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Caching by Carolina Chickadees: Minimizing Starvation Risk Vs Maximizing Harvest Rate

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CACHING BY CAROLINA CHICKADEES:
MINIMIZING STARVATION RISK VS. MAXIMIZING HARVEST RATE

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This thesis is submitted in partial fulfillment of

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ABSTRACT

Food storage by chickadees may function in one of two ways. When food access is limited, caching may increase available food harvest from the habitat. Alternately, caching may reduce starvation risk by increasing food availability during times when the habitat is unproductive. By manipulating body weight and food availability in captive chickadees, the relative importance of these factors was determined. Results support the starvation risk hypothesis, with birds caching more at low body weights, and caching less at the end of the day. The effect of variable access times was unclear, as seasonal influences on caching rates were substantial. Birds were found to retrieve seeds less at higher weights, but no diurnal pattern was found. Retrieval rates followed the same seasonal trends found in caching rates. Recaching activity was observed, and was found to occur when caching activity was greatest.

CACHING BY CAROLINA CHICKADEES:

MINIMIZING STARVATION RISK VS. MAXIMIZING HARVEST RATE

INTRODUCTION

Caching, the movement of potential food items from one location to another for eating at some later time (Smith & Reichman 1984), occurs in at least twelve species of birds, and in many species of mammals and hymenoptera (Roberts 1979, Sherry 1985). The most commonly stored items are seeds, which are fairly resistant to spoilage, although other plant materials and many types of animal matter are also stored.

For caching behavior to evolve, the cacher must have a better chance than other hetero- or conspecifics of recovering the cache (Anderson and Krebs 1978). Species may use landmarks, microhabitats, or spatial memory to recover stores (Vander Wall 1982, MacRoberts 1970, Cowie et al 1981). Caching may be short-termed, lasting a few hours or days before recovery occurs, or long-termed, lasting many weeks or months.

The two categories of caching, larder hoarding and scatter hoarding, differ by the number of caches and the number of items per cache. Larder hoarders store many food items in a central cache within the home range. Larder hoarders are usually territorial animals whose caches are defendable against conspecific and interspecific competition. Scatter hoarders store few (usually single) food items in many caches that are distributed throughout the home range. Scatter hoard caches are generally not defendable and depend on either the utilization of a safe microhabitat or the maintenance of spacing between caches such that the density of caches in a given area is kept below a level where theft is economical (Smith and Reichman 1984).

Caching occurs primarily in the fall and winter months and is thought to function to ensure a steady supply of energy in a stochastic environment. An individual's fitness can be increased by storing food when the cost of obtaining food is low (usually due to superabundance) and utilizing that food store when costs of obtaining food or gains by ingestion are inflated. Situations in which this fitness has been demonstrated include: (1) avoiding adverse effects of interspecific competition, demonstrated in caching by subordinant animals to prolong use of a patch; (2) retrieving cached food late in the day when it may have greater value, since this represents the last opportunity for adding to overnight reserves; (3) meeting the increased food requirements associated with reproduction, such as the provisioning of young; (4) surviving seasonal food shortages; (5) uncoupling the need for food with the need to forage (individuals can than forage when it is most profitable, or when risks of predation, to themselves or their young, are minimal). Overall, caching results in a change in food value - food of relatively little value at the time it is encountered is changed to food of higher relative value by investing the time and energy to store it (Smith & Reichman 1984, Sherry 1985).

Many species of the Paridae family of birds, including titmice, chickadees, and European tits, scatter hoard seeds and insects, generally placing their caches in bark crevices of trees or in moss or soil on the ground. These caches are of short duration, usually 48 hours or less. Much field and laboratory work investigating the mechanics of cache recovery, particularly the role of memory, has been done with marsh tits, Parus palustrus, and black-capped chickadees, P. atricapillus (Cowie et al. 1981, Sherry et al. 1981, Shettleworth and Krebs 1982, Shettleworth 1983, Sherry 1984, Stevens and Krebs 1986, Baker et al. 1988). These birds utilize spatial memory in the recovery of stored caches. As with most caching birds, tits and chickadees are not dependent on olfactory or visual cues from the seeds for successful recovery. When given multiple opportunities to recover stores, black-capped chickadees have been found to avoid previous harvested cache sites, as well as caches they previously found to be pilfered, and when allowed to store different seed types, they recover the more preferred seed type before recovering other stores (Sherry 1984). This suggests the birds have a memory not only for the cache sites, but also for the contents of the caches.

In Europe, parids that cache are smaller, subordinate species; in these birds, caching may be a technique to more fully utilize food patches they may be driven out of by more dominant birds (Cowie et al. 1981, Shettleworth and Krebs 1982). Caching may also be an energetic neccessity since food reserves consumed just prior to their over-night fast may be critical to winter survival (Sherry 1985).

Caching by chickadees may function in one of two ways in the natural history of the species. (1) Maximizing Harvest Rate. The handling time needed to eat a seed is much greater than the handling time to cache a seed. When food access is limited, caching may function to increase the availability of food from the habitat by allowing the bird to handle more seeds within the limited time frame, thus maximizing harvest rates. (2) Minimizing Starvation Risk. Chickadees experience a low survival rate, especially in the winter, due in large part to starvation. Caching may reduce the threat of starvation by increasing the availability of food during times when the habitat is unproductive.

This study simultaneously tests two variables that should define the relative importance of two factors: variability in food availability, and the influence of body weight.

If maximizing food harvests is the most critical factor, the birds should cache whenever food becomes available, regardless of food access time patterning or time of day. The birds should also cache whether at high or low body weights, and whether they are increasing or decreasing weight. Therefore, if caching functions to maximize food harvest, the birds should always cache.

If minimizing starvation risk is the most critical factor, then different caching patterns should emerge. When food access time is varied, the birds may cache more when there are fewer long access periods than when there are many shorter access periods. Since eating a seed requires more time than caching, if the birds eat a seed during a short access period it will proportionately have a greater limiting effect on possible seed caching time than when eating during a long access period.

Foraging expectations may also fluctuate over the course of a day, with various environmental and energetic components influencing the bird's expectations. In the morning, when the birds are at their lowest body weights, one might expect seed eating instead of caching, as the birds meet more immediate needs. Eating may also take priority over caching in the evenings, as the birds prepare for their overnite fast (Sherry 1985).

Body weight should also influence caching rates. When at low body weight, meeting immediate needs by eating may take precedence over caching. When at high body weight, the threat of starvation is reduced, and predation risk is increased due to less maneuverability (Lima 1986), and caching behavior may again be suppressed. Caching activity should then be greatest at intermediate body weights. The birds might also be expected to cache less when losing weight, especially if they are at low or intermediate weights, since meeting immediate needs is again most important.

MATERIALS & METHODS

Four Carolina chickadees, _Parus carolinensis_, were captured in suburban woodlands of Williamsburg, Virginia in September of 1986. In the laboratory, the birds were housed individually in wire cages (61 x 61 x 91 cm.), connected by sliding doors to net aviaries (2.13 x 2.13 x 2.13 m.). The aviaries were maintained at a constant temperature (20 - 22°C.) on a 10hr:14hr light:dark cycle, with lights on at 0800. The birds were admitted into the aviaries between 0900 and 1600, where they were fed sunflower hearts from automatic feeders. The feeders consisted of seed trays with sliding covers that were wired to electromagnets and timers, so that access to food was limited to certain preset intervals.

Each aviary contained three 'trees', approximately 2 meters tall, and 2.5-10.0 cm. in diameter. Eleven to twenty-two holes (.5 cm. in diameter, 1-1.5 cm. deep) were drilled into the trees 15 - 20 cm. apart to provide cache sites for the birds, so that 46-50 holes were present in each aviary. On vertical surfaces, dowel perchs were installed 2.5 cm. below the cache holes.

After an initial feeder training period in the aviary, the birds were trained to one of two feeder schedules. On Schedule 1, the birds received 00:02:50 minutes (+/- 10 sec.) of access to sunflower hearts every hour, 7 times daily. On Schedule 2, the birds received 00:05:00 minutes (+/- 10 sec.) of access to sunflower hearts every two hours, 4 times daily. Total automatic feeder access time for both schedules totalled 00:20:45 minutes (+/- 20 sec.) per day. The birds were trained to each schedule for 5-7 days before data collection began. Two birds were placed on Schedule 1, two birds were placed on Schedule 2; after 45-60 days of data collection, they were then switched to the alternate schedule (schedule 2 and schedule 1) and after another 5-7 day acclimation period, 45-60 more days of data were collected.

Body weight was recorded each morning. The chickadees were drawn into removable nestboxes and the box, +/- the bird, were weighed on a triple-beam balance. Each bird was subjected to a regime of diets designed to vary the body weight of the individual between 100% of normal body weight (as defined by the body weight maintained under ad libitum food availability) and approximately 75% of normal body weight. Body weight was manipulated by altering the amount of food fed to the birds in their cages overnight. Overnight diets consisted of the following:

0 - 3 gm. sunflower hearts
1 - 10 mealworms
1 - 10 peanut hearts
.625 - 1.25 cm^3 grated carrot
.625 - 1.25 cm^3 grated egg
2.5 -7.5 cm^3 dry insectile mix (Aleckwa)

Daily caching data were recorded relative to body weight and change in body weight, as measured by weight loss or gain from one morning to the next, on both reducing and gaining diets. Data recorded for each feeder opening included handling sequence, handling time, location, and fate of each seed taken. [Handling time began when a seed was taken from the feeder, and ended when the seed was cached, dropped and not retrieved, or eaten completely]. If caching occurred, birds were observed at least 45 min./day (in 15 min. increments) for retrieval information. Recaching was recorded when a bird retrieved a seed and then cached the seed again in another location without having eaten it. Seeds that were known to have been cached for more than 5 days were removed.

The experiment was run from October 1986 through June 1987. In addition to the data on the four chickadees, limited data on 3 other birds (caught in September and October) from this study will be presented. For ease of analysis and comparisons, the different schedule runs were assigned a season. A schedule completed before January 1 was designated as a Fall schedule, a schedule completed before April 1 was designated as a Winter schedule, and any schedule that began later than March 15 was designated as a Spring schedule. A pilot study for this experiment was conducted January - May 1986, at another location.

RESULTS

Three of the four principal chickadees, chickadees #2, #3 and #4, cached during both schedules. The fourth bird, chickadee #5, did not cache on his second schedule, the 1 hour schedule. Chickadees #6, #7 and #8 were each run on only one schedule. (Table 1) The time neccessary to cache a seed was found to be significantly less than that needed to eat a seed. [Total mean time to eat = 99.40 sec.; Total mean time to cache = 15.02 sec., $p < .05$]. Each bird could have handled significantly more seeds if it had always cached. (Table 2 and Figure 1)

The birds cached more in late morning than early or late in the day. (Figure 2) These results are supported by Multiple Regression Analysis (Table 3 column A) which shows % cached as a function of Feeding time (FT) and the square of Feeding Time (FT^2). A positive coefficient for FT and a negative coefficient for FT2 indicate that the unimodal peak during the midday is statistically significant ($p < .05$). During the day, the birds tended to eat during the first daily access period and then began caching, regardless of

TABLE 1
NUMBER OF SEEDS CACHED & NUMBER OF SEED EATEN

Bird	Schedule	Season	# Cached	# Eaten	% Cached	Total # Handled
c2	1 hour*	winter	531	457	53.74	988
	2 hour	fall	621	350	63.95	971
c3	1 hour	fall	936	339	73.4	1275
	2 hour	winter	518	393	56.86	911
c4	1 hour	winter	544	358	60.31	902
	2 hour	spring	79	412	16.08	491
c5	1 hour	spring	0	575	0	575
	2 hour	winter	175	461	27.5	636
c6	1 hour	spring	18	151	10.65	169
c7	2 hour	spring	37	87	29.84	124
c8	2 hour	spring	179	395	31.18	574

* : 1 hour means Schedule 1, with food available at 1 hr. intervals; 2 hour means Schedule 2, 2 hr. intervals.

TABLE 2
TIME TO EAT AND TIME TO CACHE

Bird	Schedule	Time to Eat (seconds)	Max. seeds handled if eaten (theoretical)	Time to Cache (seconds)	Max. seeds handled if cached (theoretical)
c2	1 hour	74.64*	2.3	+11.60	25.8
	2 hour	81.24*	2.1	+13.20	22.7
c3	1 hour	73.92*	2.3	+13.24	22.7
	2 hour	76.26*	2.2	+12.36	24.3
c4	1 hour	139.74*	1.2	+13.53	22.2
	2 hour	154.11*	1.1	^14.77	20.3
c5	1 hour	104.40*	1.6		
	2 hour	102.86*	1.6	^30.95	9.7
c6	1 hour	78.86+	2.2	^13.92	21.6
c7	2 hour	114.71^	1.5	^13.52	22.2
c8	2 hour	92.73*	1.8	*13.16	22.7
		x = 99.4		x = 15.02	

* - Mean time of 100 seed handlings.
\+ - Mean time of 150 seed handlings.
^ - Mean time of all seeds handled.

Figure 1.

Number of seeds handled and cached on either schedule.

