

**Winter Food-caching, Feeding, and Body Weight
in Relation to Social Dominance
in Black-capped Chickadees (*Poecile atricapillus*)**

by
Michael J. Boisvert

Department of Psychology

Submitted in partial fulfilment
of the requirements for the degree of
Master of Arts

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
September, 1999

©Michael J. Boisvert 1999



**National Library
of Canada**

**Acquisitions and
Bibliographic Services**

395 Wellington Street
Ottawa ON K1A 0N4
Canada

**Bibliothèque nationale
du Canada**

**Acquisitions et
services bibliographiques**

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-42127-9

Canada

Abstract

The present study examined the influence of social dominance on winter food-caching, feeding, and body weight in Black-capped chickadees (*Poecile atricapillus*.) Food-caching and eating were observed by direct visual observation in an outdoor aviary. An automated bird-feeder continuously recorded the time of visits by the birds as well as body weight at each visit. The times required to cache and to eat a seed, obtained by independent observation were used to classify unobserved feeder visits as representing caching or eating of a seed. Results indicated that birds of different dominance rank used different behavioral strategies. Birds displayed different diurnal patterns of caching and eating, and differed in their responses to environmental conditions. However, the most dominant and least dominant bird maintained the same body weight and showed the same pattern of gain in body weight through the day. Cache pilferage by the subordinate birds probably accounts for this finding.

Keywords: food-caching, body weight, social dominance, feeding, body fat, temperature, daylength, Black-capped chickadees, *Poecile atricapillus*, Parids, cache pilferage, energy regulation, foraging.

Acknowledgements

I would like to thank David Sherry for his support, advice, and CDs. Yaoping Hu wrote the computer software. John Orphan and Dan Pulham put many hours into building and modifying the feeder apparatus. Many thanks to Bill Roberts, Peter Ossenkopp, and Mark Cole for serving on my examining board. Bill and Peter also provided valuable comments at earlier stages. Vladimir Pravosudov provided helpful comments as well as advice on weighing birds. Bob Gardner provided statistical advice. Finally I would like to thank my family and friends for their support and encouragement, especially my mom and dad, Dave Brodbeck, Shelley Cross-Mellor, and Jen Sutton.

TABLE OF CONTENTS

	Page
CERTIFICATE OF EXAMINATION.....	ii
ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	v
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
INTRODUCTION.....	1
1. Measuring Body Fat.....	3
2. Natural Variation in Body Weight.....	4
3. External Energy Reserves.....	7
4. Natural Variation in Food-caching.....	8
5. Integrating the Two Modes of Energy Storage.....	10
6. Energy Regulation in Relation to Social Dominance.....	14
7. The Present Study.....	17
METHOD.....	18
1. Subjects.....	18
2. Apparatus.....	19
3. Procedure.....	21
RESULTS.....	24
1. Social Dominance.....	24
2. Directly Observed Caching and Eating.....	24

3. Automated Record of Feeder Visits.....	29
4. Body Weight.....	45
DISCUSSION.....	48
1. Food-caching and Eating.....	48
2. Body Weight.....	51
3. Integrating Food-caching and Body Weight.....	54
4. Future Research.....	55
REFERENCES.....	56
CURRICULUM VITAE.....	64

LIST OF TABLES

Table	Description	Page
I	Predicted Within-Day Patterns in Food Caching by McNamara, Houston and Krebs (1990) and Lucas And Walter (1991).....	12
II	Outcomes of Competitive Interactions Between Pairs Of Birds (OW, GR, and GY).....	25

LIST OF FIGURES

Figure	Description	Page
1	Photograph of the Automated Feeder.....	20
2	Distribution of Times to Cache and to Eat a Seed by OW.....	27
3	Distribution of Times to Cache and to Eat a Seed by GR.....	28
4	Distribution of Times to Cache and to Eat a Seed by GY.....	29
5	Mean Number of Seeds Eaten and Cached per Day for all birds.....	31
6	Distribution of Unobserved Feeder Visits for OW (α -bird).....	32
7	Distribution of Unobserved Feeder Visits for GR (β -bird).....	33
8	Distribution of Unobserved Feeder Visits for GY (γ -bird).....	34
9	Scatterplot of Daily Caches and Daylength for β -bird.....	36
10	Scatterplot of Daily Caches and Overnight Temperature for β -bird...	37
11	Scatterplot of Daily Caches and Daylength for γ -bird.....	33
12	Scatterplot of Daily Eating and Daily Temperature for α -bird.....	40
13	Scatterplot of Daily Eating and Daylength for β -bird.....	41
14	Within-day Pattern of Caching for All Birds.....	43
15	Within-day Pattern of Eating for All Birds.....	44
16	Within-day Pattern of Weight Gain for α - and γ -bird.....	47

One obvious change in the ecology of many non-migratory bird species is the seasonal change in social organization that occurs when mated pairs stop defending breeding territories and form winter flocks. Generally, flock formation begins in late summer or early fall and by late August or early September flocks are fully formed and persist through the winter (Welty & Baptista, 1990). In the case of Parids (chickadees and titmice), flocks contain between two and twelve members, and are usually comprised of paired adults and foreign juveniles (Smith, 1991). Flocks occupy home ranges that are much larger than individual breeding territories and home ranges may be defended from other flocks (Smith, 1991). Flocks are hierarchically organized: typically, adults dominant juveniles and males dominate females. Dominance relationships also exist in mixed-species flocks, where, for instance, woodpeckers and nuthatches exclude chickadees and kinglets from food sources (Smith, 1991).

Regardless of its dominance status, a diurnal bird living at northern latitude is faced with two problems during the winter. First, the number of daylight hours available for foraging is limited. This means that birds must acquire adequate reserves during short days to survive long overnight fasts. Second, cold temperatures increase metabolic costs, as more energy is required to maintain body temperature. This problem is exacerbated by the small body size of birds like Parids (chickadees and tits). Small bodies have higher surface area:volume ratios than large bodies and small birds suffer greater heat loss per unit of mass than large birds (Welty & Baptista, 1990). Of course other problems exist. Food supply may be limited due to the reduced activity of insects, the covering of food by snowfall, and the need to rest during periods of harsh weather conditions.

Over-wintering birds must ensure that they have adequate reserves to withstand unpredictable interruptions in foraging during the day, and long periods of fasting overnight. Most birds, indeed most animals, rely exclusively on energy stored within the body. Three main internal energy stores exist for birds: carbohydrates, proteins, and lipids (Blem, 1990). Carbohydrates are stored mainly in the liver and in muscle tissues as glycogens. In small birds they are depleted within a few hours and appear to be used only during periods of inactivity (Blem, 1990). Carbohydrates provide about half the energy of lipids (Blem, 1990; Welty & Baptista, 1990). Proteins appear to be used as a last resort. Proteins are incorporated in muscle tissue; their breakdown is inefficient, and may produce toxins and reduce muscle mass (Blem, 1990). Lipids are the primary energy source for birds (Blem, 1990; Welty & Baptista, 1990). Fat is stored primarily in subcutaneous and intraperitoneal sites, and in small birds is located mostly around the furcula (Welty & Baptista, 1990). The mass of stored body fat is often more than 100% of lean body mass and increases in body fat are positively correlated with increases in body mass (Blem, 1990).

Birds add body fat in anticipation of two times of energetic stress: winter and the nightly fast (see below). Birds rarely carry the maximum amount of body fat that they can support, however, and this has led to the view that there may be costs to carrying fat. Most workers follow Lima (1986, 1988) in assuming that levels of body fat reflect a tradeoff between the risk of starvation and the risk of predation (e.g. Carrascal & Polo, 1999; Lucas & Walter, 1991; McNamara, Houston, & Krebs, 1990; Pravosudov & Grubb, 1997a, b). On the one hand, birds should maintain high levels of body fat to guard against the risk of starvation. However, doing so will incur costs in terms of the increased energy

needed to maintain a larger body size. In addition, increases in time spent foraging and, possibly, decreases in agility or take-off speed may increase the risk of predation (Witter & Cuthill, 1993). Thus, there may be benefits to being lean. Body fat, then, may reflect a trade-off between these two forces.

