., pp. 315-341.

Brownlee, A. and W. Moss. 1959. Changes in size of the gastro-intestinal tract, liver and kidneys of the labor-atory rat at different live weights and on different dietary regimens. Brit. Vet. J. 115(7):1-10.

Caldwell, G.S. 1981. Attraction to tropical mixed-species heron flocks: proximate mechanism and consequences. Behav. Ecol. Sociobiol. 8:99-103.

Caraco, T. 1979a. Time-budgeting and group size: a theory. Ecol. 60:611-617.

__________. 1979b. Time-budgeting and group size: a test of theory. Ecol. 60:618-627.

Cody, J.L. 1974. Competition and the Structure of Bird Communities. Monogr. Popul. Biol. No. 7. Princeton Univ. Press.

Cody M.L. and J.M. Diamond, eds. 1975. Ecology and Evolution of Comunities. Belknap Press of Harvard Univ. Press.

Colwell, R.K. and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecol. 52:567-576.

Conley, W. 1976. Competition between Microtus : A be-havioral hypothesis. Ecol. 52:224-237.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In Cody and Diamond, eds., pp. 460-490.

Connelly, J.W., H.W. Browers and R.J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. J. Wildl. Manage. 52(4):679-688.

Crome, F.H.J. 1978. Foraging ecology of an assemblage of birds in lowland rainforest in northern Queensland. Australian J. of Ecol. 3:195-212.

Cullen, J.M. 1980. Rolling bird survey. Atlas Newsletter No. 16, R.A.O.U. Melbourne.

Culver, D.C. 1975. Interaction between competition and predation in cave stream communities. Int. J. Speleol. 7:229-245.

Custer, T.W. 1974. Population ecology and bioenergetics of Lapland longspur (*Calcarius lapponicus*) near Barrow, Alaska. Disssertation. University of California, Berkeley, California, USA.

Custer, T.W. and F.A. Pitelka. 1972. Time-activity patterns and energy budgets of nesting Lapland longspur (*Calcarius lapponicus*) near Barrow, Alaska. Pages 160-164 *in* Proceedings of the 1972 Tundra Biome Symposium, Lake Wilderness, Washington, USA.

Davis, J. 1961. Some seasonal changes in morphology of the rufous-sided towhee. Condor 63:313-321.

Dawson, D.G., P.J. Dilks, P.D. Gaze, J.G.R. McBurney, and P.R. Wilson. 1978. Seasonal differences in bird counts in forests near Reefton, South Island New Zealand. Nortornis 26:53-61.

Dayton, P.K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

__________. 1973. Two cases of resource partitioning in an intertidal community: Making the right prediction for the wrong reason. Am. Nat. 107: 662-670.

DeBenedictis, P.A. 1974. Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica:* An experimental field study. Ecol. Monogr. 44:129-151.

Dolnik, V.R., and T.I. Blyumental. 1964. Bioenergetika migratsii ptits. Uspekhi Sovremennoi Biologii. 58:280-301.

Drobney, R.D. 1984. Effect of diet on visceral morphology of breeding wood ducks. Auk 101:93-98.

Drobney, R.D. and L.H. Fredrickson. 1979. Food selection by Wood Ducks in relation to breeding status. J. Wildl. Manage. 43:109-120.

Emlen, J.M. 1973. Ecology: An Evolutionary Approach. Addison-Wesley.

Enemar, A. 1962. A comparison between the bird census results of different ornithologists. Var. Fagelvarld 21:109-120.

Ettinger, A.O. and J.R. King. 1980. Time and energy budgets of the willow flycatcher (Empidonax traillii) during the breeding season. Auk 97: 533-546.

Fell, B.F. 1969. Morphology of the absorptive surfaces of the alimentary tract. Pages 295-344. In D. Cuthbertsson (ed.), Nutrition of animals of agricultural importance. Part 1. The science and nurtrition o ffarm livestock. Internatl. Encyclopedia of Food and Nutrition 17. Pergamon Press, Oxford, London and New York. 592 pp.

Fraser, D.F. 1976. Coexistence of salamanders in the genus Plethodon : A variation of the Santa Rosella Theme. Ecol. 57:238-251.