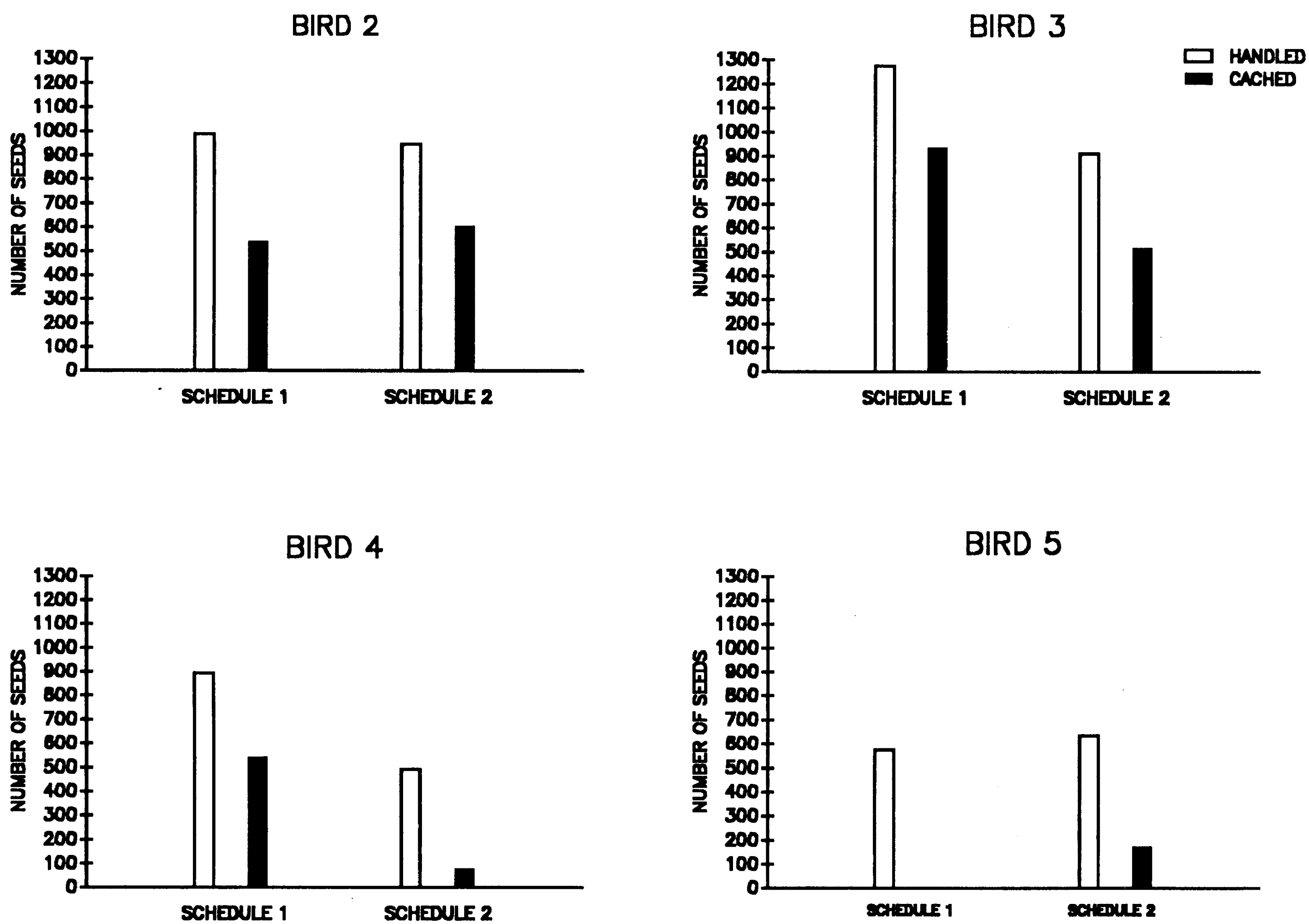
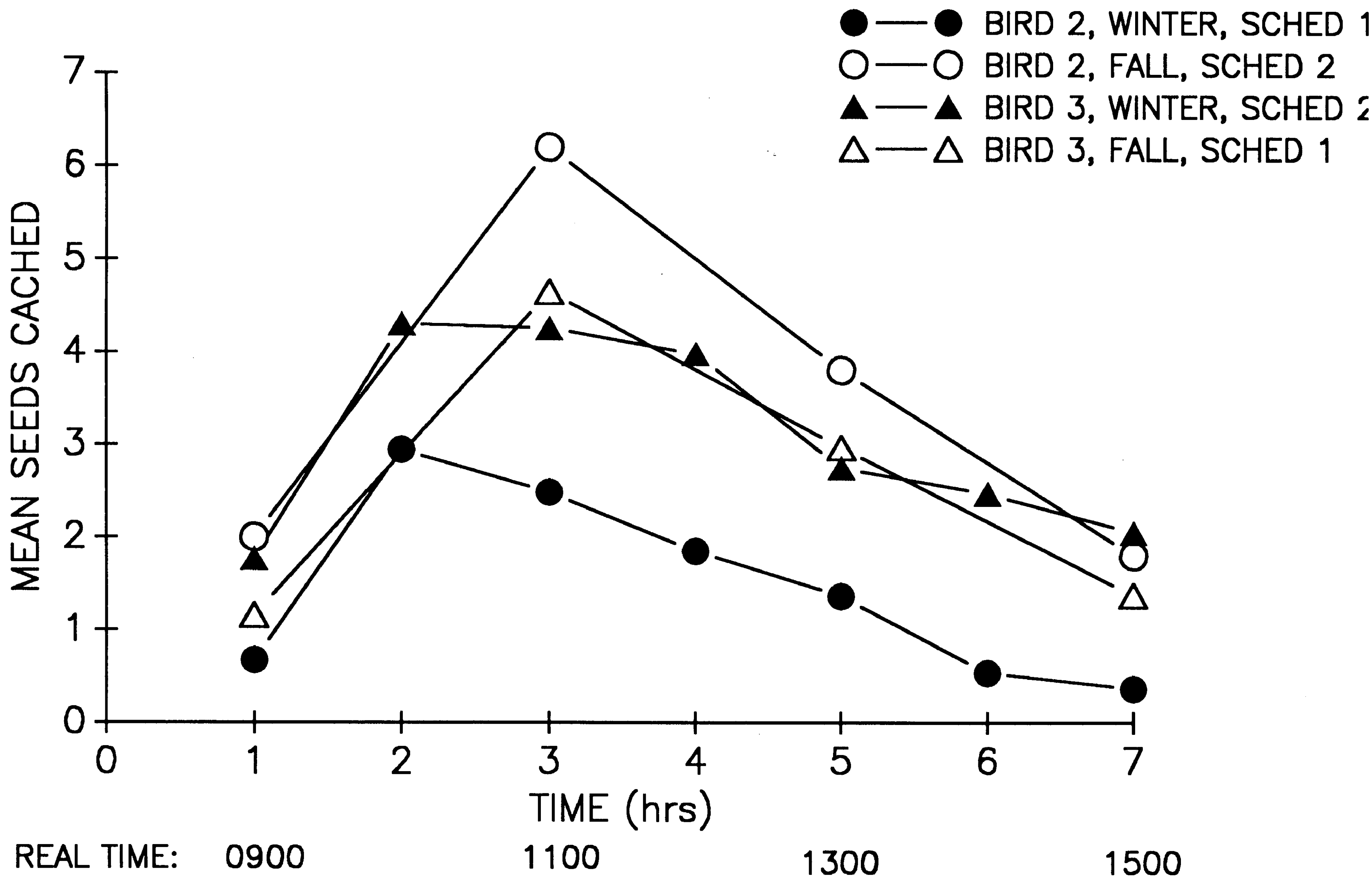

BIRD 2
BIRD 3
BIRD 4
BIRD 5
HANDLED
CACHED
NUMBER OF SEEDS
SCHEDULE 1
SCHEDULE 2
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300

Figure 2.

Mean number of seeds cached per hour vs. time of day.

2a depicts chickadees 2 and 3

2b depicts chickadees 4 and 5


BIRD 2, WINTER, SCHED 1
BIRD 2, FALL, SCHED 2
BIRD 3, WINTER, SCHED 2
BIRD 3, FALL, SCHED 1
MEAN SEEDS CACHED
0
1
2
3
4
5
6
7
TIME (hrs)
REAL TIME:
0900
1100
1300
1500

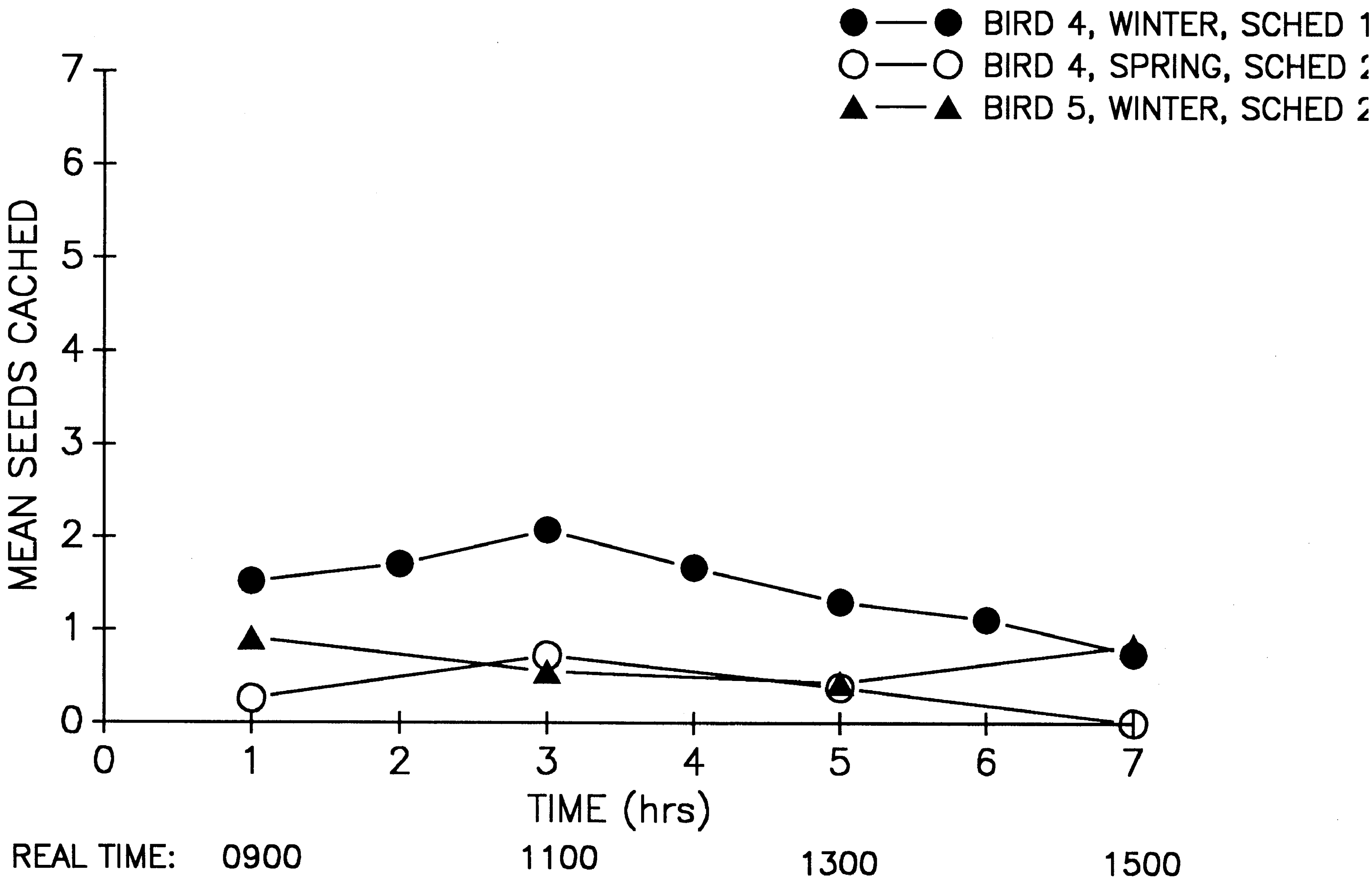

BIRD 4, WINTER, SCHED 1
BIRD 4, SPRING, SCHED
BIRD 5, WINTER, SCHED
MEAN SEEDS CACHED
0
1
2
3
4
5
6
7
TIME (hrs)
REAL TIME: 0900 1100 1300 1500

TABLE 3
SUMMARY OF MULTIPLE REGRESSION
ANALYSIS OF PERCENT OF SEEDS CACHED.

column:	A		B		C		D	E	r2	DF
	FT	FT2	WT	WT2	CHWT	CHWT2	DAY	WT*DAY		
FALL										
c2/2*	++	--	++		-	--	++	--	.48	148
c3/1	++	--	--		++	--	--	++	.22	268
WINTER										
c2/1	++	--	-		NS	+	--	NS	.44	286
c3/2	++	--	-		+		NS	NS	.24	179
c4/1	(+)	(-)	_--		++	-	-	+	.52	320
c5/2	-	+	-		+		--	+	.20	248
SPRING										
c4/2	-		NS		NS		NS	NS	.06	220
c7/2	NS		-		++		-	+	.24	52

2/2 = Chickadee # 2 on Schedule 2, with access to food every 2 hours.
FT(2)= feeding time (squared)
WT(2)= body weight (squared)
CHWT(2)= changing body weight (squared)
Day = # days the bird has been on a particular schedule.
WT*day= interaction of body weight and days into the study

++ and + indicate a positive coefficient for the variables
-- and - indicate a negative coefficient for the variables

++ and -- indicate $p < .01$
+ and - indicate $p < .05$
(+) and (-) indicate $p < .1$

____

their body weight. Caching activity then increased, as the birds presumably reached more intermediate body weights, and began to restock the caches. At the end of the day, caching activity decreased as the birds prepared for the overnight fast.

To examine the effect of body weight on proportion cached the body weight data was divided into 3 categories: 1, low; 2, intermediate; and 3, high body weight. With the exception of chickadee 2 on schedule 2, the birds were found to cache more at low and intermediate body weights than at high body weights (Figures 3 and 4). Multiple Regression Analysis showed a significant negative coefficient for body weight (WT), also indicating a decrease in caching activity at higher body weights. (Table 3, column B). Chickadee 2, the lightest bird, cached more at high weight when on the 2 hour schedule.

Three-dimensional graphics were generated to examine predictions concerning changing body weight. Changing body weight, CHBW, was recorded as either positive or negative, relative to each body weight category. Positive CHBW was recorded when the bird gained weight from one morning to the next, negative CHBW when the bird lost weight from one morning to the next. Generally, the birds cached more when gaining rather than losing weight (Figure 5). Even chickadee

Figure 3.