Measuring Body Fat

Historically, the most popular method of assessing body fat in birds has been carcass analysis (Brown, 1996). The major advantage of carcass analysis is that it gives the most detailed information about the compositions of lipids, proteins, and minerals in the body. Though variations exist in how this method is applied, carcass analysis always requires sacrificing the subject. Thus, its major weakness is that individual animals cannot be studied longitudinally. The general procedure involves killing an animal and then dissecting its carcass. Once tissue types (e.g. stomach, heart, liver, etc.) have been separated they are ground, dried, treated with petroleum ether, and the lipids extracted. Often, following lipid extraction, the remaining carcass is burned to determine its ash and mineral content. Carcass analysis results in the most complete index of body fat and is used to evaluate the accuracy of other, nondestructive, methods (Brown, 1996).

Carcass analysis is the only method of assessing body fat that cannot be repeated on the same animal. A simple, repeatable and commonly used method of assessing body fat is measuring body weight (e.g. Haftorn, 1989; Hurly, 1992; Lucas & Walter, 1991; Pravosudov & Grubb, 1997b). Changes in body weight correlate with changes in body fat levels and with repeated sampling this method provides a good estimate of body fat levels (Brown, 1996).

Natural Variation in Body Weight

During the non-breeding season, birds display adaptive changes in body weight that anticipate or respond to periods of energetic stress. For instance, body weight changes on a seasonal basis, anticipating the onset of winter. Using an electronic balance as a feeding table Haftorn (1989) recorded over 13000 body weights from five species of European tits. For all species four measures of body weight (morning body weight, midday body weight, evening body weight, and mean daily body weight) increased beginning in September and peaked in December. The midwinter peak represented a 2-8% increase over the autumn levels. Similar patterns have been shown in a variety of species (Blem, 1976; Chaplin, 1974; Haftorn, 1992; Lehikoinen, 1987; Koivula, Orell, Rytönen, & Lahti, 1995).

During winter, a predictable period of stress occurs on a daily basis: the nightly fast. For Haftorn's (1989) tits, average evening body weight was between 7-12% higher than morning body weight. Maximum body weight also has been shown to occur in the evening in other species (Willow tits: Koivula et al., 1995; Tufted titmice: Pravosudov & Grubb, 1997a).

Such increases in body weight are most likely due to increases in fat levels. Chaplin (1974) used carcass analysis to measure fat levels in Black-capped chickadees caught and sacrificed in the early morning or early evening at four times of the year. She measured lean dry weight and fat weight as a percentage of total body weight. Lean dry weight did not differ statistically on a seasonal or daily basis, but fat content was significantly higher in November and February than in September or April.

The seasonal and daily variation in body weight described above raises the question of what proximate factors produce these phenomena. Among the proximate variables hypothesized to produce variation in body weight are changes in temperature, daylength, and food supply. Although few experiments have systematically manipulated temperature, existing data suggest that birds may be sensitive to changes in temperature. In one of the few experimental investigations of temperature, Bednekoff, Biebach and Krebs (1994) exposed captive Great tits (*Parus major*) to constant and variable temperature regimes while holding constant the light:dark cycle. Birds were exposed to a constant temperature of 8.5 °C for several days, then given a block of consecutive days where the daily temperature was pseudorandomly set to either 1.5 °C or 15.5 °C. Following this variable block, birds were re-exposed to the constant temperature (8.5 °C) for several consecutive days. Evening weights were significantly higher during the variable treatment than during the two control phases. In another experimental investigation of temperature on body weight, Ekman and Hake (1990) showed that captive Greenfinches (*Carduelis chloris*) exposed to a 5 °C drop in ambient temperature increased their body weight relative to a control group maintained on constant temperature.

Field-based investigations of the influence of temperature on body weight have yielded conflicting results. In his comparative study of European tits, Haftorn (1989) found significant correlations between daily temperature and both daily weight gain and nightly weight loss, but these correlations only appeared in a few individuals, were not consistent within species, and were not consistent with respect to the direction of the relationship. In contrast, correlations between daylength and these body weight measures

were much more consistent within species, and significant correlations were always negative.

Gosler (1996) used a regression analysis to determine which of the following factors explained variation in body fat in Great tits as assessed by fat scoring: mean temperature on the day of capture, mean temperature on the day before capture, and the 30-year mean temperature for the date of capture. Only mean temperature on the day of capture explained a significant proportion of the variance in body fat. In contrast to Haftorn's (1989) results, Gosler (1996) found only a weak influence of daylength on body fat. In his analysis, daylength accounted for just 1% of the variation in body fat.

The relationship between food supply and body weight or fat reserves has been more thoroughly investigated in a range of species. This is often been shown by comparing body weight of individual birds during a "control phase," in which food is deemed to be predictable, to that during an "experimental phase" when food availability is unpredictably interrupted. The conclusion of these studies is that when the food supply is unpredictable birds increase their body weight. This has been demonstrated in Great tits (Bednekoff & Krebs, 1995), Greenfinches (Ekman & Hake, 1990), and Tufted titmice (*Parus bicolor*; Pravosudov & Grubb, 1997a).

These findings suggest that body weight is adjusted in response to environmental conditions, but there is some evidence for an endogenous role in the control of body weight. Grubb and Pravosudov (1994a) held captive House sparrows (*Passer domesticus*) on constant temperature and daylength for several months, providing them with *ad libitum* access to food. Interestingly, the birds' body weight increased significantly in December and declined in February. Pravosudov and Grubb (1997a)

suggest that seasonal patterns like winter fattening may be under endogenous control while, short-term changes in reserves may respond to environmental factors like temperature, daylength and food supply.

To summarize, natural variation in body weight occurs across and within days. Seasonal and daily peaks in body weight occur in midwinter and in the evening, respectively. Changes in body weight seem to be influenced by exogenous and endogenous factors. Among the former are predictability of the food supply, ambient temperature, and daylength.

External Energy Reserves

Not all animals are confined to a single mode of energy storage. Some species of birds and mammals store energy externally in food caches. Among birds food-caching occurs in at least 12 families (Sherry, 1985). Considerable diversity exists between species in the types of food cached, in the distribution of food caches, and in the lengths of time food is cached. Families Corvidae (jays and crows), Sittidae (nuthatches) and Paridae (chickadees and tits) are among the best-studied representatives of food-caching birds. In general, species in these families store insects and seeds in widely scattered caches and do so primarily during the nonbreeding season. Seeds and insects are often stored in the ground, in the crevices of tree bark, in clumps of needles and just about anywhere else they will fit (Haftorn, 1954, 1956a, 1956b, 1956c; Pravosudov, 1985; Vander Wall, 1990). Some species recover their caches hours or a few days after creating them (short-term caching) while others recover their caches months later (long-term caching; reviewed in Kallander & Smith, 1990). That individual parids are able to recover their own caches appears to result primarily from inter-individual (and inter-specific) differences in foraging

niches (Brodin, 1994; Haftorn, 1956c) and accurate memory for the locations of caches on the part of the storer (e.g. Balda & Kamil, 1992; Brodbeck, 1994; Brodin & Kunz, 1997; Krebs, Healy, & Shettleworth, 1990; Sherry, 1984). There is some debate at present about the duration of spatial memory in parids. Hitchcock and Sherry (1990) have shown that Black-capped chickadees are able to remember the locations of seeds cached in an indoor aviary for up to 28 days. Others argue that chickadees and titmice in the wild have much more limited cache memory that lasts only a few days (e.g. Brodin, 1994; Brodin & Clark, 1997). In any event, food-storing species seem to have a specialized memory system that has evolved to solve the unique problems presented by a food-storing lifestyle. This specialization reveals itself in behavioral and neuroanatomical differences between storing and nonstoring species (Brodbeck & Shettleworth, 1995; Sherry, Vaccarino, Buckenham & Herz, 1989).