Frederick, R.B., and E.E. Klaas. 1982. Resource use and behavior of migrating snow geese. J. Wildl. Manage. 46:601-614.

Gardarsson, A. and R. Moss. 1970. Selection of food by Icelandic ptarmigan in relation to its availability and populations in relation to its availability and populations in relatin to their food resosurces. Blackwell Scientific Publications, Oxford.

Gasaway, W.C. 1976. Cellulose digestion and metabolism by captive rock ptarmigan. Comp. Biochem. Physiol. 54A: 179-182.

Gessaman, J.A. 1973. Methods of estimating the energy cost of free existence, pp. 3-31. In Ecological energetics of Homeotherms (J.A. Gessaman, Ed.). Utah State Univ. Monogr. Ser., Vol. 20.

Gilpin, M.E. and T.J. Case. 1976. Multiple domains of attraction in competitive communities. Nature 261:40-42.

Grant, P.R. 1972. Interspecific competition among rodents. Ann. Rev. Ecol. Syst. 3:79-106.

----------. 1975. Population performance of Microtus pennsylvanicus confined to woodland habitat, and a model of habitat occupancy. Can. J. Zool. 53:1447-1465.

Hagen, Y. 1942. Totalgwichts-Studien bei norwegische vogelarten. Arch. Natur. 11:1-173.

Hayward, J.S. 1965. The gross body composition of six geographic races of Peromyscus. Can. J. Zool. 43:297-308.

Helms, C.W. and W.H. Drury Jr. 1960. Winter and migratory weight and fat: Field studies on some North American buntings. Bird-Banding 31:1-40.

Herrera, C.M. 1978. Ecological correlates of residence and non-residence in a Mediterranean passerine bird community. J. of Anim. Ecol. 47:871-890.

Hespenheide, H.A. 1973. Ecological inferences from morphological data. Ann. Rev. Ecol. Syst. 4:13-229.

Hulbert, L.C. 1985. History and use of Konza Prairie Research Natural Area. The Prairie Scout (Abilene: Kansas Corral of the Westerners, 1985), vol. V, 63-93.

Hutchinson, G.E. 1975. Variations on a theme by Robert MacArthur. In Cody and Diamond, eds., pp. 492-521.

Inozemtzev, A.A. 1964. O neketorykh prichinakh izakonomernostyakh kolebaniya vesa tela u ptits. Zoolog. Zh. 43:232-241.

Iverson, G.C., P.A. Vohs, and T.C. Tacha. 1985a. Distribution and abundance of sandhill cranes wintering in western Texas. J. Wildl. Manage. 49:250-255.

Iverson, G.C. , P.A. Vohs, and T.C. Tacha. 1985b. Habitat use by sandhill cranes wintering in western Texas. J. Wildl. Manage. 49:1074-1083.

Jaeger, R.G. 1974. Competitive exclusion: Comments of survival and extinction of species. BioScience 24:33-39.

Jayne-Williams, D.J. and M.E. Coates. 1969. The microflora of the alimentary tract of the bird and its significance in nutrition. Pages 241-59. In D. Cuthbertson (ed.), Nutrition of animals of agricultural importance. Part 1. The science of nutrition of farm livestock. Internatl. Encyclopedia of Food and Nutrition 17. Pergamon Pres, Oxford, London, and New York. 592 pp.

Johnson, S.R. and R.J. Robel. 1968. Caloric values of seeds from four range sites in northeastern Kansas. Ecol. 49(5):956-961.

Kavanagh, R. and H.F. Recher. 1983. Effects of observer variability on the census of birds. Corella 7(5):93- 100.

Kehoe, F.R. and C.D. Ankney. 1985. Variation in digestive organ size among five species of diving ducks (Aythya spp.). Can. J. Zool. 63:2339-2342.

Kendeigh, S.C. and G.C. West. 1965. Caloric values of plant seeds eaten by birds. Ecol. 46(4):553-555.

Kendeigh, S.C. 1969. Energy responses of birds to their thermal environment. The Wilson Bull. 81(4):441-449.

King, J.R. 1974. Field measurements of avian energy adaptations. pp. 4-85. In Avian Energetics (R.A. Paynter, ed.). Publ. Nutt. Ornithol. Club, No. 15, Cambridge Mass. 334 pp.