Number of seeds handled and cached
vs. body weight category:

1 — low
2 — intermediate
3 — high body weight

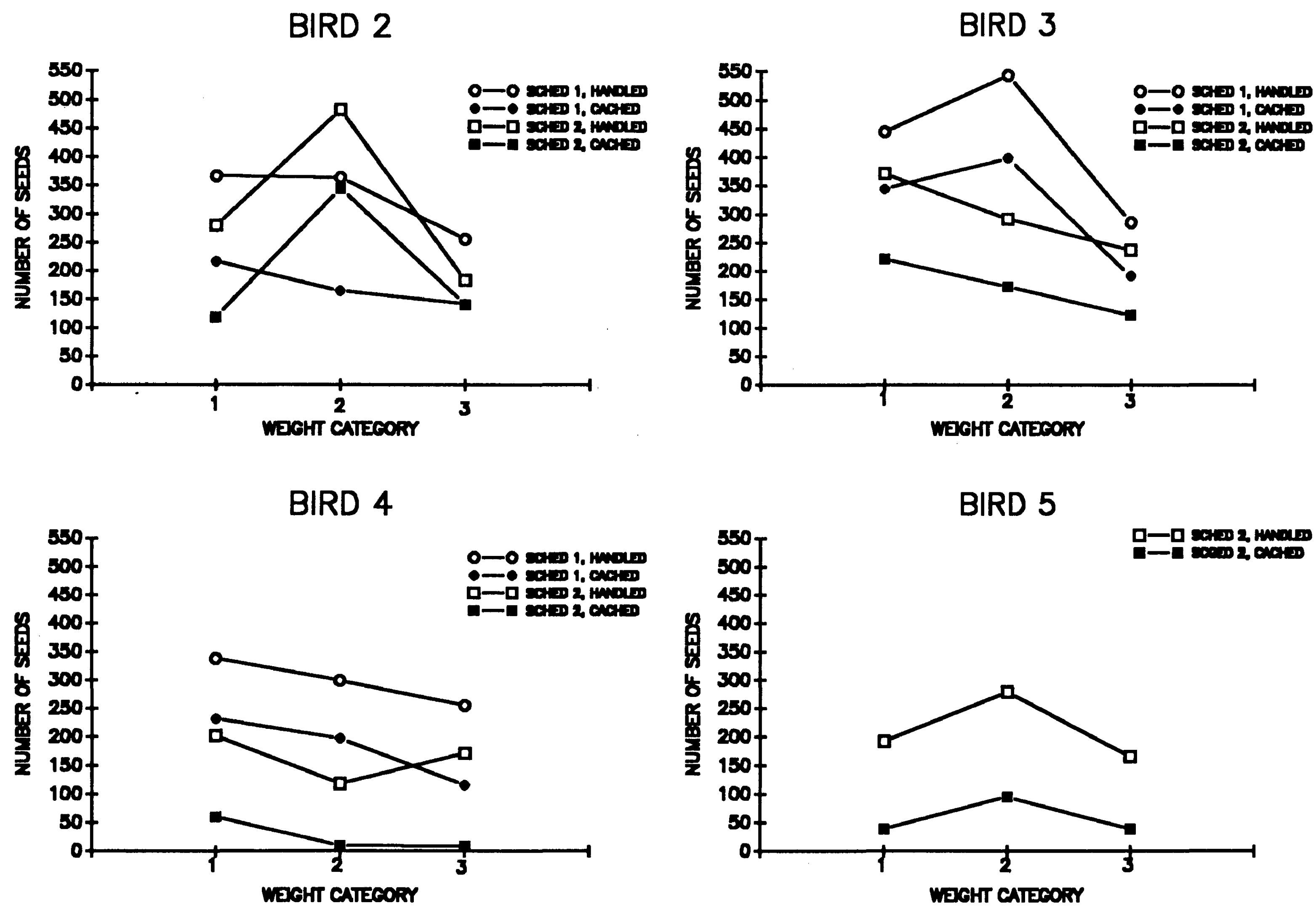

BIRD 2
NUMBER OF SEEDS
WEIGHT CATEGORY
SCHED 1, HANDLED
SCHED 1, CACHED
SCHED 2, HANDLED
SCHED 2, CACHED
BIRD 3
NUMBER OF SEEDS
WEIGHT CATEGORY
SCHED 1, HANDLED
SCHED 1, CACHED
SCHED 2, HANDLED
SCHED 2, CACHED
BIRD 4
NUMBER OF SEEDS
WEIGHT CATEGORY
SCHED 1, HANDLED
SCHED 1, CACHED
SCHED 2, HANDLED
SCHED 2, CACHED
BIRD 5
NUMBER OF SEEDS
WEIGHT CATEGORY
SCHED 2, HANDLED
SCHED 2, CACHED

Figure 4.

Percent of seeds cached
vs. body weight category:

1 – low
2 – intermediate
3 – high body weight

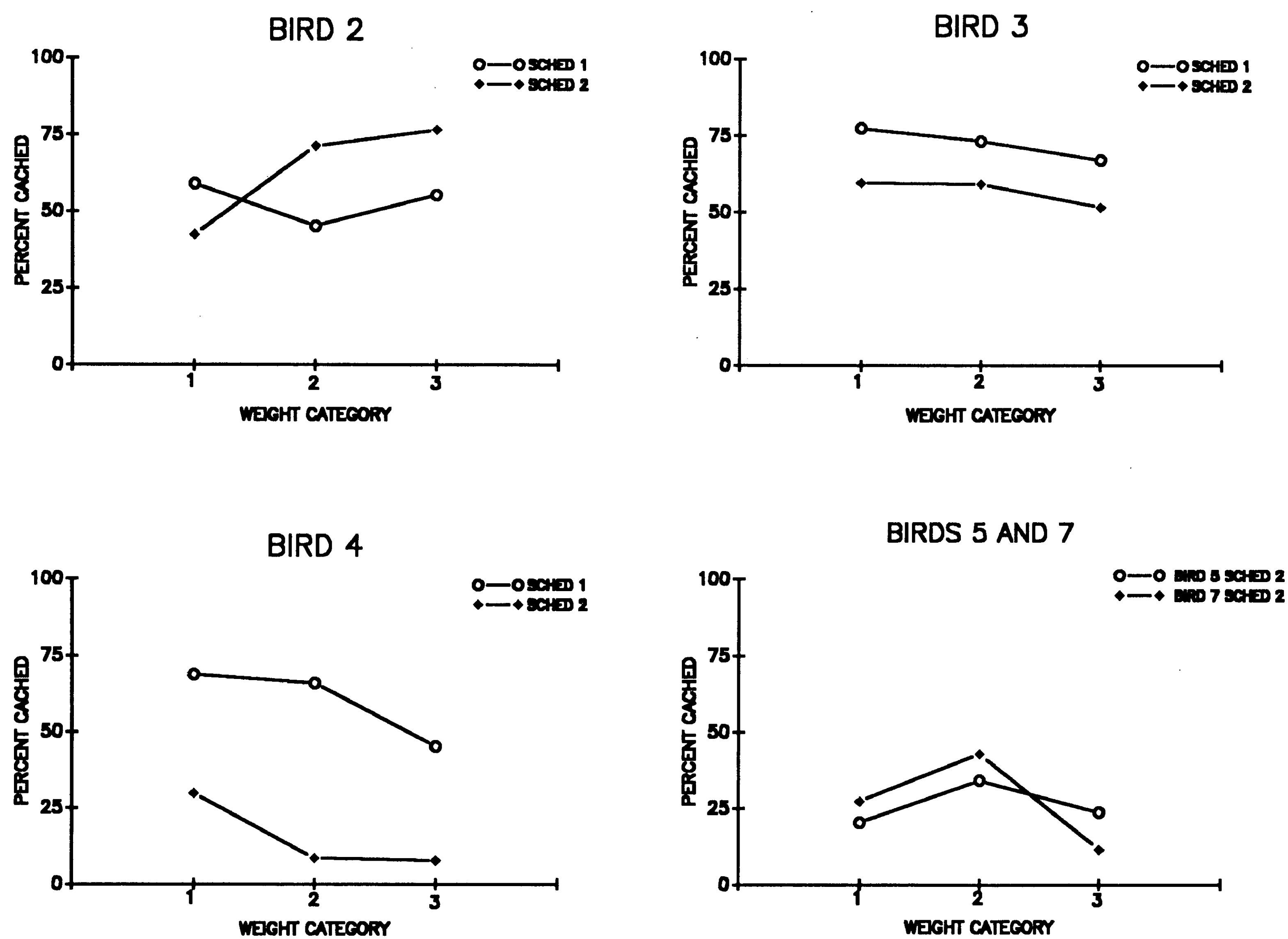
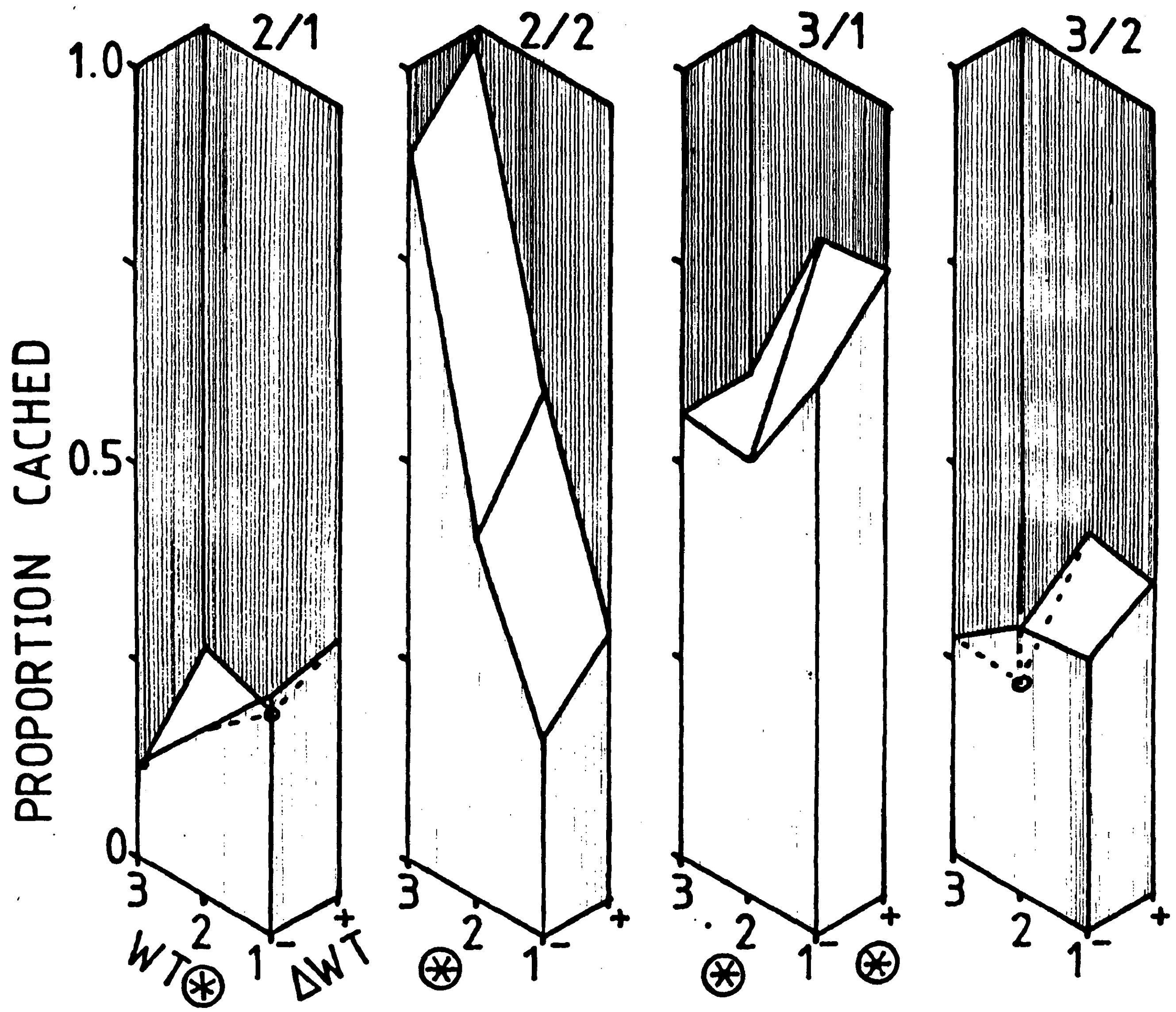
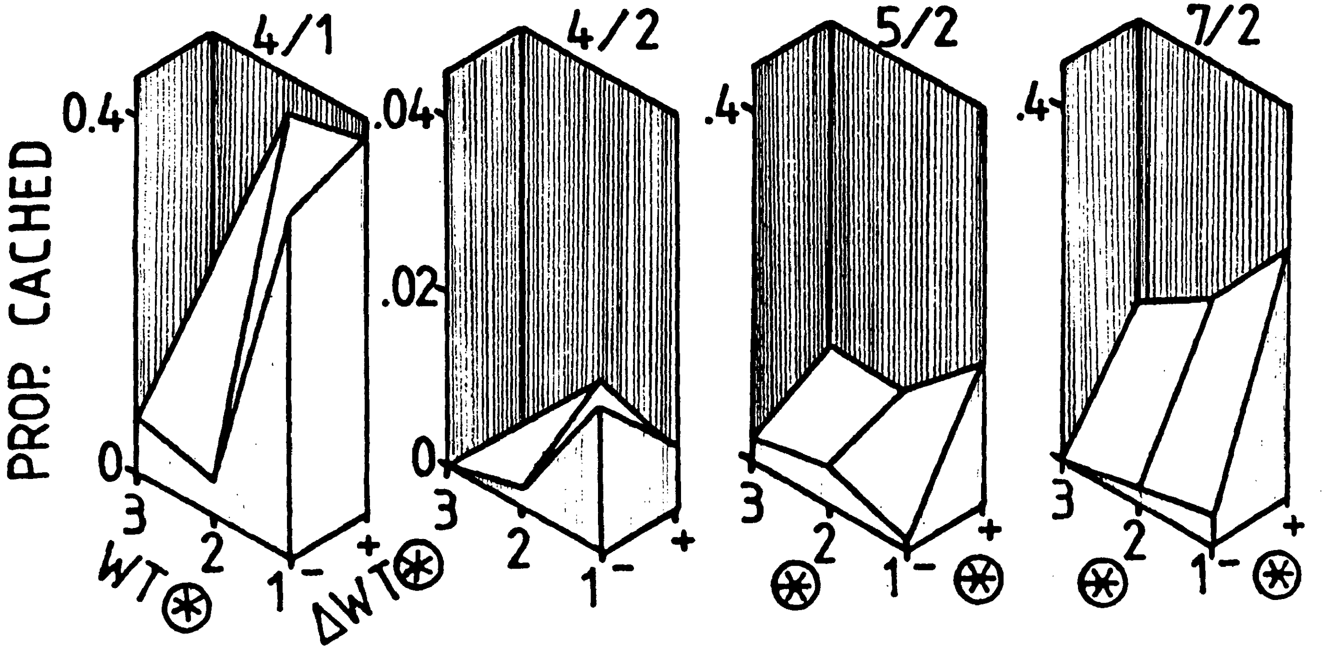

BIRD 2
SCHED 1
SCHED 2
PERCENT CACHED
WEIGHT CATEGORY
BIRD 3
SCHED 1
SCHED 2
PERCENT CACHED
WEIGHT CATEGORY
BIRD 4
SCHED 1
SCHED 2
PERCENT CACHED
WEIGHT CATEGORY
BIRDS 5 AND 7
BIRD 5 SCHED 2
BIRD 7 SCHED 2
PERCENT CACHED
WEIGHT CATEGORY

Figure 5.