Natural Variation in Food-caching

Like body weight, food-caching behavior displays seasonal changes. Ludescher (1980) and Haftorn (1956c) have shown seasonal caching patterns in several European tits. Haftorn (1956c) studied the caching behavior of three tit species in the wild and has provided the most detailed account of food caching in free-ranging birds. Coal tits (*Parus ater*), Crested tits (*P. cristatus*), and Willow tits (*P. montanus*) all cached most intensively during September and October and stored between 50-60% of the seeds they collected during these autumn months. It is generally thought this seasonal pattern is a response to seasonal changes in food supply and serves as a buffer against periods, such as the winter, when food is unavailable or hard to find (Grubb & Pravosudov, 1994; Haftorn, 1956c). However, Ludescher (1980) has shown that seasonal caching rhythms occur under

constant food conditions. He held two Willow tits in outdoor aviaries for five years and provided them with *ad libitum* access to food. Under these conditions the tits displayed pronounced seasonal peaks in caching. Ludescher's birds may have been responding to changes in daylength or temperature. For example, in the laboratory Shettleworth, Hampton and Westwood (1995) were able to stimulate increased caching by systematically shortening the number of light hours on which Black-capped chickadees were maintained. In addition, Pravosudov and Grubb (1997b) found that ambient temperature was negatively correlated with caching intensity by Tufted titmice.

Food-caching, like body weight, can also be affected by predictability or variability of the food supply. For instance, Hurly (1992) switched Marsh tits (*P. palustris*) in a counterbalanced fashion between schedules that delivered food with low variability (LV) and high variability (HV). On the LV schedule birds could feed for 10 seconds every minute, but the location of the 10-second block within a given minute was randomly determined. On this schedule the average interval between 10-second reinforcements was 50 seconds. In contrast, the HV schedule delivered food during one randomly selected 10-minute block every hour. Here the mean interval between 10-minute reinforcements was 50 minutes. Marsh tits cached significantly more seeds during the HV treatment than during the LV treatment (Hurly, 1992).

Recall that body weight in many bird species peaks late in the day, just prior to the onset of the overnight fast. This makes sense given the energetic requirements of the fast. In the case of food-caching, daily patterns are less robust across species. Haftorn (1954) showed that Crested tits cached most food between late morning and early afternoon, but overall little difference existed between caching in the first and second parts of the day

(Haftorn, 1954, Table 41). Captive White-breasted nuthatches (*Sitta carolinensis*) tended to store more food in the first half of the day than in the second half (Waite & Grubb, 1988). However, Pravosudov and Grubb's (1997b) Tufted titmice tended to do most storing in the afternoon. Other investigators have found no consistent within-day pattern among individuals (Hurly, 1992). Thus, unlike fat storage, food storing does not demonstrate a robust effect of time of day.

Integrating the Two Modes of Energy Storage

Thus far it has been emphasized that food-storing species have two places they can store energy: internal body reserves and external food caches. If we make the reasonable assumption that there are costs associated with storing energy both internally as fat and externally as caches then we would expect trade-offs to exist between these two options. Recently, investigators have explored these trade-offs by simultaneously studying food-caching and body reserves.

The trade-offs between internal and external energy storage have mostly been the focus of theoretical investigations. Two influential models are those of McNamara (McNamara et al., 1990) and Lucas (Lucas & Walter, 1991). These models use dynamic programming techniques to predict patterns in food caching and body weight. Dynamic programming models can consider simultaneously the influences of the physiological state of an individual and the state of the environment on behavior and vice versa (Clark, 1991). These models assume that some defined set of behaviors may be expressed during a specified period of time. Using field and lab data and some basic assumptions, the state of the environment and that of the organism are defined mathematically, as are the changes that occur to each when the organism interacts with its environment. The dynamic

program seeks the behavioral policy that maximizes fitness at the end of the period being considered.

The McNamara and Lucas models specify the behavioral policies that maximize the probability of surviving the winter. Each model predicts daily patterns in food-caching and fat reserves in parids. In addition, both models assume that food-storing birds have available 4 alternatives for behavior: resting, finding food and eating it, finding food and caching it, or recovering stored food. McNamara et al. (1990) predict that chickadees and tits will spend the first third of the day (hereafter Dawn) with an intermediate level of fat reserves, which will actually decline during the middle third of the day (hereafter Midday). By the final period of the day (Dusk) birds are predicted to have accumulated high levels of fat reserves. This daily pattern in fat reserves is predicted to give rise to the following daily pattern of caching: maximal caching at Dawn, less caching at Midday, and little or no caching at Dusk. These predictions are summarized in Table 1. The Lucas model predicts a different pattern of fat reserves and food-caching during a winter day. With respect to fat reserves, parids are expected to have their lowest level of reserves at Dawn, to have intermediate reserves at Midday and to have their greatest reserves at Dusk. Similarly, Lucas and Walter (1991) predict a different pattern in daily caching, with little caching occurring at Dawn, maximal caching occurring at Midday and little or no caching occurring at Dusk (Table 1). Notice that although the models predict different diurnal patterns for both internal and external reserves, in each case maximal caching accompanies intermediate fat levels and less caching occurs as internal reserves reach minimum or maximum levels. The reasoning behind this is that when fat levels are low, storing energy internally should be most important because starvation becomes an immediate risk. Thus,

Table 1. Predicted within-day caching patterns of two theoretical models.

Time of Day:	McNamara et al. (1990)	Lucas & Walter (1991)
Dawn	Maximal caching occurs	Little caching occurs
Midday	Less caching occurs	Maximal caching occurs
Dusk	Little or no caching occurs	Little or no caching occurs

Note. Each model predicts that maximal caching will occur at intermediate body weight. McNamara et al. (1990) predict that intermediate body weight will occur at Dawn, but Lucas and Walter (1991) predict intermediate body weight will occur at Midday.

birds should favour finding food and eating it immediately over finding food and storing it for later use. When internal reserves are high, however, predation is assumed to become a more important risk than starvation and so birds are predicted to rest rather than forage and expose themselves to predators. At intermediate fat levels, immediate starvation is not a threat, but birds must ensure they accumulate enough reserves by Dusk to survive the overnight fast. Caching is favored over eating at this weight range because birds are expected to delay weight gain until late in the day as a hedge against the increased risk of predation associated with higher body weight. Thus, they are predicted to make food-caches, which they can retrieve later in the day to add body fat.

As discussed above, many species demonstrate a daily pattern of weight gain with low morning levels and evening peaks, supporting the prediction of Lucas and Walter (1991). It is difficult to evaluate the predictions for daily caching patterns given the variability that exists among species. However, Lucas and Walter (1991) did test the prediction that most caching should occur when birds are at intermediate body weight. Three of the four Carolina chickadees they studied cached most at midday, when they were at intermediate weight and cached the least at dawn and at dusk.

Most empirical studies of fat and cache dynamics have investigated the influence of changes in temperature, daylength, or food supply on energy regulation (Bednekoff et al., 1994; Bednekoff & Krebs, 1995; Ekman & Hake, 1990; Hurly, 1992; Lucas & Walter, 1991; Pravosudov & Grubb, 1997). But, a striking feature of the nonbreeding season is the change in social organization of many species from territorial mated pairs to membership in dominance-structured winter flocks. Differences in social status among flock-members may create differences between birds in foraging behavior and predation

risk. Indeed, dominant birds have priority of access to food resources (Koivula et al., 1995; Lahti et al., 1998; Piper, 1997; Pulliam & Caraco, 1984), forage in higher quality microhabitats than subordinates (Piper, 1997), and forage in habitats that are safer from predators (Koivula, Lahti, Rytönen, & Orell, 1994; Lahti et al., 1997). Perhaps not surprisingly, subordinates may suffer from higher mortality rates (Koivula et al., 1994; Lahti, Koivula, & Orell, 1997).