Klem, D., Jr., M.A. Parker, W.L. Sprague, S.A. Tafuri, C.J. Veltri and M.J. Walker. 1984. Gross morphology and general histology of the alimentary tract of the American robin (Turdus migratorius). In Proceedings Of The Pennsylvania Academy of Science. 58(2):151-158.

Kontogiannis, J.E. 1968. Effect of temperature and exercise on energy intake and body weight on the White-throated Sparrow, Zonotrichia albicollis. Physiol. Zool. 41:54-64.

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

Korschgen, C. E. 1976. Breeding stress of female American Eiders (Somateria mollissima dresseri Sharpe). Unpublished Ph.D. dissertation. Orono, Maine, Univ. Maine.

Krebs, J.R. 1973. Social learning and the significance of mixed species flocks of chickadees (Parus spp.) Can. J. Zool. 51:1275-1288.

Kushlan, J.A. 1977. The significance of plumage color in the formation of feeding aggregations of ciconiiforms. Ibis 119:361-364.

------------. 1978. Commensalism in the little blue heron. Auk 95:677-681.

Lack, D.L. 1971. Ecological Isolation in Birds. Blackwells, Oxford.

Lack, D.L. 1974. Darwin's Finches. Cambridge Univ. Press. Cambridge, Mass.

Lazarus, J. 1979. The early warning function of flocking in birds: an experimental study with captive quelea. Anim. Behav. 27:855-865.

Leopold, A.S. 1953. Intestinal morphology of gallinaceous birds in relation to food habits. J. Wildl. Manage. 17:197-203.

Levin, R.J. 1969. The effects of hormones on the absorptive, metabolic and digestive functions of the small intestines. J. Endocrinol. 45(2):315-348.

Levin, V. 1963. Reproduction and development of young in a population of California quail. Condor 65(4):249-278.

Levins, R. 1975. Evolution in communities near equilibrium. In Cody and Diamond, eds., pp. 51-73.

MacArthur, R.H. 1972. Geographihcal Ecology. Harper and Row, New York.

MacArthur, R.H. and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. PNAS 51:1207-1210.

MacArthur, R.H. and E.R. Pianka. 1966. On optimal use of patchy environment. Am. Nat. 100:603-609.

Menge, B.A. 1972. Competition for food between two intertidal starfish species and its effect on body size and feeding. Ecol. 53:635-644.

Miller, M.R. 1975. Gut morphology of mallards in relation to diet quality. J. Wildl. Manage. 39(1):168-173.

Morse, D.H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr.

40:119-168.

Morse, D.H. 1975. Ecological aspects of adaptive radiation in birds. Biol. Rev. 50:17-214.

----------. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during winter. Ibis 120:295-312.

Moss, R. 1969. Rearing red grouse and ptarmigan in captivity. Avicultural Mag. 75(7):256-261.

Moss, R. 1972. Effects of captivity on gut lengths in red grouse. J. Wildl. Manage. 36(1):99-104.

Moss, R. 1974. Winter diets, gut length, and interspecific competition in Alaskan ptarmigan. Condor 85:185-193.

Moss, R. 1983. Gut size, body weight, and digestion of winter foods by grouse and ptarmigan. Condor 85:185-193.

Moss, R. and J.A. Parkinson. 1972. The digestion of heather (Calluna vulgris) by red grouse (Lagopus lagopus scoticus). Brit. J. Nutr. 27:285-298.

Newton, I. and P.R. Evans. 1966. Weights of birds in winter. Bird Study 13:96-98.

Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109:33-98.

Orians, G. 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31:285-312.

Paine, R.T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecol. 52:1096-1006.

Paulus, S.L. 1982. Gut morphology of gadwalls in Louisiana in winter. J. Wildl. Manage. 4(2):483-489.

Paulus, S.L. 1988. Time-activity budgets of mottled ducks in Louisiana in winter. J. Wildl. Manage. 52(4):711-718.

Pearson, O.P. 1954. The daily energy requirements of a wild Anna hummingbird. Condor 56:317-322.

Pendergast, B.A. and D.A. Boag. 1973. Seasonal changes in the internal anatomy of spruce grouse in Alberta. Auk 90:307-317.

Peters, R.H. 1976. Tautology in evolution and ecology. Am. Nat. 110:1-12.