Percent of seeds cached vs. body weight category
for gaining and losing weight:

+ indicates gained weight from one morning to the next
– indicates lost weight from one morning to the next


2/1
2/2
3/1
3/2
1.0
0.5
0
PROPORTION CACHED
WT⊛
ΔWT

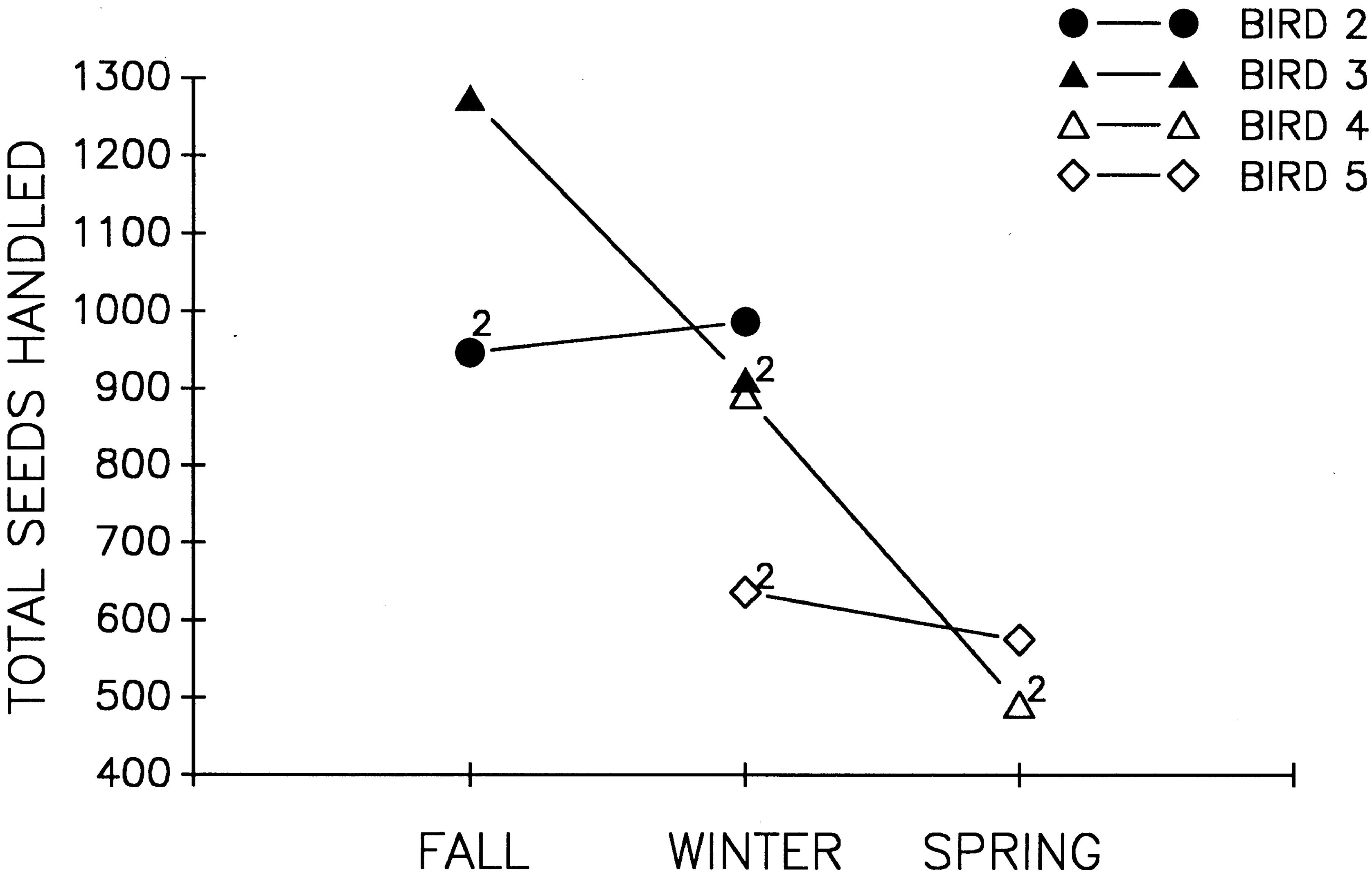

PROP. CACHED
4/1
4/2
5/2
7/2
0.4
0
.04
.02
.4
3
2
1
-
+
WT⊛
ΔWT⊛
⊛

2, with the anomolous body weight caching trends, exhibited this pattern. Regression analysis of CHBW data showed that caching increased as CHBW increased. As CHBW became large, a reversal in trends occurred in two of the birds and they began to cache less at large CHBW (CHBW coefficient is +, CHBW2 coefficient is -). (Table 3, column C) This indicates that those birds were caching at a maximum rate at intermediate changes in body weight.

If caching to minimize starvation risk, the birds were predicted to cache more on schedule 2, the 5 minute/ 2 hour food access schedule, than schedule 1, the 2.5 minute/ 1 hour schedule. Two birds cached significantly more ($P < .05$) on the 1 hour schedule, and one bird cached more on the 2 hour schedule. (Table 2) Seasonal trends seemed to overshadow any schedule variations, since the birds cached most in the fall, less in the winter, and rarely in the spring (Figures 6, 7, and 8). Examining the regression analysis, one finds that with the exception of chickadee 2- schedule 2, the birds cached less (the coefficient is neg.) as the number of days into the schedule increased (Table 3, column D). An examination of the interaction of wt * day in the regression analysis (Table 3, column E), also supports this result. The correlations of body weight and caching behavior became weaker as the days

Figure 6.

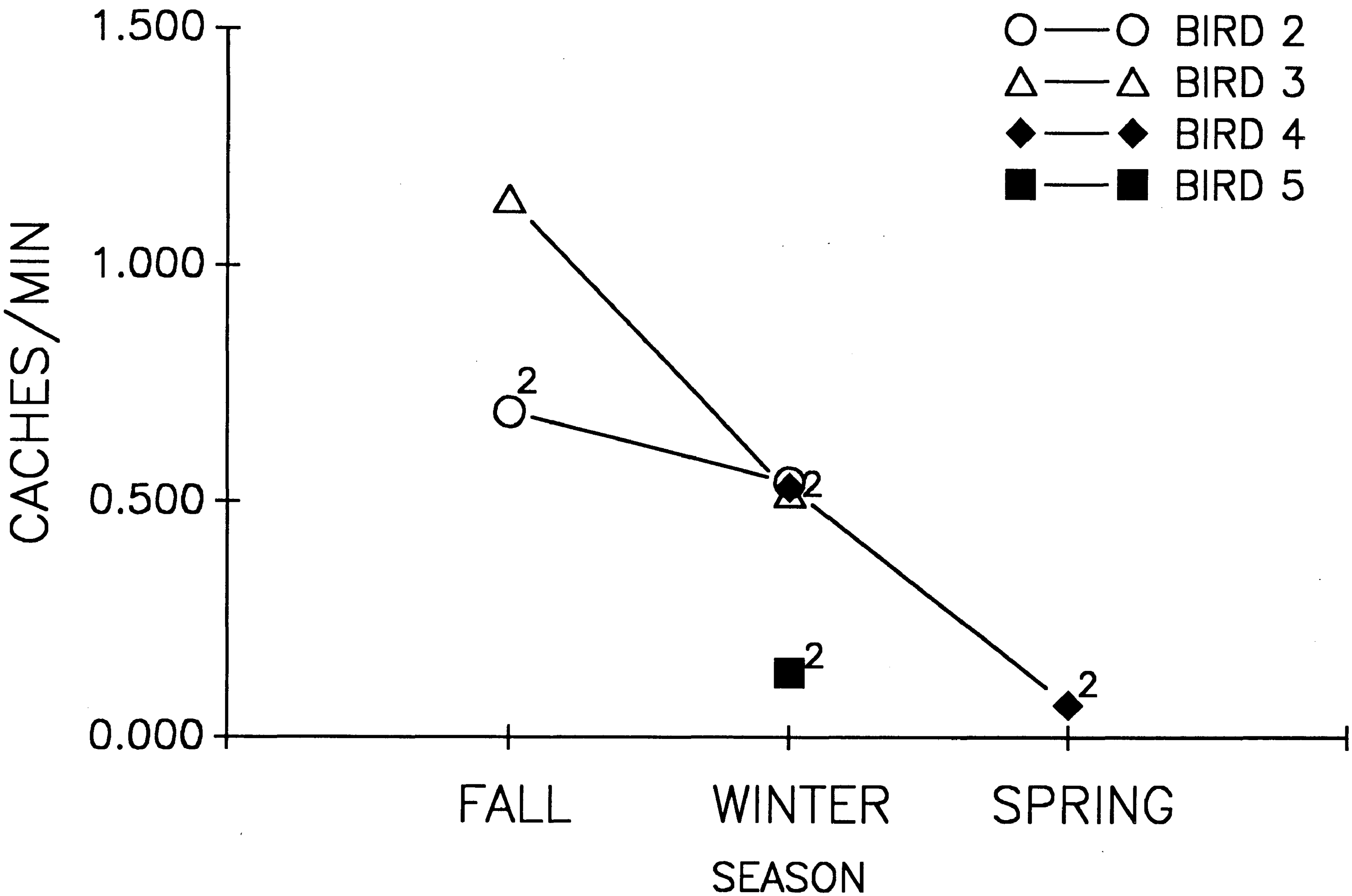
Total seeds handled vs. season.



2 denotes schedule 2

Figure 7.

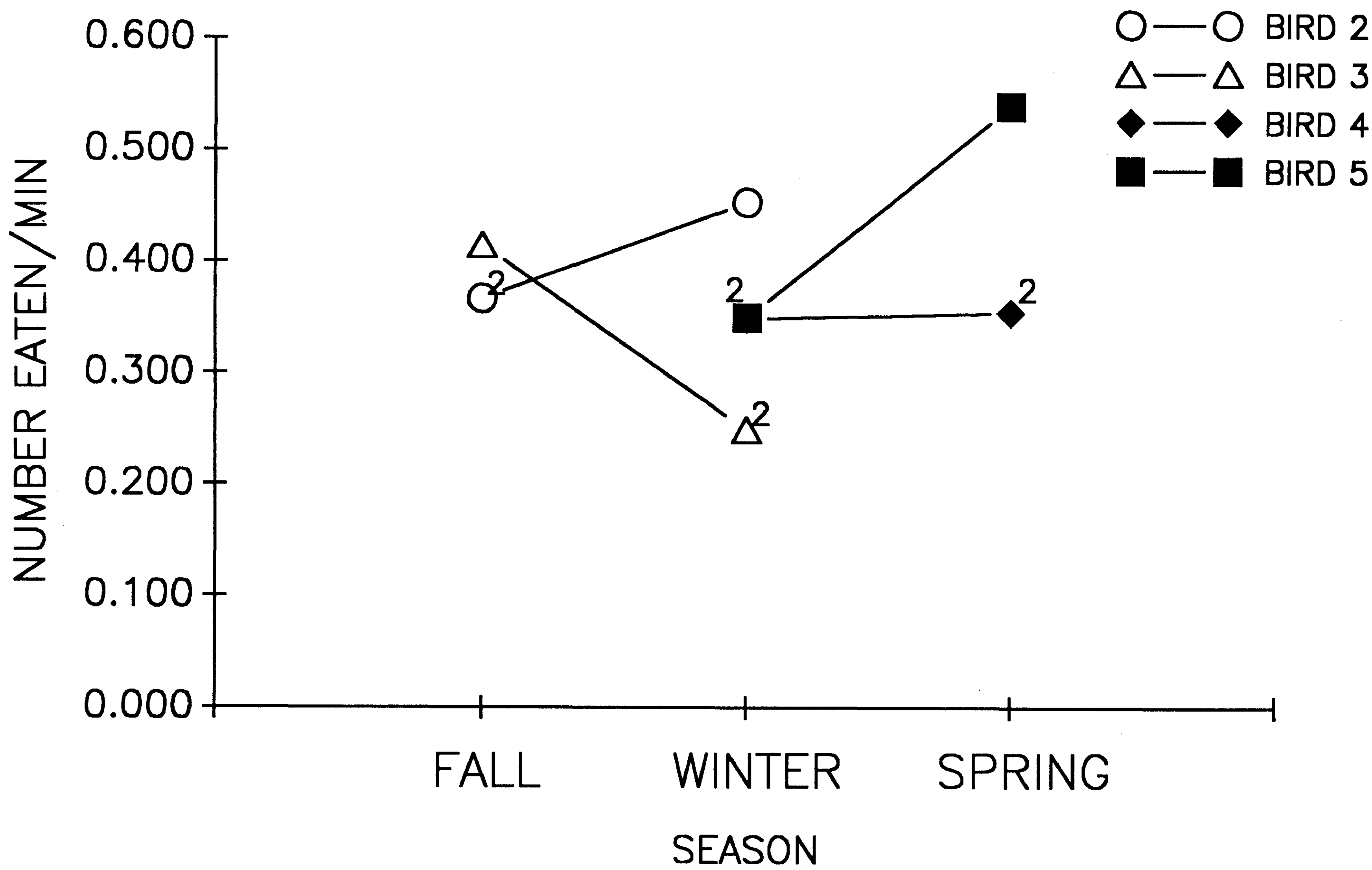
Number of seeds cached vs. season.