Energy Regulation in Relation to Social Dominance

It seems reasonable to hypothesize that the differences in foraging behavior and predation risk that distinguish dominants from subordinates may influence the energetic strategies adopted by each dominance class. Although all over-wintering birds must adjust their energy reserves to cope with environmental conditions, not all members of a flock may make adjustments in the same ways. Dominance status seems to influence regulation of body weight but in complex ways. For instance, Hake (1996) showed that in flocks of Greenfinches subordinates maintained significantly higher body weights than did dominants, and increased their body weight more than dominants when food predictability was lowered. Ekman and Lilliendahl (1993) found the same pattern in a population of Willow tits in Sweden. But, Koivula et al. (1995) found that dominants maintained higher evening body weight than subordinates in a population of Willow tits in northern Finland, a pattern also found for Willow tits in Norway (Verhulst and Hogstad, 1996). Together, these results suggest that there is no simple predictive relationship between social status and body weight. The differences in results may be due to differences in predation risk, food supply, or weather conditions.

Dominants have priority of access to food. One often suggested consequence of this is that subordinates may perceive the food supply as being less predictable than dominants (Ekman & Lilliendahl, 1993; Hake, 1996; Koivula et al., 1995; Lahti et al., 1998; Piper, 1997; Piper & Wiley, 1990; Verhulst & Hogstad, 1996). This has led some authors to predict that subordinates should maintain larger reserves than dominants in order to hedge against periods when food cannot be obtained (Ekman & Clark, 1995; Ekman & Lilliendahl, 1993; Witter & Swaddle, 1995). For instance, Ekman and Lilliendahl (1993) showed that subordinate Willow tits maintained higher body weight than dominants. They predicted that if they removed the dominant, the remaining subordinate birds would lower their reserves due to reduced competition for food. They removed the dominant member of five flocks and compared body weight of the remaining flock members to that of members of unmanipulated control flocks. Body weight of subordinate birds decreased in response to removal of dominants, but no changes in body weight occurred in control flocks. The authors concluded that dominance was causally related to body weight. However, because removal of the dominant bird was confounded with a change in group size, it is not clear whether removal of the dominant *per se* was responsible for the changes observed. Perhaps, the removal of any bird would have had the same effect, since fewer birds were competing for the same number of resources. Witter and Swaddle (1995) performed a similar experiment in the laboratory with Starlings (*Sturnus vulgaris*). In addition to removing a dominant bird in one group they removed a subordinate member in a matched group. With no confound between removal of a dominant and change in group size, they found that removal of a dominant resulted in a reduction in body weight among remaining birds; removal of a subordinate had no effect.

While competition for food seems to account for differences in body weight between dominant and subdominant birds, the inconsistent findings from several field-based studies suggest that the relationship between dominance status and body weight is complex. Differences in local weather conditions, predation risks, and food-supply combined with the degree of intra- and inter-specific competition for resources may make predicting differences in body weight between dominant and subdominant birds difficult.

Of course, social dominance may also influence energy regulation with respect to food-caching. As was the case with body weight, some aspects of food-caching appear to be related to social dominance in complex ways. One difference between dominants and subordinates that has been shown in Parids and Sittids concerns the caching niche. For instance, subordinate Willow tits cached food farther from a feeder than did dominants and tended to cache food in less protected areas (Lahti et al., 1998). Similarly, Woodrey (1991) showed that subordinate female nuthatches used a broader caching niche than did dominant males.

Differences between dominants and subordinates in caching intensity are less consistent. Dominant Willow tits stored more food than subordinates (Lahti et al., 1998), but the reverse pattern was true for nuthatches (Enoksson, 1988; Moreno, Lundberg, & Carlson, 1981). Clearly, more data needs to be collected in order to determine the basis of these differences.

Some researchers have used removal experiments to determine whether dominance and food-caching behavior may be causally related. Lahti et al. (1998) conducted a field manipulation in which they removed the dominant male from several flocks and observed the caching behavior of the remaining flock members. Upon removal of the dominant, the

remaining birds cached at significantly higher rates and cached at closer distances to the feeder. This interesting result may suggest a causal link between social dominance and these features of food-caching. However, the authors did not control for the removal of the dominant by removing a subordinate and thus the removal was confounded with a change in group size.

One important difference between fat storage and caching is that caches may be lost to pilferers and cache loss can have effects on the amount of stored food. Pilferage may occur during the day or during the night when nocturnal rodents are active (Brodin, 1993). Estimates of cache loss in nature vary considerably depending on the species and location. Brodin (1994) studied free-ranging Willow tits and estimated cache loss to be less than 2% per day. Stevens and Krebs (1986), however, reported that in one area Marsh tits lost around 20% of their caches each day. We might predict that the response of a food-storer to pilfered caches would be to make fewer caches or to store food in different places. The latter prediction has been verified experimentally by Hampton and Sherry (1994). Black-capped chickadees learned to avoid storing seeds on one side of an aviary if seeds stored on that side had been “pilfered” by the experimenters. However, the prediction that decreased caching should occur under conditions of pilferage has not been supported. In fact, if anything, birds respond to experimentally induced cache loss by storing more (Lucas & Zielinski, 1998).

The Present Study

Social dominance clearly influences each of the two modes of energy storage in complex ways. Past research, however, has only investigated the influence of social dominance on a single form of energy storage, be it food-caching or body weight. The

influence of dominance on the *simultaneous* expression of food-caching and body fat has not been addressed empirically or theoretically. This may be due to the difficulty of collecting this kind of data in free-ranging animals. The following investigation of social influences on energy regulation avoided this obstacle by studying captive birds in semi-natural conditions. Another limitation in the literature concerns the species used in studies of avian energetics. Regulation of food-caching and body weight in food-storing birds has most often been investigated with European tits and in North America with Carolina chickadees (Ekman & Lilliendahl, 1993; Haftorn, 1989; Hurly, 1992; Lucas & Walter, 1991; Lucas & Zielinski, 1998). The following experiment expands the range of species studied to include the Black-capped chickadee and provides new data on the simultaneous expression of food-caching and body weight in relation to social dominance.

METHOD

Subjects

Four male Black-capped chickadees were collected between 28 August and 10 September 1998. Birds were captured with Potter traps in a woodlot on the campus of the University of Western Ontario, London, Canada (43° 11'N, 81° 18'W). Immediately after capture, each bird was brought into the lab, measured (wing length and body weight) and equipped with uniquely colored leg bands to which a transponder tag (see below) was attached. In the laboratory, birds were held individually in wire mesh cages (36 X 36 X 60 cm) under a light cycle that reflected natural daylength. Food (peanuts, striped and black-oil sunflower seeds, and a maintenance diet) and water were available *ad libitum*. On 10 September 1998 all birds were released simultaneously into a large outdoor aviary.

Apparatus

Outdoor aviary. All observations and data collection occurred in an outdoor aviary (10.13 m X 3.07 m X 2.26 m). The aviary contained 4 nestboxes, several perches, 13 trees, and many logs and wooden caching blocks. The walls of the aviary consisted of wire mesh fencing to which several tree branches, logs and the caching blocks were attached. Logs and trees were also spread across the floor of the aviary. A solid roof covered the aviary, which was otherwise exposed to natural light, temperature and weather conditions. Birds had ad lib access to water, an automated feeder that contained black-oil sunflower seeds and four small food cups that contained a maintenance diet.

Automated feeder and PIT tags. The automated feeder was located in the center of the aviary. The feeder (Figure 1) consisted of six components: a PIT-tag detector, a PIT-tag reader, an electronic balance, an interface, a perch, and a tube filled with sunflower seeds. Each bird was equipped with a passive integrated transponder (PIT) tag (Biosonics, Inc., Seattle, WA), which permitted the detection and identification of the bird when it visited the feeder.