Pianka, E.R. 1974. Niche overlap and diffuse competition. PNAS 71:2141-2145.

-----------. 1976. Competition and niche theory. In Theoretical Ecology: Principles and Applications ed. R.M. May, pp. 114-14. W.B. Saunders.

Powell, G.V.N. 1974. Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Anim. Behav. 22:501-505.

Pratt, T.K. 1984. Examples of tropical frugivores defending fruit bearing plants. Condor 86(2):123-129.

Pulliainen, E., P. Helle and P. Tunkkari. 1981. Adaptive radiation of the digestive system, heart and wings of Turdus pilaris, Bombycilla garrulus, Sturnus vulgaris, Pyrhula pyrrhula, Pinicola enucleator and Loxia pytyop- sittacus. Ornis Fennica 58:21-28.

Pulliam, H.R. 1973. On the advantages of flocking. J. Theor. Biol. 38:419-422.

Pulliam, H.R. 1975. The principle of optimal behavior and the theory of communities. In: Perspectives in Ethology (Ed. by P.P.G. Bateson & P.H. Klopfer), pp. 311-332. London: Plenum Press.

Pulliam, H.R., K.A. Anderson, A. Misztal and N. Moore. 1974. Temperature dependent social behaviour in juncos. Ibis 116:360-364.

Pulliam, H.R. 1975. Coexistence of sparrows: A test of community theory. Science 189:474-476.

Ratkowsky, A.V. and D.A. Ratkowsky. 1979. A comparison of counting methods to obtain bird species numbers. Nortornis 26:53-61.

Robbins, C.S. 1978. Census techniques for forest birds. pp.. 142-163 in Proceedings of the Workshop Management of Southern Forests for Non-game Birds. January 24-26, 1978, Atlanta, Georgia, U.S. General Technical Report SE-14.

Robel, R.J. and N.A. Slade. 1965. The availability of sunflower and ragweed seeds during fall and winter. J. Wildl. Manage. 38(4):653-664.

Robel, R.J., R.M. Case, A.R. Bisset and T.M. Clement Jr. 1974. Energetics of food plots in Bobwhite management. J. Wildl. Manage. 38(4):653-664.

Robel, R.J., A.R. Bisset, T.M. Clement Jr. and A.D. Dayton. 1979. Metabolizable energy of important foods of Bobwhites in Kansas. J. Wildl. Manage. 43(4): 982-987.

Robel, R.J. and N.G. Browning. 1981. Comparative use of woody plantings by nongame birds in Kansas. The Wildl. Soc. Bull. 9(2):141-148.

Robel, R.J., M.E. Barnes, K.E. Kemp and J.L. Zimmerman. Post mortem changes, feeding activity, and diet influences on digestive organ morphology of two emberizids. In press.

Rohwer, S. 1977. Status signalling in Harris' sparrows. Some experiments in deception. Behav. 61:107-129.

Rosenthal, R. 1969. Interpersonal expectations: effects of the experimenter's hypothesis. Pp. 181 -277 in Artifact in behavioral research (R. Rosenthal and R.L. Rosnow, Eds.). New York, Academic Press.

Rubenstein, D.I., R.J. Barnett, R.S. Ridgely and P.H. Klopfer. 1977. Adaptive advantages of mixed-species feeding flocks among seed-eating finches in Costa Rica. Ibis 119:10-21.

Schartz, R.L. and J.L. Zimmerman. 1971. The time and energy budget of the male dickcissel (Spiza americana). Condor 73:65-76.

Schoener, T.W. 1965. The evolution of bill size differences among sympatric species of birds. Ecol. 19:189-213.

-------------. 1974a. Some methods for calculating competition coefficients from resource-utilization spectra. Am. Nat. 108:332-340.

-------------. 1974b. Resource partitioning in ecological communities. Science 185:27-39.

Schroder, G.D. and M.L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between Dipodomys ordii and Dipodomys merriami. Oecologia 19:9-28.

Schultz, D.F., J.A. Cooper and M.C. Zicus. 1988. Fall flock behavior and harvest of Canada geese. J. Wildl. Manage. 52(4):679-688.