2 denotes schedule 2

Figure 8.

Number of seeds eaten vs. season.



2 denotes schedule 2

into the schedules, or as the seasons, progressed.

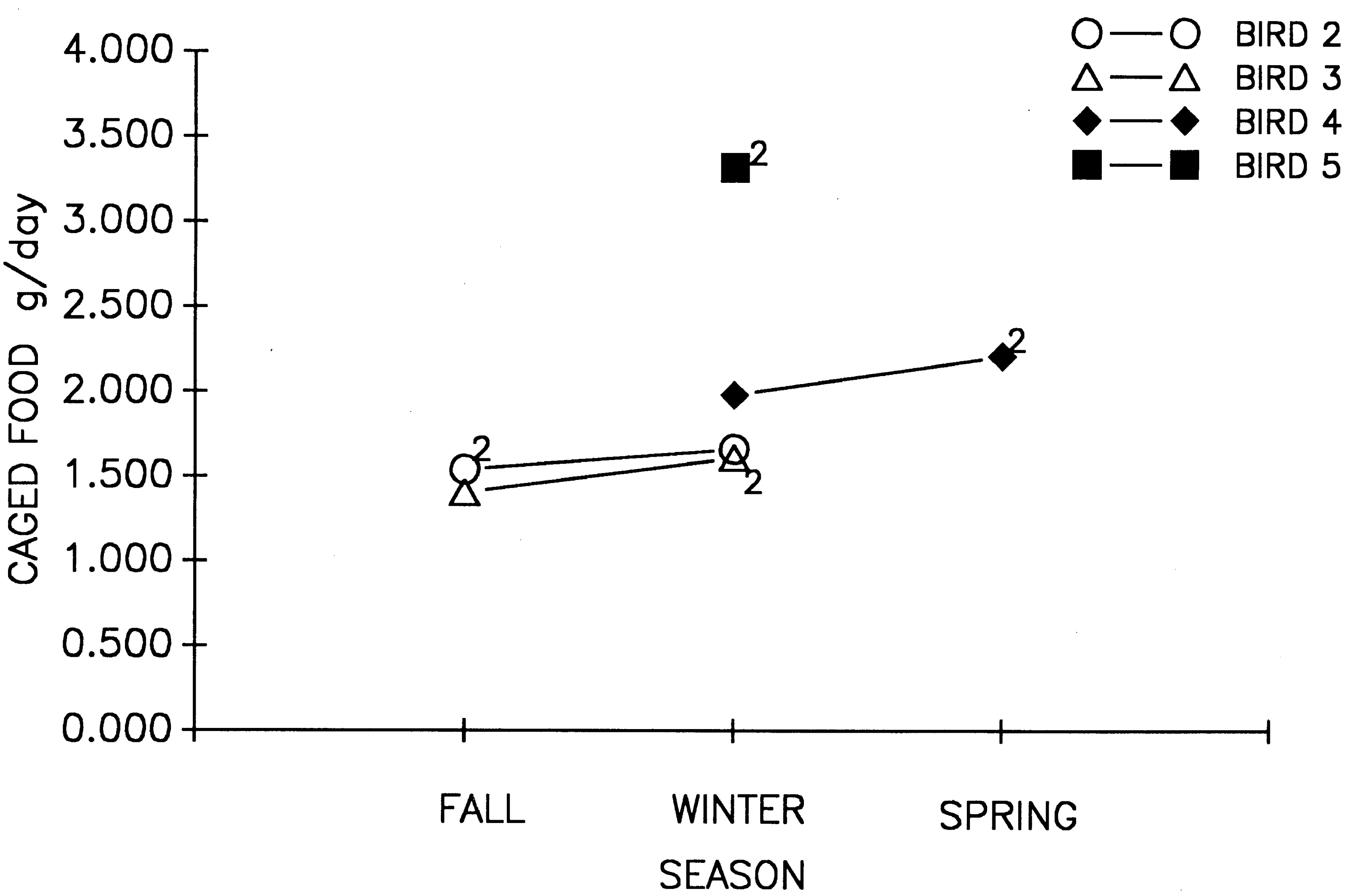
Two of the birds, chickadee #2 and #5, did tend to eat more on the 1 hour than the 2 hour schedule, irrespective of schedule order (Figure 8); and all of the birds tended to eat more cage food as the seasons progressed, although not significantly so (Figure 9).

When the combined data of chickadees 2, 3, and 4 were analysed, the same caching behavior trends are shown. Caching activity increased as body weight increased, and caching also increased (to a point) as CHBW increased. The caching activity peaked at midday, but overall caching activity decreased as the days in the study progressed (Table 4).

Retrieval and Recaching data were found to be more strongly seasonally oriented than caching data, with significant results occurring only in the fall months, that is, chickadee 3 on the 1 hour schedule, and chickadee 2 on the 2 hour schedule. While caching occured with distinct late morning peaks, retrievals showed no discernible daily patterns (Figure 10 and Table 5, column A). Recaches showed a significant ($p < .05$) late morning peak in the fall, and an overall trend to recache less at the end of the day (Figure 11). Multiple regression analysis also indicated these

Figure 9.

Food eaten in cage.



2 denotes schedule 2

TABLE 4
SUMMARY OF MULTIPLE REGRESSION ANALYSIS
OF PERCENT OF SEEDS CACHED WITH SCHEDULES COMBINED.

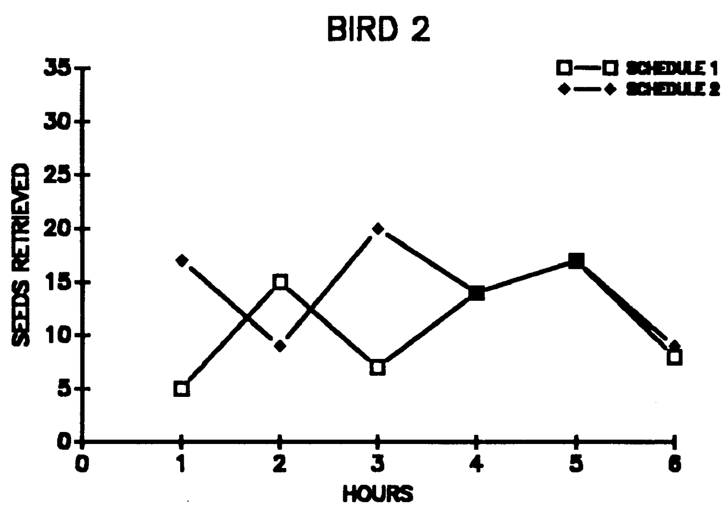
Bird	A		B		C		D		
	FT	FT2	WT	WT2	CHWT	CHWT2	DAY	SCH (1-2)	WT*SCH
c2	++	--	--				--	--	++
c3	++	--	--		++	-	-	-	
c4	-		--		++	--	--	++	

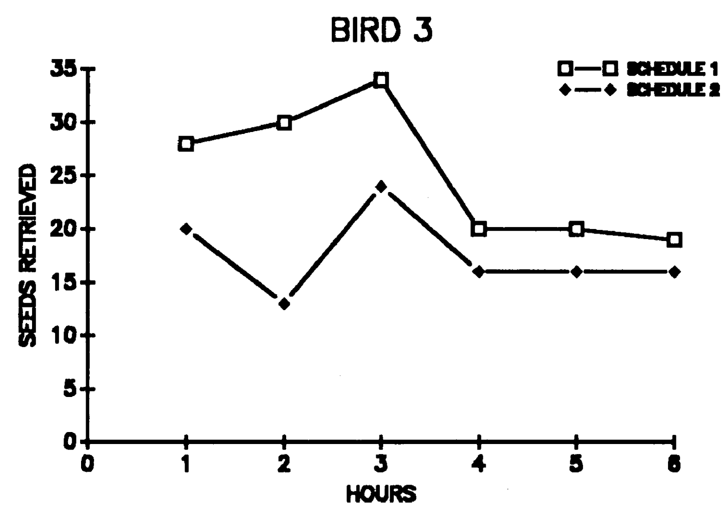
++ and --indicate p < .01
+ and - indicate p < .05

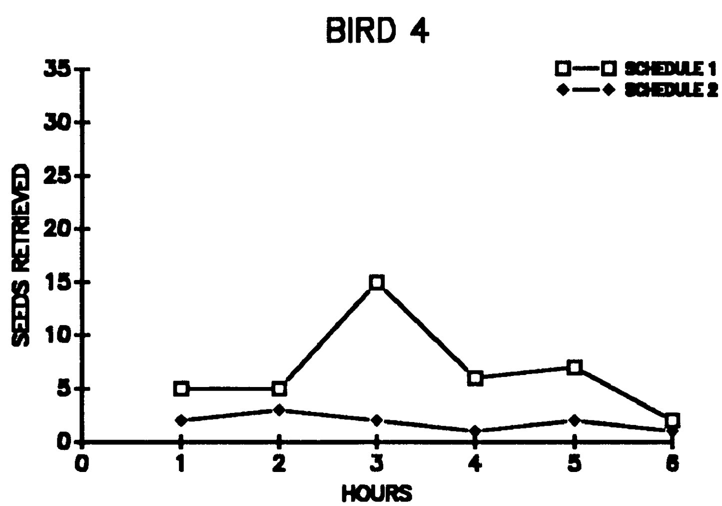
See Table 3 for explaination of column headings.

Figure 10.

Retrievals vs. time of day.


BIRD 2
SEEDS RETRIEVED
HOURS
SCHEDULE 1
SCHEDULE 2
0
5
10
15
20
25
30
35
1
2
3
4
5
6


BIRD 3
SEEDS RETRIEVED
HOURS
SCHEDULE 1
SCHEDULE 2
0
5
10
15
20
25
30
35
1
2
3
4
5
6


BIRD 4
SEEDS RETRIEVED
HOURS
SCHEDULE 1
SCHEDULE 2
0
5
10
15
20
25
30
35
1
2
3
4
5
6

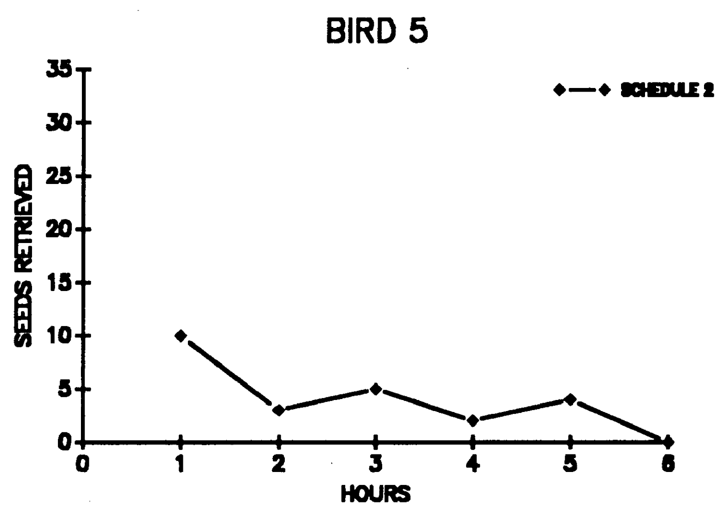

BIRD 5
SEEDS RETRIEVED
HOURS
SCHEDULE 2
0
5
10
15
20
25
30
35
1
2
3
4
5
6

TABLE 5
SUMMARY OF MULTIPLE REGRESSION
ANALYSIS OF RETRIEVALS

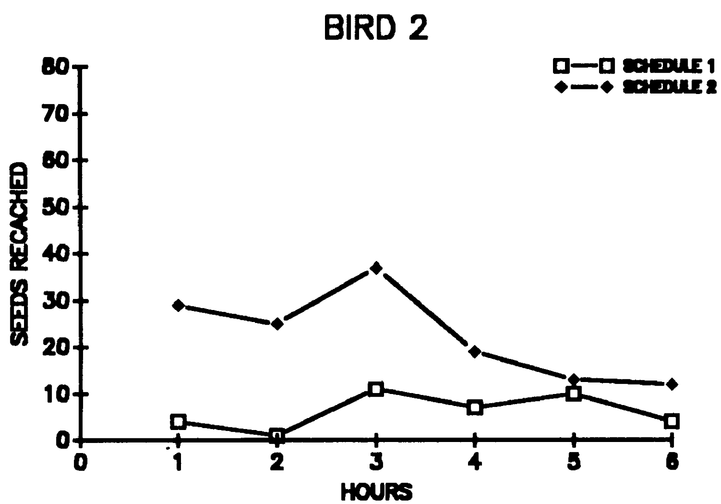
Bird/schedule	A		B		C		D	r2	df
	FT	FT2	WT	WT2	CHWT	CHWT2	DAY		
FALL									
c2/2	NS		--		NS		++	.16**	129
c3/1	NS		+	-	+		NS	.18**	162
WINTER									
c2/1	NS		NS		NS		NS	.01 NS	155
c3/2	NS		NS		+		NS	.04 NS	152
c4/1	NS	-	NS		NS		NS	.05 NS	139
c5/2	NS		NS		NS		NS	.01 NS	139
SPRING									
c4/2	+	-	NS		NS		NS	.14 NS	47
c7/2	NS		+		NS		NS	.22 NS	22