A PIT-tag consists of an integrated circuit and an electromagnetic coil, which are sealed in a glass capsule. Each tag comes with a unique factory programmed ID-code. The tags are small and lightweight (11 mm long X 2 mm in diameter, 0.07 g) and often are implanted subcutaneously in animal subjects (e.g. Fagerstone & Johns, 1986). PIT-tags have no internal power source and remain dormant until activated to transmit their code by an electromagnetic signal sent from the detector. The detector receives the code and sends it to the reader, which then decodes it and sends it to a computer. In the present study PIT-tags were not implanted in birds but, instead, were fixed to birds' leg bands with epoxy.

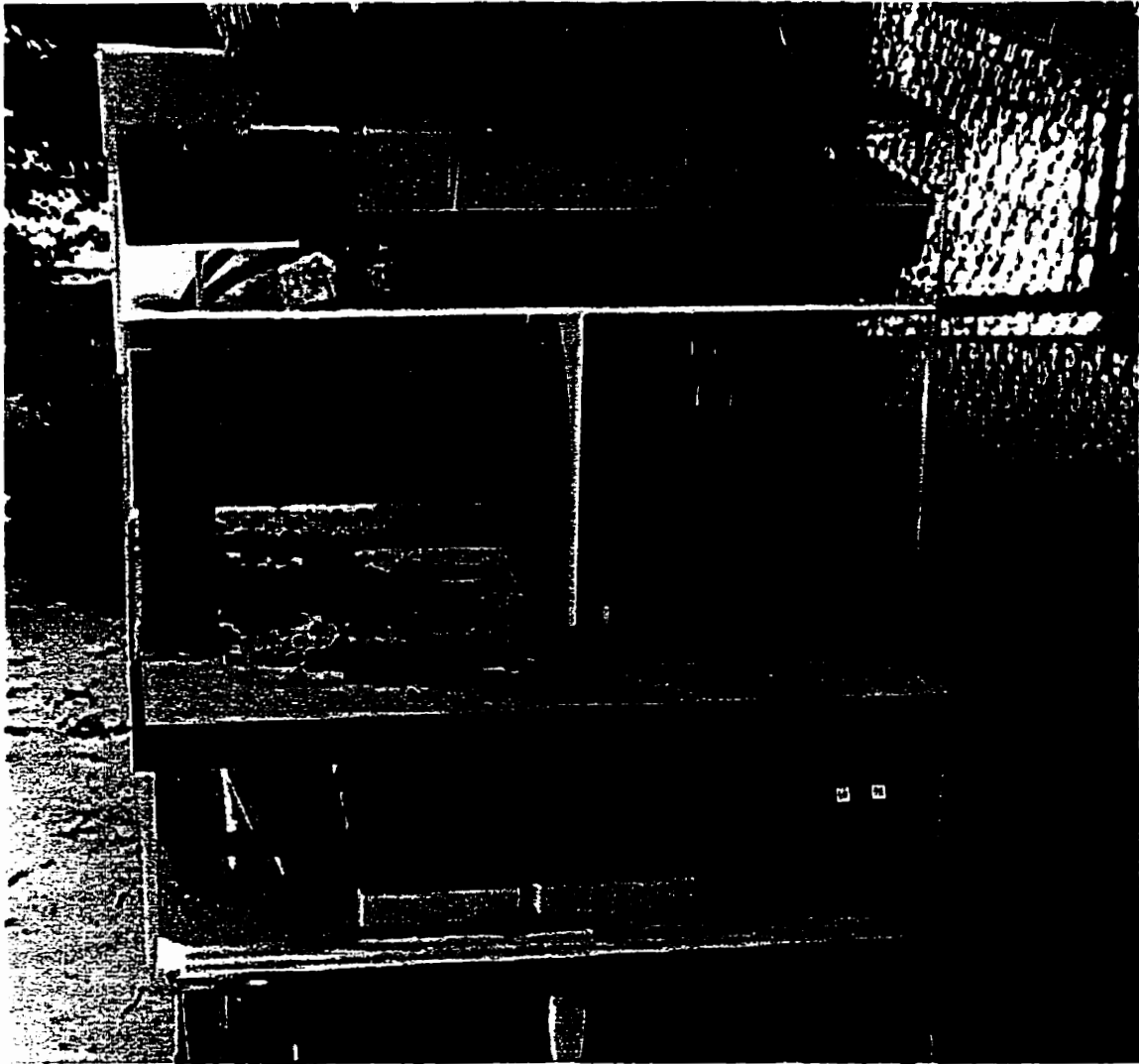


Figure 1. Photograph of the automated feeder showing (A) interface, (B) electronic balance, (C) feeder entrance, (D) PIT-tag detector, (E) perch, (F) seed tube, and (G) PIT-tag reader. The photograph was taken during training.

In the field this method of attachment proved easier to apply and resulted in no losses of tags. Moreover, it poses fewer risks for the birds.

The perch was equipped with an infrared photobeam, which was interrupted whenever a bird landed on the perch. The perch was attached to an electronic balance (Ohaus GT400, Ohaus Corp., Florham Park, NJ), and interruption of the perch photobeam sent a signal to the balance to transmit its reading to the computer. When a beam-break occurred the balance sent a weight reading to the computer every 0.25 second for 3 seconds. The interface produced a tare to the balance every 3 minutes. The balance's reading was sent to the computer every 5 minutes. Weights were recorded with .01g precision.

A custom software program coordinated the transfer of data from the automated feeder components to a 486 DX computer. On each occasion that a bird landed on the perch, the following information was recorded in a datafile: the current date and time (hh:mm:ss), the ID-code of the bird, and a list of weights collected in .25 second intervals for 3 seconds. The maximum weight reading at each visit was taken as the true weight of the bird at that time. The feeder apparatus collected data continuously.

Temperature Recorder. Ambient temperature was also continuously recorded throughout the study. A remote temperature logger (Onset Computer Corp., Pocasset, MA) inside the aviary collected temperature samples every 2 minutes. These data were stored in the logger until they could be downloaded to the computer for analyses.

Procedure

Initial Training. Birds had to find their way to the seeds located at the back of the feeder.

To first identify the feeder as a source of food, sunflower seeds were laid out on the top of

the feeder and on its side ledges (Figure 1). Birds readily came to the feeder to collect these seeds, but initially they did not enter the feeder. Until all birds demonstrated that they would take seeds from the seed tube inside the feeder, additional seeds were provided each day in the late afternoon. This seemed necessary to ensure that all birds obtained sufficient internal reserves to survive the overnight fast. This supplementary feeding was discontinued as soon as all birds were taking seeds from the tube. At this point, the automated feeder and the maintenance diet were the only sources of food provided to the birds. The seed tube was filled each day, and the maintenance diet was replenished every few days. However, birds were rarely observed to eat the maintenance diet, and the level in each cup was usually not noticeably depleted.

Assessment of Social Dominance. In the present study social dominance was defined in terms of competition for food resources. Observations of competitive interactions between pairs of birds were made between November 1998 and February 1999. A tray of black-oil sunflower seeds was placed in the aviary prior to an observation session. All interactions that involved a single pair of birds at the seed tray were recorded. Bird A was considered to have dominated Bird B if A chased B away from the tray (flight chase), if A hopped towards B and caused B to leave the tray, or if A turned towards B and this caused B to leave. Following Piper and Wiley (1990), one bird was considered dominant to another if it won at least 75% of its interactions with that individual.

Observations of food-caching and eating. Estimates of the time required to cache and to eat a single seed were made by direct visual observation. Observations were made in two periods, the first between October 14-16 1998 and the second between January 2-4 1999. All observations were made from an observation window at one end of the aviary.

Daytime temperatures recorded in the aviary ranged between +5 and +15 °C during the October observation period and between –5 and –15 °C during the January period.

Observations began when a bird entered the feeder. A stopwatch was used to time the behavior of the bird from the instant it left the feeder until its return. It was noted whether the bird consumed or cached the seed that it took from the feeder. The bird was observed for the entire period between feeder visits, unless the observer lost sight of it. A cache occurred when the focal bird cached the seed, whether it did so immediately or after an interruption (caused, for example, by dropping the seed, or by being chased by another bird). The same interruptions could occur with eating as long as the ultimate outcome was that the focal bird ate the seed it took from the feeder. The only exception to this classification system was the instance of a bird partially eating a seed and then caching it. Such cases where the same seed was both eaten and cached were rare, but, nonetheless, were discarded by the observer. These observations resulted in two distributions for each bird: one of times required to eat a seed and another of times required to cache a seed.

