J. Field Ornithol., 63(2):129-137

TIME BUDGETS OF CONFINED NORTHERN CARDINALS AND HARRIS' SPARROWS IN FLOCKS OF DIFFERENT SIZE AND COMPOSITION

THERESA W. SHUMAN, ROBERT J. ROBEL, JOHN L. ZIMMERMAN
Division of Biology
Kansas State University
Manhattan, Kansas 66506 USA

KENNETH E. KEMP
Department of Statistics
Kansas State University
Manhattan, Kansas 66506 USA

Abstract.—Activities of Northern Cardinals (*Cardinalis cardinalis*) and Harris' Sparrows (*Zonotrichia querula*) were monitored during winter under various flock conditions. Birds were housed in large flight enclosures and were provided a dispersed and unlimited food supply. Activity patterns, as determined by time budgets, differed for the two species, with the larger cardinals spending more time feeding than the smaller sparrows. Activity patterns did not change with flock size, but did when the two species were confined together. Results from this research underscore the need for theoretical ecologists to include species-specific and additional variables in their predictive models of bird flocking behavior to increase their usefulness.

PRESUPUESTOS DE TIEMPO EN BANDADAS DE DIFERENTE COMPOSICIÓN Y TAMAÑO DE INDIVIDUOS CAUTIVOS DE *CARDINALIS CARDINALIS* Y *ZONOTRICHIA QUERULA*

Sinopsis.—Las actividades de bandadas de diferente tamaño y composición de cardenales (*Cardinalis cardinalis*) y Gorriones de Harris (*Zonotrichia querula*) fue monitoreada durante el invierno bajo condiciones de cautiverio. Las aves fueron enjauladas en grandes estructuras y provistas de una cantidad ilimitada de alimento, dispersa por toda la jaula. Los patrones de actividad, determinados por los presupuestos de tiempo, variaron entre las dos especies. Los cardenales utilizaron más tiempo para alimentarse que los gorriones. Los patrones de actividad cambiaron cuando ambas especies fueron confinadas en el mismo lugar. No obstante, no hubo cambios con referencia al tamaño de las bandadas. Los resultados de este experimento señalan la necesidad de que los ecólogos teóricos incluyan en sus modelos de predicción de formación de bandadas la especificidad de especies, entre otras variables, para que sus trabajos sean de mayor utilidad.

In the last decade avian populations have served as fruitful focal points of theoretical and experimental ecologists. The development of optimal foraging theory (Zach and Smith 1981), and our understanding of foraging efficiency and resource partitioning (Pulliam 1985), effect of group size on foraging time budgeting (Caraco 1979a) and social hierarchies (Rambo 1981) have each benefitted by research on avian species. This benefit has resulted primarily because researchers often have been able to isolate the variable of interest (e.g., food abundance and distribution in foraging studies) and develop models or conduct field experiments on specific hypotheses (Mangel and Clark 1986). Rosenweig (1981) correctly recognized the importance of field testing predictions based on theory, not

merely to accept or reject specific theories, but to evaluate and modify models were appropriate.

Much of the data documenting intraspecific and interspecific avian competition and changes in frequency of aggressive encounters with flock size have relied primarily on studies of Dark-eyed and Yellow-eyed Juncos (*Junco hyemalis* and *J. phaeonotus,* respectively). Reliance on a narrow data base could jeopardize development of unified ecological theories (Mangel and Clark 1986, Rosenweig 1981).

To determine if predictions resulting from research on juncos are equally applicable to other avian species, this study assessed time-activity allocation by Northern Cardinals (*Cardinalis cardinalis*) and Harris' Sparrows (*Zonotrichia querula*) under various flock conditions. Specifically we determined (1) if avian activity patterns of these two species were altered by flock size and (2) if time budgets differed between single and mixed-species flocks of these birds.

METHODS AND MATERIALS

Our study was done during winter in outdoor enclosures on the Konza Prairie Research Natural Area, Riley County, Kansas. The enclosures were situated on a mowed brome (*Bromus commutatus*) field, 50 m from a wooded area that afforded shelter from strong prairie winds.