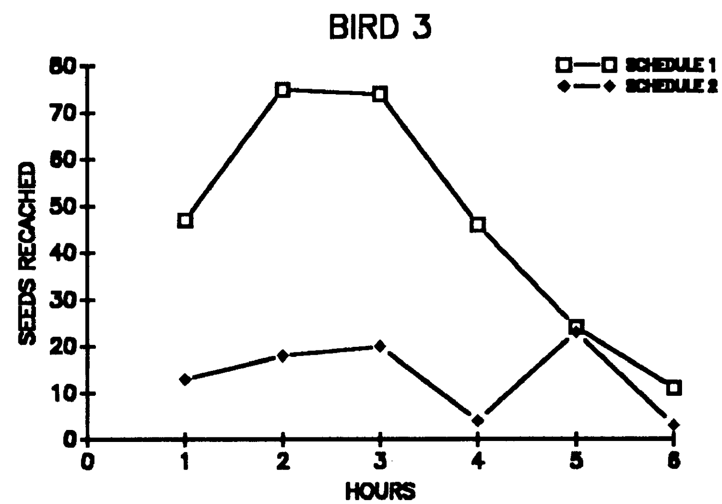
**, ++ and -- indicate $p < .05$
+ and _ indicate $p < .01$

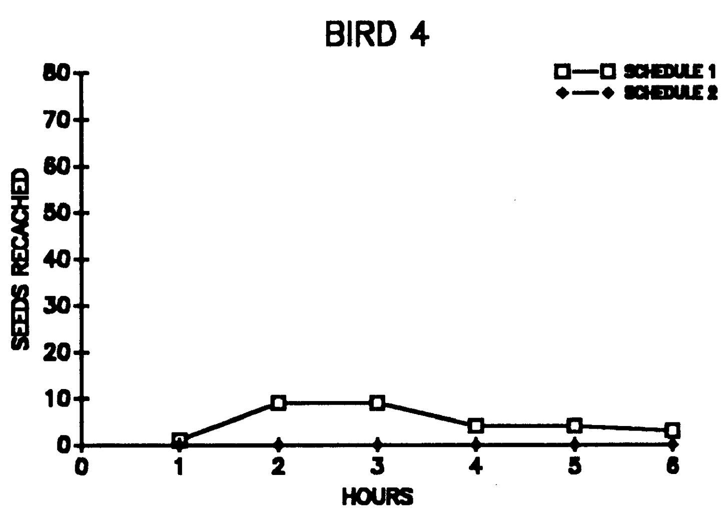
See Table 3 for an explaination of column headings.

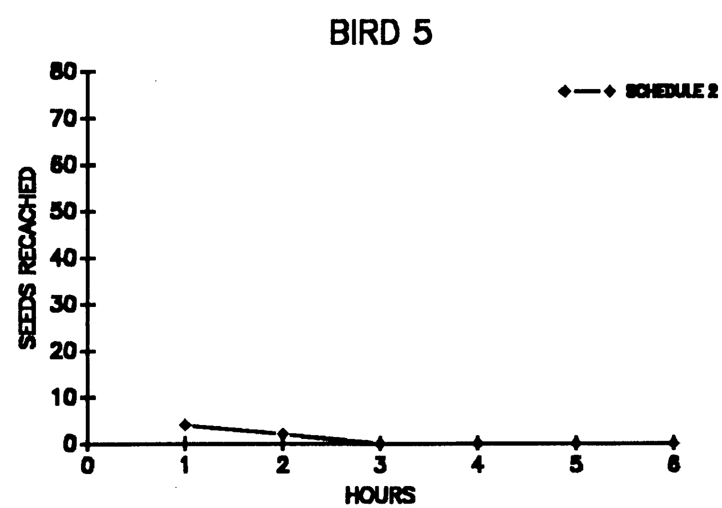
Figure 11.

Recaches vs. time of day.


BIRD 2
SCHEDULE 1
SCHEDULE 2
SEEDS RECACHED
HOURS
0 10 20 30 40 50 60 70 80
0 1 2 3 4 5 6


BIRD 3
SCHEDULE 1
SCHEDULE 2
SEEDS RECACHED
HOURS
0 10 20 30 40 50 60 70 80
0 1 2 3 4 5 6


BIRD 4
SCHEDULE 1
SCHEDULE 2
SEEDS RECACHED
HOURS
0 10 20 30 40 50 60 70 80
0 1 2 3 4 5 6


BIRD 5
SCHEDULE 2
SEEDS RECACHED
HOURS
0 10 20 30 40 50 60 70 80
0 1 2 3 4 5 6

trends, with a + coefficient for FT, and a - coefficient for FT2 (Table 6, column A).

With respect to weight categories, the birds retrieved significantly more seeds at the lower and middle body weight categories, but only in the fall (Figure 12 and Table 5, column B). Recaching also occured more at the lower and middle body weight categories, but only significantly so in the fall (Figure 13 and Table 5, column B).

When the effects of changing body weight on retrieval behavior were examined, only one bird, Chickadee 3, showed a significant pattern, retrieving more when he was gaining weight. No other patterns were significant. (Figure 14 and Table 5 column C). Regression analysis of recaching behavior for chickadee 3-1hour and chickadee 4-1hour indicate a significant trend to recache more at increasing CHBW (Table 6, column C). No other discernible patterns were found with respect to recaching and changing body weight (Figure 15).

With both retrievals and recaches, any differences between schedules were overshadowed by seasonal trends. There was a general trend to retrieve less as the seasons progress, but with only chickadee 3 showing a substantial drop in retrieval activity. (Figure 16). Regression analysis showed significant day effect for

TABLE 6
SUMMARY OF MULTIPLE REGRESSION
ANALYSIS OF RECACHES.

Bird/schedule	A		B		C		D	r2	df
	FT	FT2	WT	WT2	CHWT	CHWT2	DAY		
FALL									
c2/2	-		++		NS		++	.24**	100
c3/1	++	--	--		+		++	.28**	121
WINTER									
c2/1	NS		NS		NS		NS	.02 NS	112
c3/2	NS		NS		NS		-	.06 NS	111
c4/1	NS		NS		+	-	NS	.17**	95
c5/2	--		NS		NS		NS	.08(*)	109
SPRING									
c4/2	NO RECACHING								
c7/2	NO RECACHING								

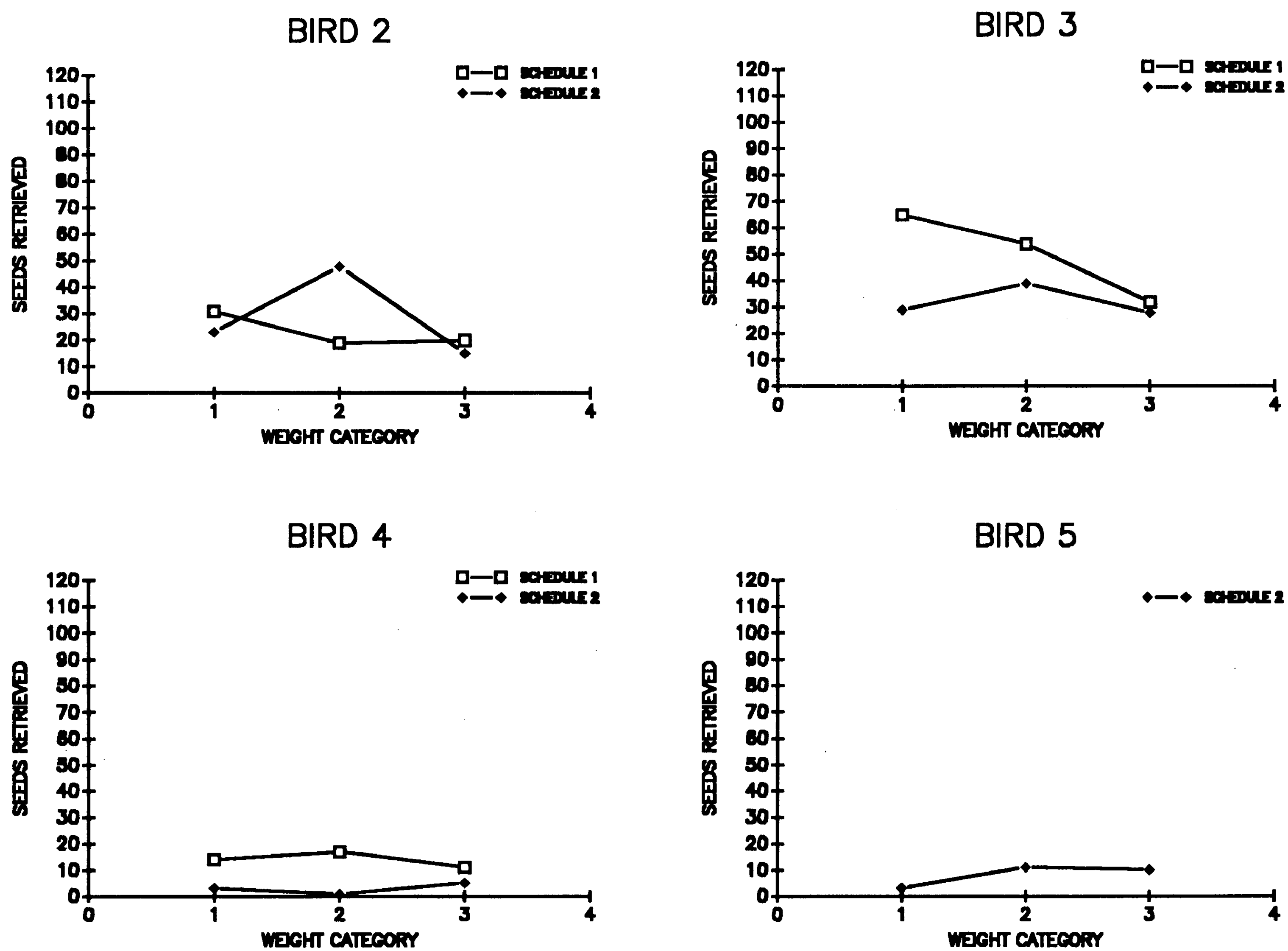
**, ++ and -- indicate p < .01
+ and - indicate p < .05
(*) indicates p < .1

See Table 3 for further explaination of column headings.

Figure 12.

Retrievals vs. body weight category:

1 – low
2 – intermediate
3 – high body weight

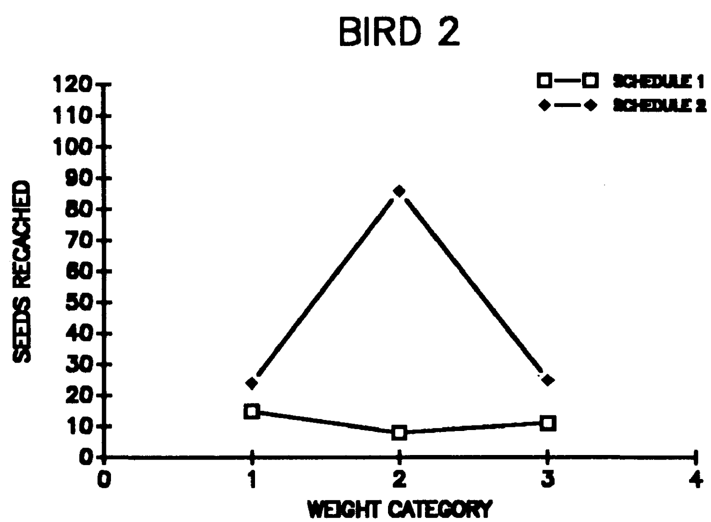


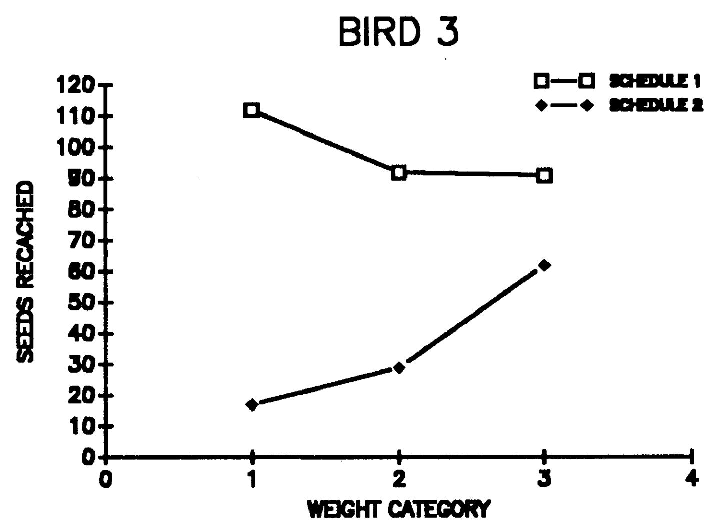
BIRD 2
SCHEDULE 1
SCHEDULE 2
SEEDS RETRIEVED
WEIGHT CATEGORY
BIRD 3
SCHEDULE 1
SCHEDULE 2
SEEDS RETRIEVED
WEIGHT CATEGORY
BIRD 4
SCHEDULE 1
SCHEDULE 2
SEEDS RETRIEVED
WEIGHT CATEGORY
BIRD 5
SCHEDULE 2
SEEDS RETRIEVED
WEIGHT CATEGORY

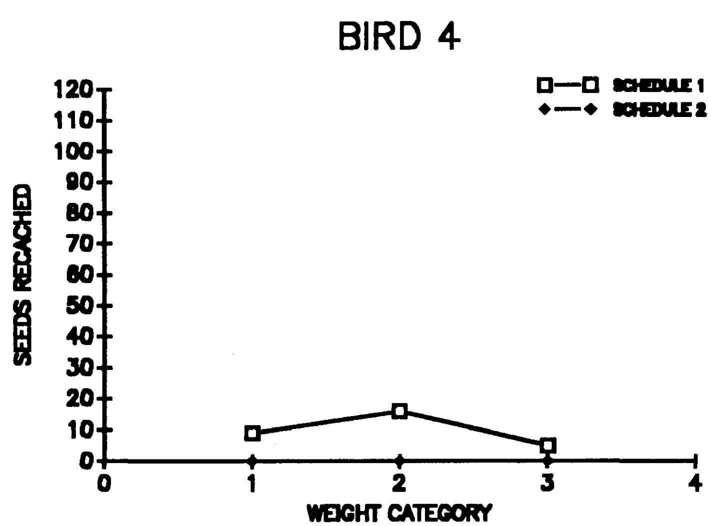
Figure 13.