Shields, W.M. 1979. Avian cnesus techniques: An analytical review. pp. 23-51 In J.G. Dickson, R.N. Connor, R.R. Fleet, J.C. Kroll and J.A. Jackson (eds.), The Role of Insectivorous Birds in Forest Ecosystems. Academic Press, New York.

Shorrocks, B. and M. Begon. 1975. A model of competition. Oecologia 19:9-28.

Shuman, T.W. 1984. Energetic responses of avian granivores to winter in northeast Kansas. A Master's Thesis. Kansas State University.

Shuman, T.W., R.J. Robel, J.L. Zimmerman and K.E. Kemp. 1989. Variance in digestive efficiencies of four sympatric avian granivores. Auk 106(2): 324-326.

Smith, D.W. 1979. Ecological isolation between Aythya spp. at Point Bay, Ontario. M.S. thesis, University of Western Ontario, London, Ontario.

Smith, J.N.M., P.R. Grant, B.R. Grant, I.J. Abbott and L.K. Abbott. 1978. Seasonal variation in feeding habits of Darwin's ground finches. Ecol. 1137-1150.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical Methods. Seventh Edition. The Iowa State University Press, Ames, Iowa.

Stiles, F.G. 1971. Time, energy, and territorialtiy of the Anna hummingbird (Calypteanna). Science 173: 818-821.

Sullivan, K.A. 1988. Ontogeny of time budgets in yellow-eyed juncos: adaption to ecological constraints. Ecol 69(1): 118-124.

Tacha, T.C., P.A. Vohs, and G.C. Iverson. 1987. Time and energy budgets of sandhill cranes from mid-continental North America. J. Wildl. Manage. 51(2):440-448.

Tarboten, W.R. 1978. Hunting and the energy budget of the black-shouldered kite. Condor 808:88-91.

Thomas, V.G. 1984. Winter diets and intestinal proportions of rock and willow ptarmigan and sharp-tailed grouse in Ontario. Can. J. Zool. 62:2258-2263.

Thompson, P.M. and J.H. Lawton. 1983. Seed size diversity, bird species diversity and interspecific competition. Ornis. Scand. 14:327-336.

Tucker, V.A. 1966. Oxygen consumption of a flying bird. Science 154: 150-151.

Ulfstrand, S. 1977. Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. Oecol. 27:23-45.

Utter, J.M. and E.A. LeFebvre. 1973. Daily energy expenditure of purple martins (Progne subis) during the breeding season: estimates using D2018 and time budget methods. Ecol. 54:597i-604.

Vandermeer, J.H. 1975. Interspecific competition: A new approach to the classical theory. Science 188:253-255.

Verbeek, N.A.M. 1964. A time and energy budget of the Brewer blackbird. Condor 66:70-74.

Wagner, J.L. 1981. Seasonal change in guild structure: Oak woodland insectivorous birds. Ecol. 62(4):973-981.

Wakely, J.S. 1978. Activity budgets, energy expenditures, and energy intakes of nesting ferruginous hawks. Auk 95:667-676.

Warlsberg, G.E. 1983. Ecological energetics: what are the questions? Pp. 135-138. In Perspectives in Ornithology. (A.H. Brush and G.A. Clark, Jr. Eds.). Cambridge Univ. Press. Cambridge.

Weathers, W.W., W.A. Buttemer, A.M. Hayworth and K.A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. Auk 101:459-472.

Wiegert, R.G. 1974. Competition: A theory based on realistic, general equations of population growth. Science 185: 539-542.

Wiens, J.A. 1977. On competition and variable environments. Am.Sci. 65:590-597.

Wiens, J.A., and G.S. Innis. 1974. Estimation of energy flow in northwestern coniferous forest bird communities. Ecology 51:350-352.

Willson, M.F. 1971. Seed selection in some North American finches. Condor 73:415-429.

Wilson, D.S. 1975. The adequacy of body size as a niche difference. Am. Nat. 109:769-784.

Wolf, L.L. and F.R. Hainsworth. 1971. Time and energy budgets of territorial hummingbirds. Ecol. 52:980-988.

Wolf, L.L. 1975. Energy intake and expenditures in a nectar-feeding sunbird. Ecol. 56:92-104.

APPENDICES

Appendix 2. DATA SHEET FOR RECORDING BEHAVIORAL ACTIVITY IN THE FIRST YEAR'S FLIGHT PEN RESEARCH DURING THE WINTER OF 1983-1984.