Two separate time budget experiments were conducted. In the first, male cardinals were configured as units of one, four and eight birds in three enclosures, with females similarly confined in three others. This design tested the hypothesis that a solitary bird and an individual bird in a flock allocate time similarly. The second experiment grouped various combinations of Harris' Sparrows and male cardinals. Five of the six enclosures housed groups of four birds: 1) four Harris' Sparrows, 2) four cardinals, 3) two Harris' Sparrows and two cardinals, 4) three Harris Sparrows and one cardinal, and 5) three cardinals and one Harris' Sparrow. The sixth enclosure contained four cardinals and four Harris' Sparrows. These configurations were designed to determine whether numbers of birds in a group, or species composition of the group, affected bird time budgets.

Wild cardinals were mist-netted in late December and early January and confined in nearly equal numbers in six 9.0 × 4.7 × 2.3-m outdoor enclosures until 13 males and 13 females were acquired for the first experiment. Each bird was fitted with a unique combination of colored plastic leg bands. The pre-study confinement period for early captured birds was a maximum of 12 d whereas birds captured later were in the enclosures for as few as 5 d. Six days after the requisite number of cardinals had been captured, they were removed from the six enclosures, randomly assigned to experimental groupings, and placed simultaneously back into one of the six enclosures. Once re-released into the designated enclosure, birds were allowed 10 d to acclimate to the conditions before time-budget data collection began.

Harris' Sparrows and male cardinals for the second experiment were

captured in mid to late February and handled in the same manner as the cardinals for the first experiment. Pre-study confinement periods for these birds ranged from 3 to 11 d. After randomly assigning birds to experimental groupings, they were simultaneously re-released into designated enclosures and allowed 10 d to acclimate before data collection began.

Birds were provided a mixed diet of white proso millet (*Panicum miliaceum*), smooth sunflower (*Helianthus annuus*), and a hen layer mash in excess at six feeders in each enclosure. Water was available *ad libitum* adjacent to a dense red cedar (*Juniperus virginiana*) shelter centrally placed in each enclosure. Mid-day ambient temperatures during the study period ranged from −10 C to 15 C. Bird activity data were recorded by observers hidden in wooden blinds 2 m from the middle of the long side of each enclosure.

In both experiments, time budgets of individual birds were constructed from activity data collected by six observers during four quarters of the day (early morning, late morning, early afternoon and late afternoon). The duration of each experiment was determined by the time required to complete a data set (activity data from all birds during all four quarters of the day); 12 d for the first experiment and 15 d for the second. Activity data were recorded at 10-s intervals using the metronome method (Wiens et al. 1970). Seven discrete activity categories, plus miscellaneous, were recorded as follows: 1) Flying: physically airborne in the enclosure regardless of cause of flight; 2) Perching: stationary with no movement except head turning; 3) Feeding: consuming food at a feeder or foraging on ground; 4) Drinking: imbibing water from water font or droplets on vegetation; 5) Interacting, neutral: displacement and non-aggressive movement towards or away from other birds; 6) Interacting, aggressive: threatening or otherwise aggressive movements towards other birds; 7) Interacting, submissive: movement away or cowering from aggressive overtures of other birds; and 8) Miscellaneous: preening, bathing, hopping and other activities not readily included in the above categories.

Prior to data collection, observers were trained to recognize the selected bird activities but were not informed specifically of the study design or current theories. The same six observers were used to gather time-budget data throughout both experiments.

An activity measurement consisted of tallying bird activity at each 10-s interval for 4 min (24 activity scores). Eight activity measurements were completed during a 32-min period by each observer each quarter of the day. This resulted in 48 activity measurements per observer per quarter producing 192 activity measurements per enclosure. For single bird enclosures, all 192 activity measurements were on the same bird, whereas in multiple bird enclosures, the 192 activity measurements were subdivided equally among the birds in the enclosure. The tallies of each activity (i.e., present or absent) in a series of 10-s intervals for each 4-min activity measurement were then counted and the number of blocks in which the activity was present were noted; these values (0–24) were the response variables subsequently analyzed. The results are presented as percentages

for easier comprehension and comparability to the time-budget literature.