Recaches vs. body weight category:

1 – low
2 – intermediate
3 – high body weight


BIRD 2
SCHEDULE 1
SCHEDULE 2
SEEDS RECACHED
WEIGHT CATEGORY


BIRD 3
SCHEDULE 1
SCHEDULE 2
SEEDS RECACHED
WEIGHT CATEGORY


BIRD 4
SCHEDULE 1
SCHEDULE 2
SEEDS RECACHED
WEIGHT CATEGORY

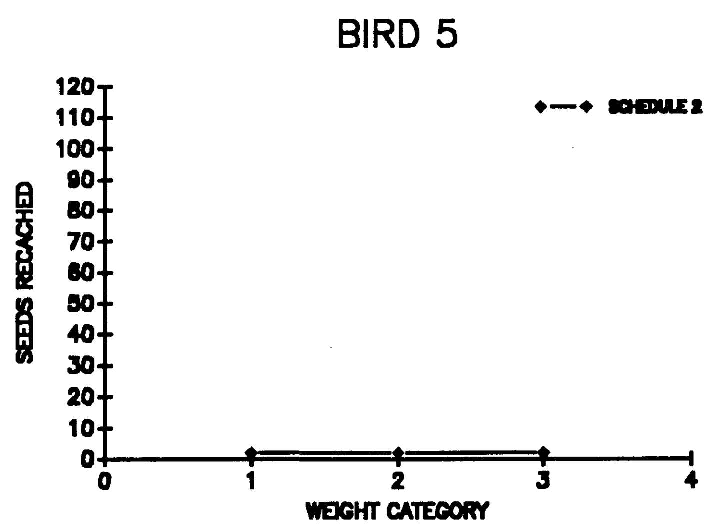
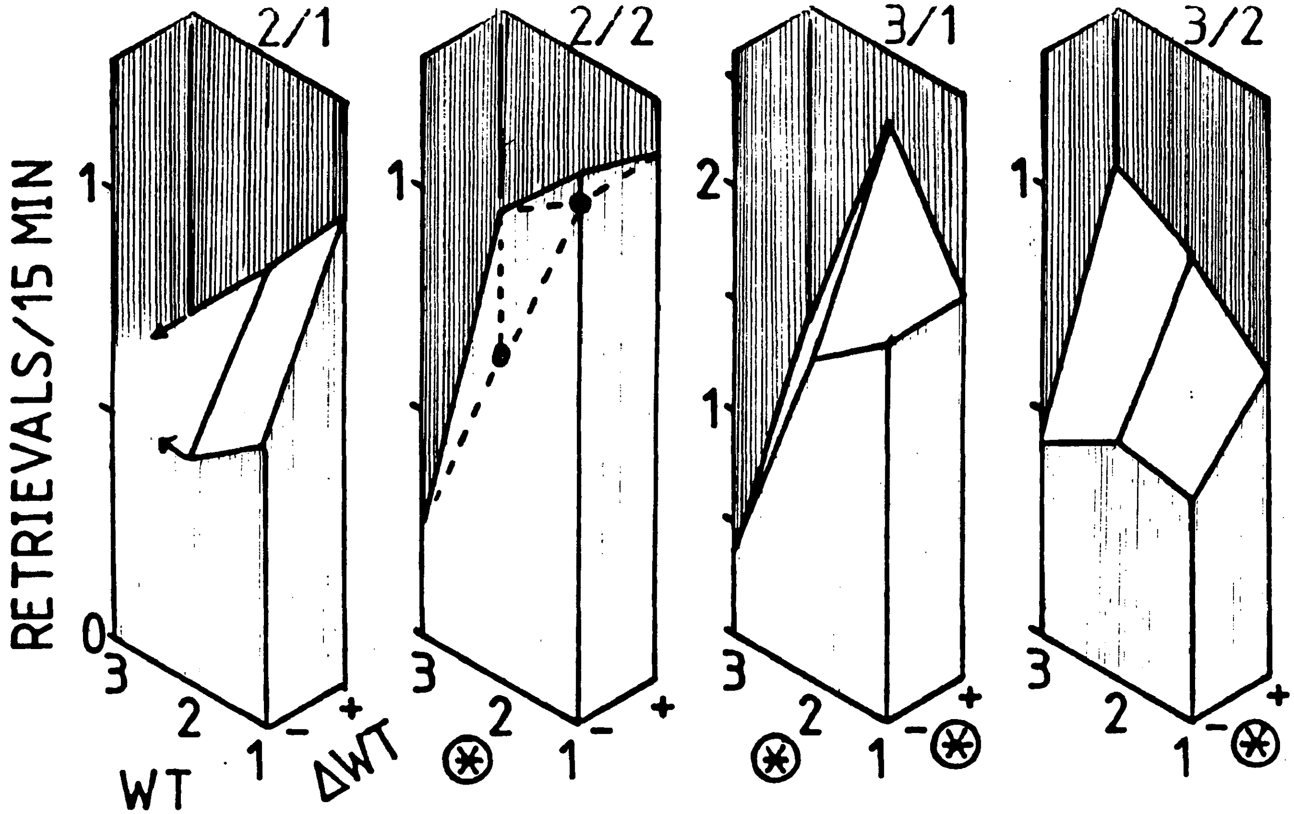

BIRD 5
SCHEDULE 2
SEEDS RECACHED
WEIGHT CATEGORY

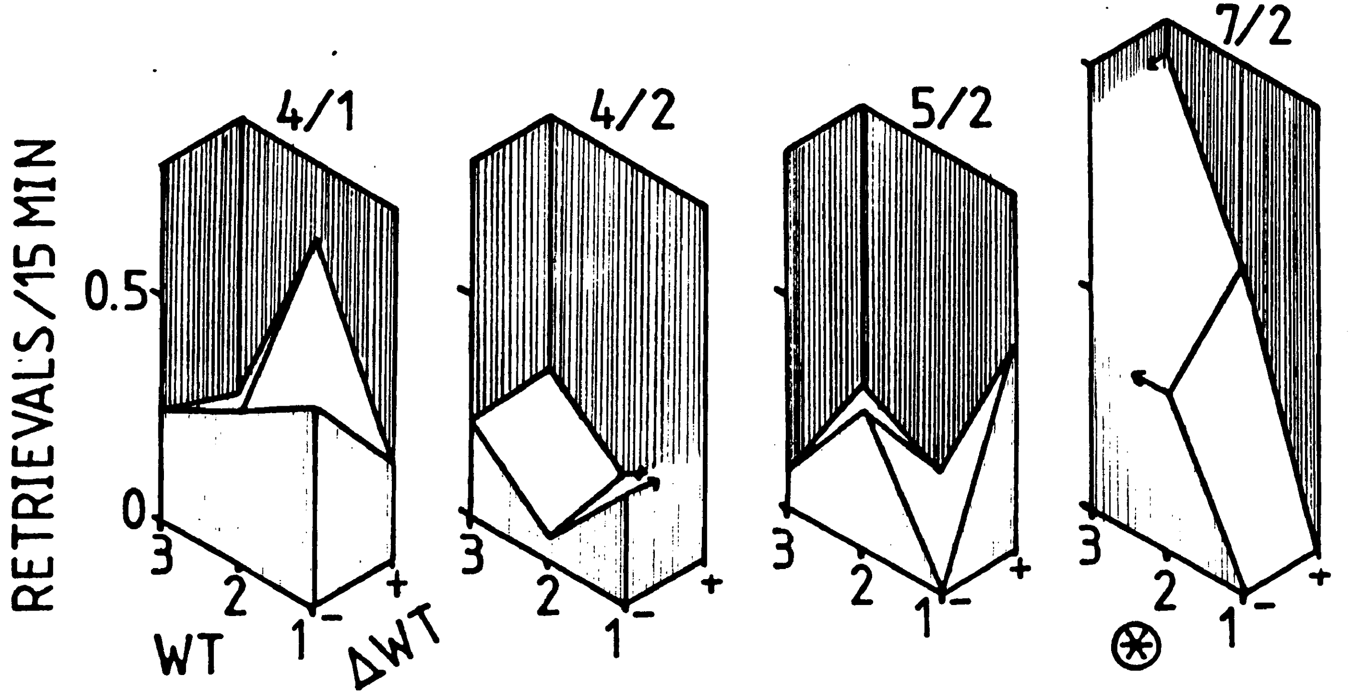
Figure 14.

Retrievals vs. body weight category
for gaining and losing weight:

+ indicates gained weight from one morning to the next
– indicates lost weight from one morning to the next

14a depicts chickadees 2 and 3
14b depicts chickadees 4 and 5


RETRIEVALS/15 MIN
2/1
2/2
3/1
3/2
WT
ΔWT
0
1
2
3
-
+



RETRIEVALS/15 MIN
0.5
0
4/1
4/2
5/2
7/2
3
2
1
WT
ΔWT
+
-
⊛

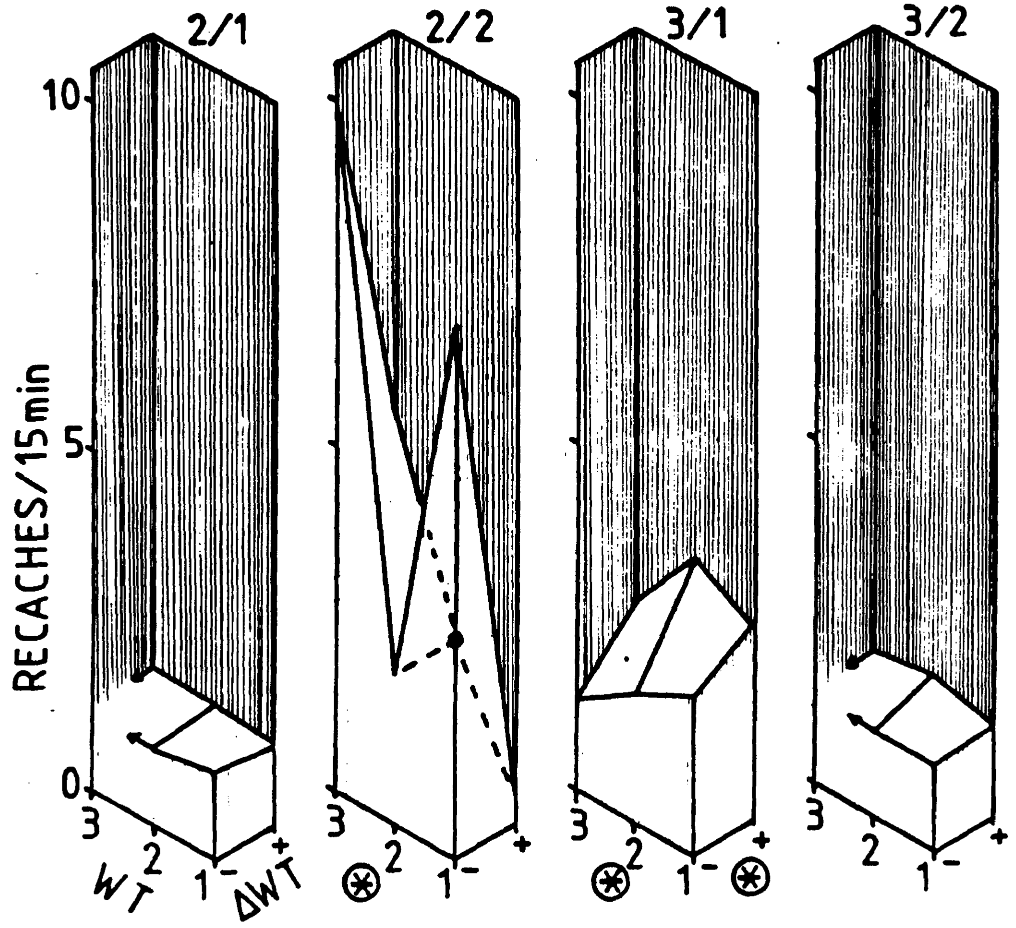
Figure 15.