The data-file created by the custom software contained a chronological record of the date and time each bird took a seed from the feeder; the majority of feeder visits were not directly observed by the investigator. To classify unobserved feeder visits as representing either eating or caching of a seed, a statistical rule for two-group discrimination (Marascuilo & Levin, 1983) was applied to each bird's distributions. For each bird the result was a "cut-off" time, which was used to separate intervals between unobserved visits (intervisit-intervals) into caches and eats. Intervisit-intervals below the cut-off time were classified as caches. No bird was ever observed to enter the feeder to the point of the detector and leave without taking a seed. Eats could not be classified

simply as those intervals above the cut-off time, because many intervals were very long and probably reflected the termination of a particular foraging bout. An upper time limit was, therefore, determined for each bird as being that value two standard deviations above the mean for the distribution of observed eat times. Thus, unobserved intervisit-intervals that fell between the cut-off time for caches and this upper limit were classified as eats. Data were collected during January and February, 1999.

RESULTS

One bird died during training, thus, only data from three birds are presented here. All statistical analyses were performed with SPSS 9.0 for Windows.

Social Dominance.

In all, 79 competitive interactions involving a single pair of birds were observed. The outcomes of these interactions were arranged in a dominance matrix (Table 2). OW won 97 % of its contests with GR, and 100% of its contests with GY. GR won 100% of its contests with GY. Thus, the birds were arranged in order of most to least dominant: OW, GR, and GY. These birds will also be described in the text as the α -, β -, and γ -birds, respectively to indicate their dominance rank.

Directly Observed Caches and Eats. For each bird the distributions of times required to eat or to cache a single seed showed little or no overlap (Figures 2-4). The mean time required by the α -, β -, and γ -bird to eat a seed was 81.32 s (SD = 31.15), 98.44 s (SD = 40.41), and 91.20 s (SD = 34.75), respectively. Caching, however, required much less time. The mean cache times for the α -, β -, and γ -birds were 20.37 s (SD = 9.81), 24.35 s (SD = 7.83), and 21.5 s (SD = 7.67), respectively. For each bird, two independent t-tests

Table 2. Matrix of the outcomes of competitive interactions between pairs of birds during the observation period (November 1998 to February 1999).

	OW	GR	GY
OW	---	33	30
GR	1	---	15
GY	0	0	---

Note. Individuals are identified by their colored leg bands. Row entries describe the winner in competitive interactions, and column entries describe the loser. For instance, OW won 33 competitive interactions with GR. GR won 1 competitive interaction with OW.

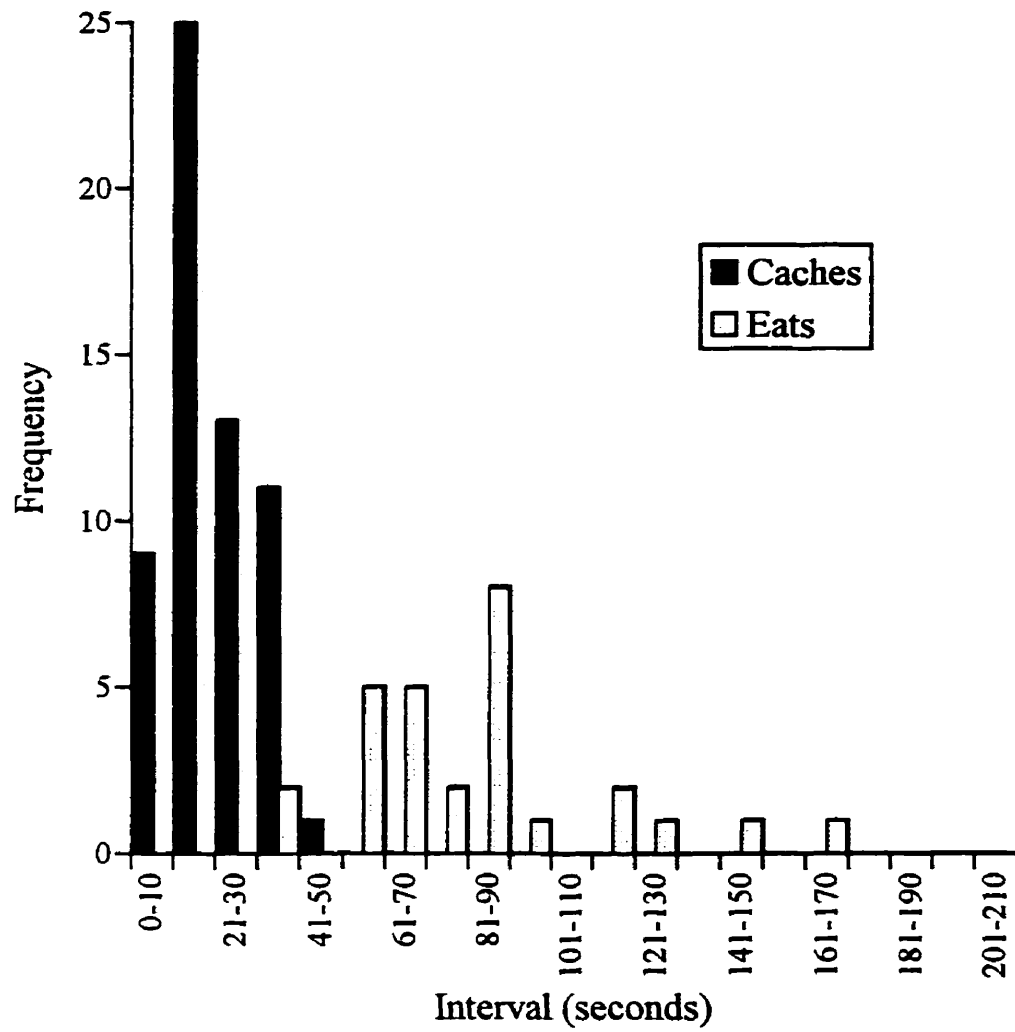


Figure 2. OW's distribution of times required to cache and to eat a seed taken from the feeder.