Each experiment consisted of a Latin Square design with six flock treatments (blocking on observer and order in which observer monitored enclosures) that scheduled each observer to monitor each enclosure in random order. Data were analyzed by ANOVA and Fisher's LSD at a 0.05 level of significance.

RESULTS

Experiment I

There were no dramatic differences in general activity patterns among male and female cardinals confined individually or as members of four- or eight-bird flocks (Table 1). Combining flock size and sex data, cardinals spent approximately 74% of their time perching, 13% feeding and 5% flying.

Flying.—The solitary male and individual males in the flock of eight flew significantly ($P < 0.05$) less than males in a four-bird flock (Table 1). The solitary female cardinal flew significantly less than females in flocks. Females in all situations flew significantly more than males in the flock of eight and the solitary male.

Feeding.—Feeding occupied the second largest amount of time in the daily time budget of male and female cardinals (Table 1). Individual males in the eight-bird flock spent significantly more time feeding than males or females in any other flock configuration (Table 1). In a flock of four, individual females fed as long as a single female but longer than females in the eight-bird groups (Table 1). Individual females in an eight-bird flock spent less time feeding than individual males in an eight-bird flock.

Perching.—Males in the flock of eight spent significantly less time perching than the solitary male or individual males in a flock of four. There was no significant difference between the perching times of a solitary female cardinal and those in four- and eight-bird groups.

Interactions.—Birds spent very little time interacting under any of the test situations (Table 1). The observed time spent interacting in various configurations ranged from 0 to 0.17% of the daily time budget. Neutral encounters did not vary significantly with treatment for males or females. Individual females in a flock of eight held their position in an encounter significantly more often than females in the flock of four. Males relinquished their position more often in a group of eight than in a group of four.

Drinking and miscellaneous.—There was no flock effect on miscellaneous activities; males, females, single birds and birds in flocks of four or eight allocated a similar amount of time to these activities. The same was true for time spent drinking.

Experiment II

When comparing intraspecific activity data of birds in all configurations in which they were confined, the proportion of time spent flying reflected

TABLE 1. Mean time allocations (% of 192 observations each) of Northern Cardinals confined in outdoor enclosures in different flock configurations.

Activity	Flock configuration						Variance	
	1 Male	1 Female	4 Males	4 Females	8 Males	8 Females	LSD[a]	SE
Flying	2.92A[b]	5.42B	8.59D	7.42CD	1.96A	6.79C	1.32	0.49
Feeding	11.25AB	11.38AB	7.00A	13.96B	20.67	7.21A	4.46	1.65
Perching	77.29C	74.71BC	77.83C	72.00AB	70.04A	77.08C	4.99	1.85
Interaction, neutral	—	—	0.04	0.04	0.07	0.02	N.S.	0.03
Interaction, submissive	—	—	0.00A	0.09AB	0.15B	0.07AB	0.09	0.03
Interaction, aggressive	—	—	0.00A	0.04A	0.07A	0.17	0.10	0.04
Drinking	0.15	0.35	0.13	0.19	0.30	0.15	N.S.	0.10
Miscellaneous	8.42	8.13	6.42	6.25	6.75	8.50	N.S.	0.88

[a] LSD not given (N.S.) when F-test was not significant at $P = 0.05$ and no means compared.
[b] Means within a row followed by the same letter do not differ ($P \geq 0.05$) by Fisher's LSD.

TABLE 2. Mean (±SE) time allocations (% of 48 to 192 observations) of Northern Cardinals and Harris' Sparrows in various flock configurations.