TIME BUDGET DATA SHEET

10 Second Interval	Activity	10 Second Interval	Activity
1		25	
2		26	
3		27	
4		28	
5		29	
6		30	
7		31	
8		32	
9		33	
10		34	
11		35	
12		36	
13		37	
14		38	
15		39	
16		40	
17		41	
18		42	
19		43	
20		44	
21		45	
22		46	
23		47	
24		48	

DATE ______________

QUARTER ______________

EXPERIMENT ______________

OBSERVER ______________

PEN ______________

BIRD I.D. ______________

COMMENTS ______________

TEMPERATURE ______________

RELATIVE HUMIDITY ______________

10 Second Interval	Activity
1	
2	
3	
4	
5	
6	
7	
8	
9	
10	
11	
12	

Appendix 3. DATA SHEET FOR RECORDING BEHAVIORAL ACTIVITY IN THE SECOND YEAR'S UNCONFINED RESEARCH DURING THE WINTER OF 1984-1985.

TIME BUDGET DATA SHEET

10 Second Interval	Activity	10 Second Interval	Activity
1		25	
2		26	
3		27	
4		28	
5		29	
6		30	
7		31	
8		32	
9		33	
10		34	
11		35	
12		36	
13		37	
14		38	
15		39	
16		40	
17		41	
18		42	
19		43	
20		44	
21		45	
22		46	
23		47	
24		48	

DATE ______

QUARTER ______

EXPERIMENT ______

OBSERVER ______

Field ______

Species ______

COMMENTS ______

TEMPERATURE ______

RELATIVE HUMIDITY ______

Windspeed ______

10 Second Interval	Activity
1	
2	
3	
4	
5	
6	
7	
8	
9	
10	
11	
12	

APPENDIX 4. List of abbreviations used for behavioral activities in the second year's unconfined research during the winter of 1984-1985.

F = Feeding

FLY = Flying

SING = Singing

DR = Drinking

SIT = Sitting

MSC = Miscellaneous activities including preening, hopping, walking, bathing, predator scanning, etc.

SUB = Submission; when a bird physically exhibited the characteristics associated with submitting to an attack or show of dominance by another bird.

AC = Attack with contact; when an attack occurred resulting in actual physical contact.

AV1 = Attack with visual threat; when an attack or display of dominance (wings spread, feathers erect, etc.) occurred but no physical contact was made.

AVO = Attack with vocal threat; when an attack or display of display of dominance occurred in which vocalizations were the threat but no physical contact was made.

AV2 = Attack with visual and vocal threat; when an attack or display of dominance occurred in which both visual and vocal threats were made but no physical contact occurred.

Appendix 5. Frequency results for observer inconsistencies in species during the second year's unconfined research during the winter of 1984-1985. Values are frequencies followed by (percent).

	Species		
Observer	Cardinal	Harris	Total
1	14 (26.42)	39 (73.58)	53
2	36 (52.94)	32 (47.06)	68
3	19 (41.30)	27 (58.70)	46
4	39 (30.00)	91 (70.00)	130
Total	108	189	297

BEHAVIORAL AND MORHPHOLOGICAL RESPONSES
IN AVIAN GRANIVORES TO DIETS
IN NORTHEAST KANSAS

BY

JANICE M. JOHNSON

B.A., SOUTHERN ILLINOIS UNIVERSITY, 1983

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Time budgets of three captive emberizid species (cardinals, Harris' sparrows and tree sparrows) were recorded during the winter of 1983-1984 in northeast Kansas in order to assess the effects of: 1) flock composition, 2) flock size and 3) reduced resource availability.

Time budgets were also recorded the following winter on two of the previous examined species, cardinals and Harris' sparrows, in the wild in order to assess the effects of food quality and availability.

Concurrent research also investigated the visceral morphological responses of these birds to differential diets.

The captive birds exhibited many of the characteristics associated with flocking behavior in the wild and provided insights into species specific behavior.

The wild bird time budget study provided data illustrating typical winter songbird behavior for temperate zone birds.

The morphological study demonstrated that passerines as well as gallinacious birds and waterfowl possess the ability to alter their morphology in response to their diet.