Recaches vs. body weight category

for gaining and losing weight:

\+ indicates gained weight from one morning to the next

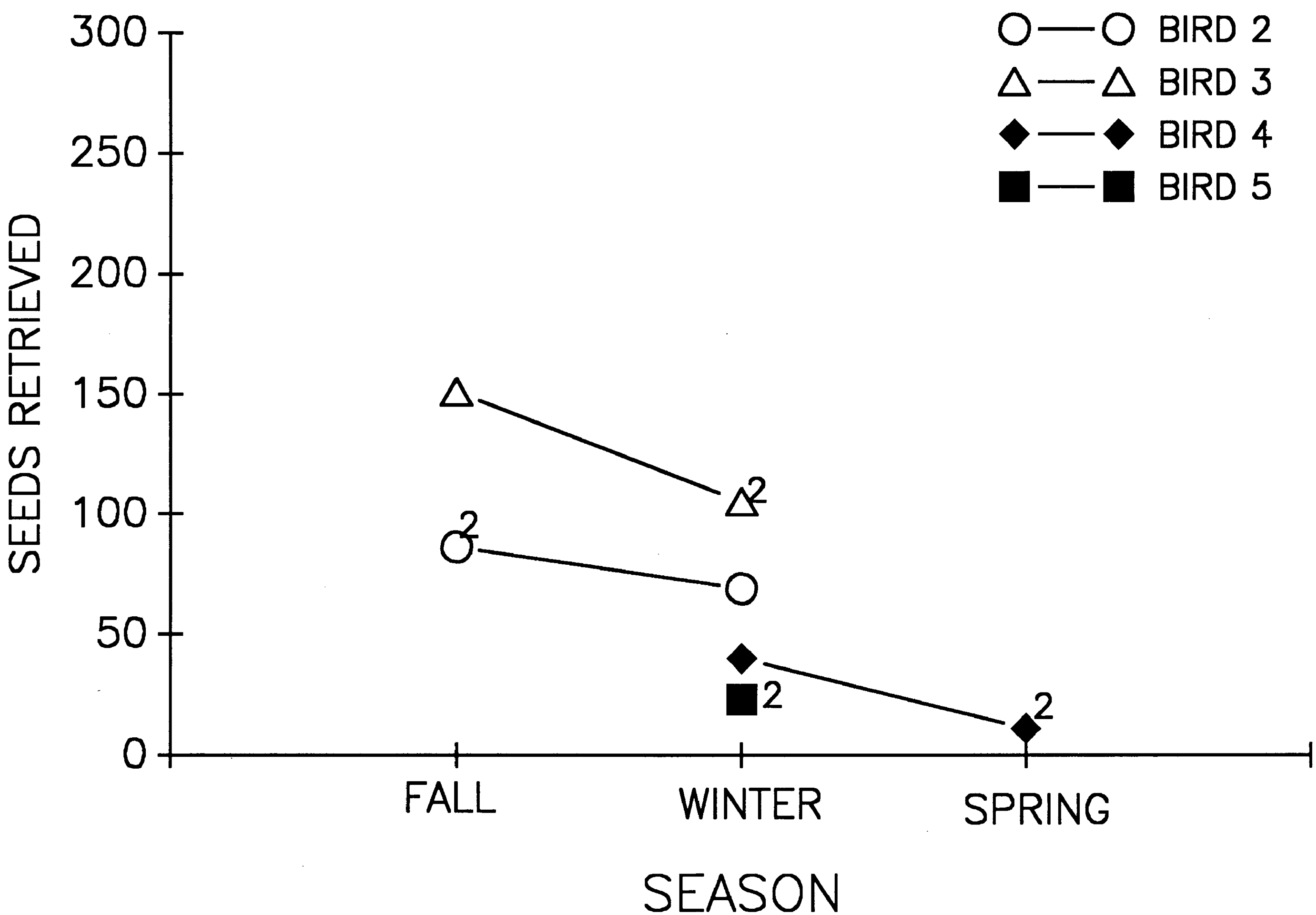
– indicates lost weight from one morning to the next



RECACHES/15min
10
5
0
2/1
2/2
3/1
3/2
WT
ΔWT
3
2
1
-
+

Figure 16.

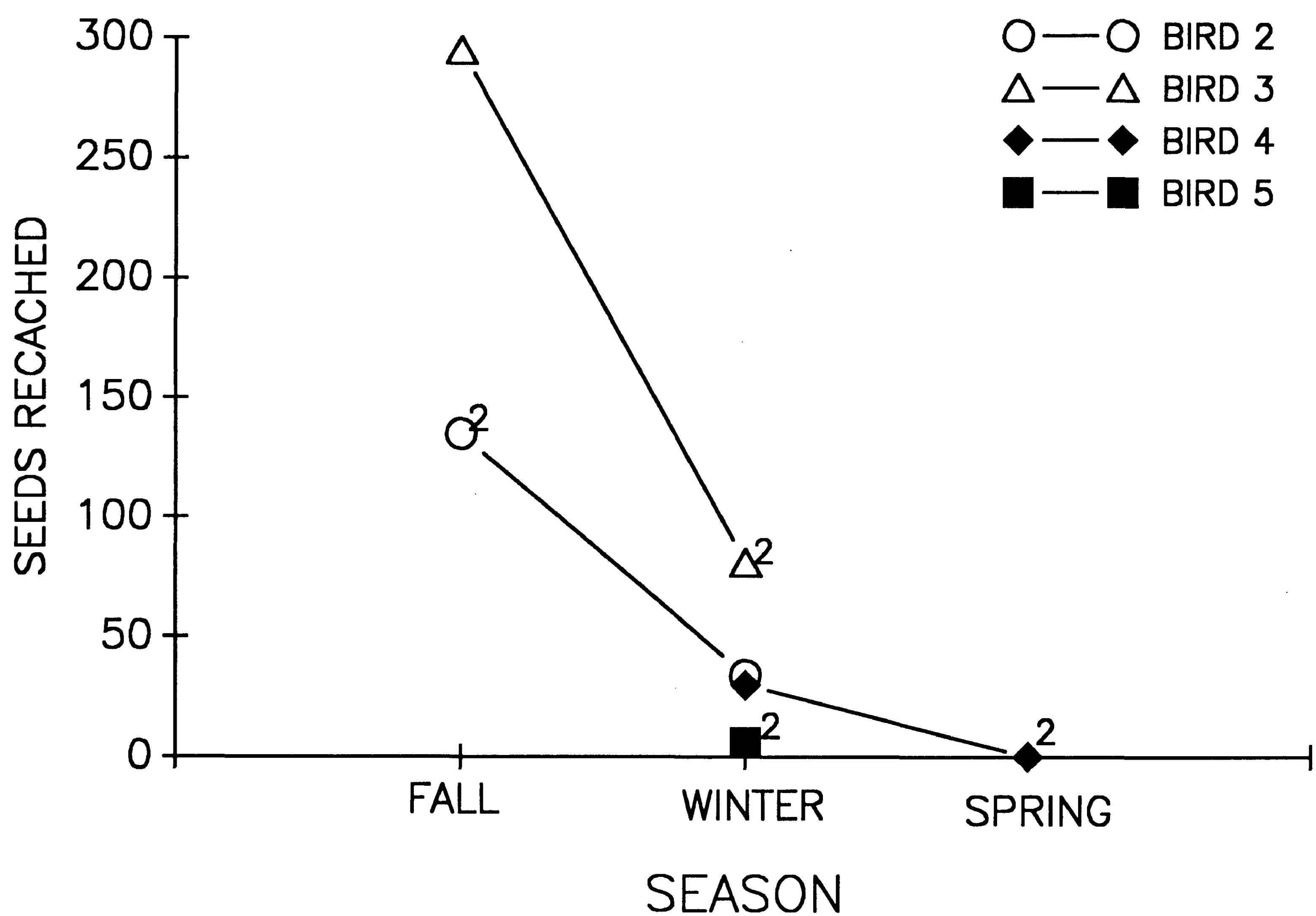
Retrievals vs. season.


BIRD 2
BIRD 3
BIRD 4
BIRD 5
SEEDS RETRIEVED
300
250
200
150
100
50
0
2
2
2
2
FALL
WINTER
SPRING
SEASON

one fall schedule bird, chickadee 2, who retrieved more as the days into the fall schedule progressed (Table 5, column D). With respect to recaches, both chickadee 2 and chickadee 3 recached more as the days into the fall schedule progressed. Chickadee 3 was then significantly less active with recaches as the days into the winter schedule progressed. No other regression results were significant (Table 6, column D). There was very little retrieving, and no recaching by any of the birds in the spring (Figure 17).

Figure 17.

Recaches vs. season.



SEEDS RECACHED
300
250
200
150
100
50
0
FALL
WINTER
SPRING
SEASON
BIRD 2
BIRD 3
BIRD 4
BIRD 5
2
2
2
2

DISCUSSION

If maximizing harvest rate was the critical variable regulating caching behavior in Carolina chickadees, then time of day, body weight, change in body weight and food access time should have had no effect on caching rates. The results did not support this hypothesis. Caching behavior peaked in the late morning. Early in the day, when the birds were presumably at their lowest body weights, meeting immediate needs by eating took precedence over future needs. Late in the day, two factors may have influenced caching rates. First, in the wild, the possibility of overnight pilfering decreases the potential value of stored seeds. Secondly, the need to eat and increase fat reserves for the overnight fast becomes paramount as the day ends. Mueller (1974) found no daily pattern to the caching behavior of American kestrels; and Tomback (1977) found that Clark's Nutcrackers stored pine seeds all day. James and Verbeek (1984) found caching rates of Northwestern crows to be equal in the morning and afternoon, with food availability determining caching patterns. Lohrl

(1958) found nuthatches stored more in the morning than at other times of day.

In support of the starvation risk minimization hypothesis, the birds cached less at higher body weights, with the exception of chickadee2-schedule2. [Chickadee 2, the lightest bird, cached more at high weight when on the 2 hour schedule. This opposite caching trend might be predicted for birds under high stress, possibly reflected by low body weight (pers. comm. Dr. J.R. Lucas, June 1988)]. If a bird has sufficient fat stores, the investment of time and energy required to cache may not be worthwhile when one considers how short a time seeds remain cached. Lima (1986) addressed the trade off between starvation risk and predation risk. At high body weight more foraging time is necessary to maintain the higher energetic cost of existence; but time spent feeding is also time spent exposed to predation. Increased mass associated with fat reserves may also reduce maneuverability during an attack. Thus, safe alternatives to foraging, such as perching, may be preferable at high body weight.

Rogers (1987) compared the amount of body fat of various passerine foragers in winter, noting that several species maintain fat reserves below physiological capabilities. Ground foraging birds who may be subjected to longer periods of food deprivation in the winter tended to have more body fat reserves than tree foragers. Since chickadees and most caching birds are tree foragers, they may be storing excess food as caches instead of as body fat.

The threat of starvation faced by foragers has been generally addressed under the name of risk sensitive foraging behavior. If caching is a method chickadees use to avoid starvation, their behavior should follow general risk theory. Caraco (1980, 1981) and others have shown that some birds and mammals respond to mean reward rate and variability of reward rate, and will choose among alternate habitats such that they minimize the chance of a shortfall. The risk proneness of the forager is determined by the expectation (during a foraging period) of meeting its energy requirements (Weissburg 1986). When the mean reward rate exceeds the minimum foraging requirements, the animal should be risk averse, preferring a constant reward rate. When the minimum foraging requirements exceed the mean reward rate, the animal should be risk prone (Caraco, 1983). Thus when the animal is on a positive energy budget one might expect risk averse behavior, and when on a negative energy budget, risk prone behavior (Barnard and Brown, 1985). Caching by chickadees should then be considered as a risk averse strategy, since caching occurs when the birds are at low and intermediate body weight categories, but are gaining weight. By caching, the birds are likely to reduce the variability of the food supply. The use of retrieved seeds that occurred when the birds were in the lower weight categories demonstrates the risk averse strategy of caching, as the retrieved seeds were eaten in order to 'level out' variance in food availability.

In this study, no daily pattern of retrieval behavior was found. Mueller (1974) found a trend in kestrels to retrieve more in the evening than in the morning or at noon. Stevens and Krebs (1986), looking at retrievals by Marsh tits, reported that "it appears that there may be an afternoon peak on each day with a 'trough' in the number of recovery attempts during the middle of the day." The expectation of cage food fed to the birds at the end of the day in this study, together with the fact that they were maintained at a constant temperature, possibly influenced the behavior shown by the birds and may have weakened the tendency to retrieve caches late in the day in preparation for the natural overnight fast.

Recaching has rarely been mentioned in caching research. Pruett-Jones & Pruett-Jones (1985) describe fruit caching and recaching by the male MacGregors Bowerbird; and some squirrel species have been observed recaching stored nuts (pers. comm. Dr. JR Lucas). In both cases, it appears that the birds or mammals would cache items as rapidly as possible, and then would return to retrieve and in some cases recache the items whenever time permitted, perhaps moving the caches to a more accessible or safe location. During this study, after the access period ended when a bird had been caching heavily, it would sometimes move a seed or seeds in quick succession from one cache site to another site at close proximity, in a bout that might last 3-5 minutes. Recaching was stimulated by the same variables that stimulated caching behavior; at midday peaks, at lower and intermediate body weight categories, and when the birds were gaining weight. Recaching would seem to be an counter-productive behavior, for conspecifics would then have a greater chance of seeing a cache site. Shettleworth and Krebs (1986) found that seeds encountered (but not retrieved) when foraging, were remembered equally as well as seeds the birds had stored themselves. However, Baker et al. (1988) found that chickadees observing caching by other birds did not seem to be able to memorize the seed location. Baker theorized that some part of the physical act of caching was necessary for memorization of the cache site.

The relationship of change in body weight to caching, retrieval, and recaching behaviors was not well defined. The amount of food fed to the birds in their cages overnight did not sufficiently control the weight of the birds, since the birds were able to maintain their body weights almost entirely on aviary food. Since the birds were weighed only once daily, in the morning, this study was unable to address the effect of change in body weight within a day on the caching and retrieval behavior of the birds. Within day changes in body weight may have significant effects on caching behavior, and in part explain the decrease in caching by the birds at the end of the day. When a bird is at a relatively low body weight, each seed eaten would add proportionally more mass to the bird than when the bird is heavy. This daily gain may be sufficient to reduce caching behavior by the relatively heavier bird at the end of the day.

The effect of seasonality on caching behavior was strong and unexpected, since the birds were maintained in controlled laboratory conditions throughout the study. Coupled with the decrease in caching, retrieval and recaching activity that occurred in the spring, was an increase in the amount of cage food (high protein insectile mix and egg) the birds ate when not in the aviary.

Because of physical and behavioral changes in the birds, as well as an increase in the availability of insects, the birds tend to eat fewer seeds and more insects in the spring. In addition, food is more likely to be abundant and more predictable in the spring, so the need to cache, even short-termed, is reduced. Chickadee social structure changes from a social, mixed-species feeding flock to territorial breeding pairs. Competition for food at a given patch would then be reduced, and in turn reduce the need to scatter hoard. Time constraints may also reduce caching behavior. In the winter, most active time is spent foraging, so the added time to cache and then later retrieve and eat a seed is not important. In the spring, mating and territorial defense should reduce the time available for foraging, and may reduce the value of maintaining caches. Chaplin (1976) found a seasonal pattern to the nocturnal hypothermic response of Black-capped chickadees, that "may depend on a circannual rhythm of sensitivity to low ambient temperatures." This rhythm may also play a role in determining the amount of caching activity exhibited by the birds. It appears that behaviors that might be expected in the field are driven, at least in part, by endogenous behavioral changes that were expressed in the laboratory.

This study has shown that many factors influence the caching behavior of Carolina chickadees. Time of day, and body weight both appear to have strong effects on the behavior of the birds; with caching activity strongest at midday, and at low and intermediate body weight categories. Thus, this study has shown that chickadees are caching, not to maximize harvest rates, but instead to minimize starvation risk.

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VITA

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