Flock configuration	Observations	Activity		
		Flying	Feeding[d]	Perching[d]
1) 4 Harris' Sparrows[ac]	192	1.48 ± 0.26A*	5.88 ± 0.72	75.75 ± 1.45
2) 4 Cardinals[bc]	192	3.88 ± 0.45bc§☆	9.90 ± 1.41	80.14 ± 1.59
3) 3 Cardinals +	144	4.72 ± 0.52[bc]	10.47 ± 1.62	77.22 ± 1.83
1 Harris' Sparrow	48	3.38 ± 0.52B	1.74 ± 1.44	75.52 ± 2.89
Enclosure[c]	192	4.38 ± 0.41§	8.29 ± 1.27	76.80 ± 1.55
4) 2 Cardinals +	96	2.30 ± 0.64a	12.24 ± 1.99	77.99 ± 2.25
2 Harris' Sparrows	96	1.82 ± 0.36A	3.95 ± 1.02	72.63 ± 2.04
Enclosure	192	2.06 ± 0.37*	8.08 ± 1.12	75.31 ± 1.52
5) 3 Harris' Sparrows +	144	2.08 ± 0.30A	3.96 ± 0.83	72.66 ± 1.67
1 Cardinal	48	5.90 ± 0.90c	7.83 ± 2.81	80.38 ± 3.18
Enclosure	192	3.04 ± 0.32☆	4.92 ± 0.94	74.59 ± 1.48
6) 4 Harris' Sparrows +	96	3.82 ± 0.36B	3.78 ± 1.02	76.17 ± 2.04
4 Cardinals	96	6.03 ± 0.64c	8.03 ± 1.99	77.65 ± 2.25
Enclosure	192	4.92 ± 0.37§	5.92 ± 1.12	76.91 ± 1.52

[a] Means of time allocations for Harris' Sparrows within a column followed by the same uppercase letter do not differ ($P \geq 0.05$) by Fisher's LSD.

[b] Means of time allocations for Northern Cardinals within a column followed by the same lowercase letter do not differ ($P \geq 0.05$) by Fisher's LSD.

[c] Means of flying activity for all birds in an enclosure, followed by the same symbol (§, ☆, or *) do not differ ($P \geq 0.05$) by Fisher's LSD.

[d] F-test was not significant so no means were compared.

significant differences between Harris' Sparrows and cardinals, as did the miscellaneous activity category of Harris' Sparrows (Table 2). For all enclosures combined, the sparrows and cardinals differed significantly in time allocated to flying, feeding, perching and miscellaneous behavior. Cardinals devoted more time to flying, feeding and perching than did Harris' sparrows, but less time to miscellaneous activities.

Flying.—Individual cardinals flew least when confined with two sparrows and another cardinal, whereas individual Harris' Sparrows flew least in groups of four in which conspecifics equalled or outnumbered cardinals (Table 2). In a group of four in which sparrows were outnumbered three to one by cardinals and in the group of eight (four of each species), individual Harris' Sparrows flew significantly more than their conspecifics in the other configurations. Four cardinals alone averaged significantly less flying than four cardinals in a group with four Harris' Sparrows and a group of four in which cardinals were outnumbered three to one. For both species, individuals flew more (although not always significantly) as its species became outnumbered or gathered in the largest flock configuration. Regardless of species ratio, all five groups of four individuals produced mean flying times less than that for the group of eight; significantly less in two cases. Harris' Sparrows spent significantly less time flying than cardinals.

TABLE 2. Continued.