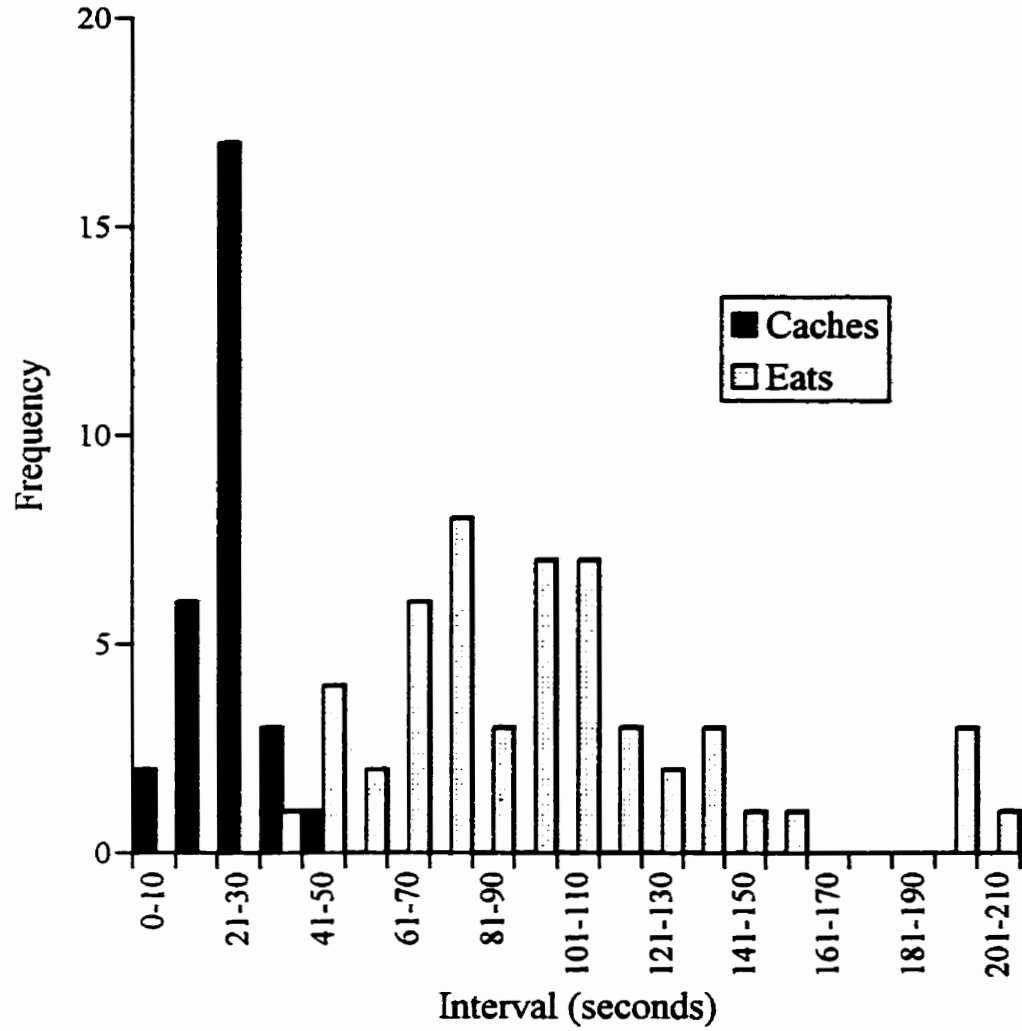


Figure 3. GR's distribution of times required to cache and to eat a seed taken from the feeder.

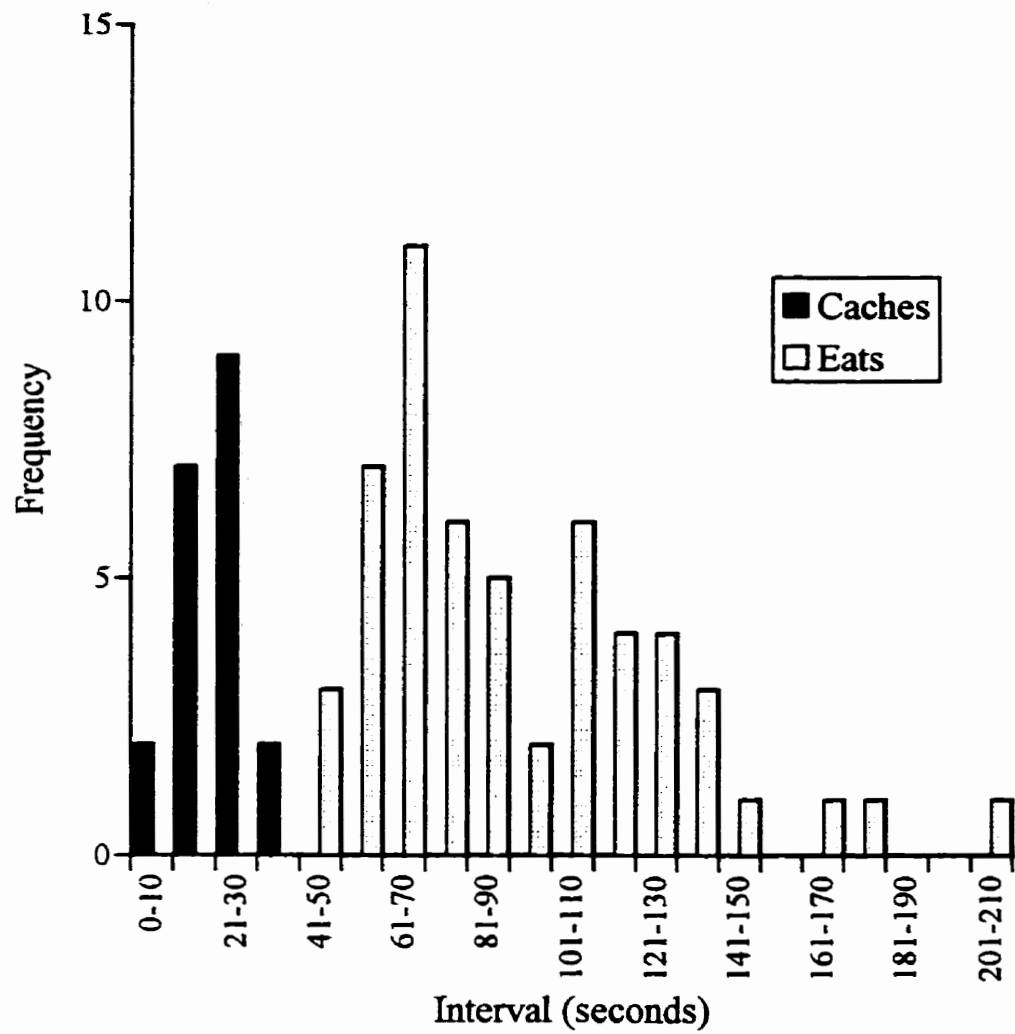


Figure 4. GY's distribution of times required to cache and to eat a seed taken from the feeder.

were used to compare eat and cache intervals between observation periods. In no case was there a significant difference between the two periods in the amount of time required to eat or to cache a seed. Thus, data from both observation periods were pooled for each bird to obtain cut-off times.

For each bird, the following statistical rule (Marascuilo & Levin, 1983) was used to obtain a criterion time for classifying unobserved feeder visits as representing either eating or caching of a seed:

$$C = [N_e(X_e/SD_e) + N_c(X_c/SD_c)] / [(N_e/SD_e) + (N_c/SD_c)],$$

where N_e is the number of observed eats, N_c is the number of observed caches, X_e and X_c are the mean eat and cache times respectively, and SD_e and SD_c are the standard deviations of the eat- and cache-time distributions. The cut-off times obtained for the α -, β -, and γ -birds were 28, 43, and 47 seconds respectively. Thus, intervisit-intervals (IVIs) in the automated record that were below a bird's cut-off time were classified as caching of a seed taken from the feeder (as described in the METHODS). For each bird, any IVI that was greater than its cut-off time but less than two standard deviations above its mean eat-time was classified as eating of a seed taken from the feeder. The upper limit on IVIs classified as eating was imposed to eliminate long intervals that could not reasonably be classified as eating or caching.

Automated Record of Feeder Visits

Food-Caching and Eating.

For each of the three birds, two measures related to feeding were obtained: number of seeds eaten per day, and number of seeds cached per day. These results are shown in Figure 5. Multivariate analysis of variance showed a significant effect of bird for

these two variables taken together ($F(2,149) = 133.52, p < .01$). Significant univariate differences among birds on the two variables were also obtained (Caches: $F(2,150) = 22.36, p < .01$; Eats: $F(2,150) = 43.27, p < .01$). Tukey's HSD tests were conducted to test the differences between birds on the two measures. Only the differences between the α -bird and β -bird (Caches: $q(3,150) = 8.39$; Eats: $q(3,150) = 10.95$) and between the α -bird and the γ -bird (Caches: $q(3,150) = 7.98$; Eats: $q(3,150) = 11.79$) were significant ($p's < .01$). Differences between the two subordinate birds in daily caching and eating were not significant. Daily monitoring of the food in the aviary indicated that birds were not using the maintenance diet.

Interestingly, the bi-modal shape of the directly observed distributions were not as apparent when each bird's distribution of unobserved feeder intervals was plotted for the month of February (Figures 6-8). The α -bird's distribution is clearly uni-modal (Figure 6). The β -bird's distribution shows an initial peak between 11-20 seconds (Figure 7). However, the γ -bird's distribution is clearly bi-modal. These data suggest that it would be useful to collect a larger sample of observations of eating and caching with which to predict unobserved feeder visits. The shapes of the distributions will also be affected by seasonal differences in caching intensity. Thus, direct observations need to be collected on a monthly basis.