Activity				
Neutral interactions[d]	Submissive interactions[d]	Aggressive interactions[d]	Drinking[d]	Miscellaneous
0.02 ± 0.06	0.13 ± 0.04	0.09 ± 0.05	0.17 ± 0.06	16.46 ± 1.20A
0.00a ± 0.05	0.02 ± 0.03	0.11 ± 0.05	0.22 ± 0.09	5.75 ± 0.76a
0.12 ± 0.06	0.12 ± 0.04	0.14 ± 0.06	0.14 ± 0.11	7.04 ± 0.88a
0.26 ± 0.11	0.00 ± 0.08	0.00 ± 0.10	0.17 ± 0.12	18.92 ± 2.39AB
0.16 ± 0.05	0.09 ± 0.04	0.11 ± 0.05	0.15 ± 0.08	10.01 ± 0.89
0.09 ± 0.08	0.00 ± 0.05	0.04 ± 0.07	0.13 ± 0.13	7.20 ± 1.08a
0.04 ± 0.08	0.00 ± 0.06	0.00 ± 0.07	0.09 ± 0.08	21.48 ± 1.69B
0.06 ± 0.05	0.00 ± 0.04	0.02 ± 0.05	0.11 ± 0.8	14.34 ± 1.00
0.09 ± 0.07	0.06 ± 0.06	0.14 ± 0.06	0.06 ± 0.07	20.95 ± 1.38B
0.00 ± 0.11	0.00 ± 0.07	0.00 ± 0.10	0.00 ± 0.18	5.92 ± 1.52a
0.07 ± 0.06	0.04 ± 0.04	0.11 ± 0.05	0.04 ± 0.07	17.21 ± 1.10
0.26 ± 0.08	0.04 ± 0.06	0.22 ± 0.07	0.30 ± 0.08	15.42 ± 1.69A
0.17 ± 0.08	0.00 ± 0.05	0.00 ± 0.07	0.13 ± 0.13	8.00 ± 1.08a
0.22 ± 0.05	0.02 ± 0.04	0.11 ± 0.05	0.22 ± 0.08	11.71 ± 1.00

Feeding and perching.—Confinement configuration did not affect time allocated to feeding or perching by cardinals and Harris' Sparrows (Table 2). Harris' Sparrows devoted less of their daily activity budget to feeding and perching (3.6 and 73.9%, respectively) than cardinals (10.0 and 77.9%, respectively).

Interactions.—Flock configurations did not alter the amount of time devoted to interactions within or between species (Table 2). In the mixed species groups, no increase was recorded in submissive interactions by the smaller Harris' Sparrow, and no increase was evident in aggressive interactions by the larger cardinal.

Miscellaneous.—Harris' Sparrows allocated a significantly greater proportion of their daily time budget to miscellaneous activities (19.5%) than did cardinals (7.2%). In all four-bird groups, the amount of time tallied for miscellaneous activity was higher when Harris' Sparrows were present (Table 2).

DISCUSSION

Our results show that cardinals and Harris' Sparrows allocate time differently, with cardinals flying, feeding and perching more than Harris' Sparrows, but spending less time in what we termed miscellaneous activities.

Of the differences between the species, flying and feeding allocations are especially revealing, the former activity because of its energetic costliness and the latter because of its relation to energy intake. Cardinals are heavier than Harris' Sparrows and, thus, are expected to require more energy for weight maintenance (Kendeigh 1949). A lower digestive efficiency of cardinals (80.4%) than Harris' Sparrows (87.9%) (Shuman et

al. 1989), coupled with greater body weight and more flight activity, could explain why cardinals needed more food and, thus, allocated more time to feeding. Cardinals also perched more than Harris' Sparrows, and this could have been another mechanism to offset the high energetic cost of flying.

Differences in the amount of time allocated to feeding may not be an exact reflection of differences in energy usage by cardinals and Harris' Sparrows because we did not monitor energy intake. The food mix contained low energy items (mash and millet seeds) and high energy items (sunflower seeds). If cardinals fed primarily on sunflower seeds and Harris' Sparrows on millet, the measured difference in the amount of time allocated to feeding would minimize the difference in energy usage. A reversed food selection would overestimate the energy usage difference. We did not monitor which foods were consumed by our birds and thus could not estimate the true relationship between feeding time activity and energy usage.

Species differences in time allocations were much more pronounced than those manifested by changes in flock sizes. Increasing flock size did not result in a distinct continuum of changes in allocation of time as predicted by Caraco's (1979a, b) models. A solitary cardinal behaved like an individual in a flock of four in some cases and like an individual in a flock of eight in others. Time spent perching by our solitary male cardinal was more than that by a male in a group of eight, but similar to that by a male with three flock mates. Female cardinals allocated the same amount of time to perching whether they were alone or in groups of four or eight. It appears that male and female cardinals may respond differently to changes in flock size and such may need to be considered as predictive models of avian behavior are developed.

Harris' Sparrows flew more when grouped with any number of cardinals, when conspecifics became increasingly outnumbered and as flock size increased. In general, flock composition rather than flock size appeared to have a greater impact on Harris' Sparrow activity. Hutto (1988) suggested that some species adjust their activities when in mixed species flocks and our results support that hypothesis.

We did expect both species to spend more time interacting as flock size increased. Balph (1977) found that Dark-eyed Juncos had more encounters per individual per minute as the number of birds increased. Our study of cardinals and Harris' Sparrows did not show this relationship, however. The lack of an effect of flock size on the frequency of interactions in our study may have been due to our dispersed and unlimited food supply. Our food was provided in unlimited amounts at six locations in each enclosure, providing conditions that could decrease interactions at even the largest flock sizes (eight) we used. Fugle et al. (1984) showed that reduced food supplies increased interactions, and Theimer (1987) suggested that a homogeneous distribution of food decreased interactions. Food abundance and distribution should be factored into models designed to predict behavioral activity of birds in different sized flocks.

Results from our studies suggest that research on flocking behavior of different species of small birds should be conducted before modeling generalizations of avian behavior are justified. Such studies should include single- and mixed-species flocks of different size.

ACKNOWLEDGMENTS

This study was supported by the National Science Foundation (Grant DEB-8022568), the Kansas Agricultural Experiment Station (Contribution 89-414-J), and the Division of Biology, Kansas State University. Portions of this study were conducted at the Konza Prairie Research Natural Area, a preserve of The Nature Conservancy operated by the Division of Biology, Kansas State University. We thank Diane Bentrup, Sharon Collinge, Robin Hughes, Jim Lickey, Gary Schilts and the late Scott Haller for collecting data. John Shuman assisted with statistical analyses. A critical review of Thomas Rambo and the editorial assistance of Ken Yasukawa greatly improved this paper.

LITERATURE CITED

BALPH, M. H. 1977. Winter social behavior of Dark-eyed Juncos; communication, social organization and ecological implications. Anim. Behav. 25:859–884.

CARACO, T. 1979a. Time budgeting and group size: a theory. Ecology 60:611–617.

———. 1979b. Time budgeting and group size: a test of theory. Ecology 60:618–627.

FUGLE, G. N., S. I. ROTHSTEIN, C. W. OSENBERG, AND M. A. MCGINLEY. 1984. Signals of status in wintering white-crowned sparrows *Zonotrichia leucophrys gambelii*. Anim. Behav. 32:86–93.

HUTTO, R. L. 1988. Foraging behavior patterns suggest a possible cost associated with participation in mixed-species bird flocks. Oikos 51:79–83.

KENDEIGH, S. C. 1949. Effect of temperature and season on the energy resources of the English Sparrow. Auk 66:113–127.

MANGEL, M., AND C. W. CLARK. 1986. Towards a unified foraging theory. Ecology 67: 1127–1138.

PULLIAM, H. R. 1985. Foraging efficiency, resource partitioning, and the coexistence of sparrow species. Ecology 66:1829–1836.

RAMBO, T. C. 1981. Social hierarchy and activity in caged flocks of Dark-eyed Juncos, *Junco hyemalis*. Ohio J. Sci. 81:24–28.

ROSENZWEIG, M. L. 1981. A theory of habitat selection. Ecology 62:327–335.

SHUMAN, T. W., R. J. ROBEL, J. L. ZIMMERMAN, AND K. E. KEMP. 1989. Variance in digestive efficiencies of four sympatric avian granivores. Auk 106:324–326.

THEIMER, T. C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate Dark-eyed Juncos, *Junco hyemalis*. Anim. Behav. 35:1883–1890.

WIENS, J. A., S. C. MARTIN, W. R. HOLTHAUS, AND F. A. IWEN. 1970. Metronome timing in behavioral ecology studies. Ecology 51:350–352.

ZACH, R., AND J. N. M. SMITH. 1981. Optimal foraging in wild birds? Pp. 95–113, *in* A. C. Kamil and T. D. Sargent, eds. Foraging behavior. Garland STPM Press, New York, New York.

Received 27 Mar. 1990; accepted 25 Jul. 1991.