Temperature and Daylength.

Each day three measures of environmental condition were calculated. Mean daily temperature was defined as the average temperature between sunrise and sunset for each day. Mean overnight temperature was defined as the average temperature between sunset of the previous day and sunrise of the current day. Daylength was defined as the number

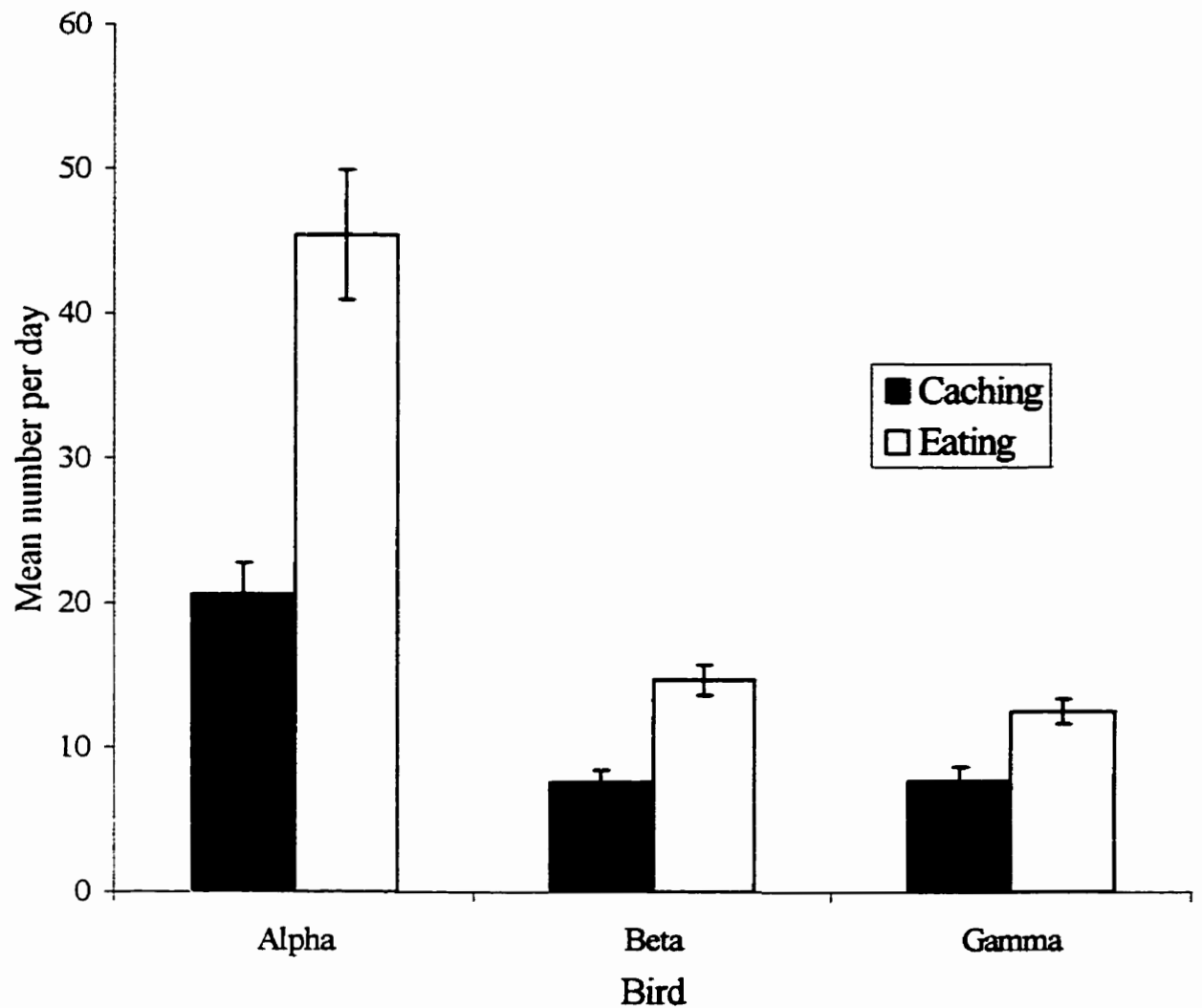


Figure 5. Mean number of seeds cached and eaten per day by the three birds. Solid bars show the mean number of seeds cached. Open bars show the mean number of seeds eaten. The error bars show the standard error of measurement.

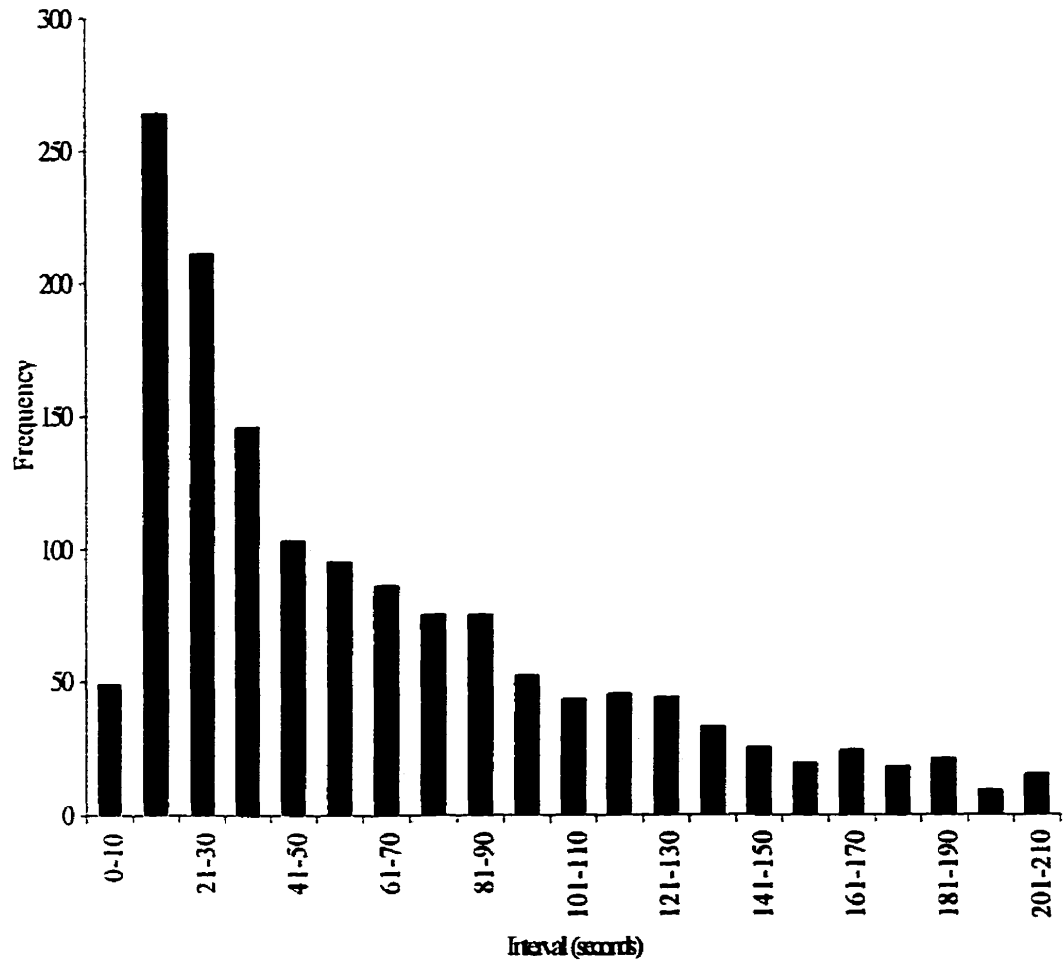


Figure 6. Distribution of unobserved feeder intervals during February for OW (α -bird).

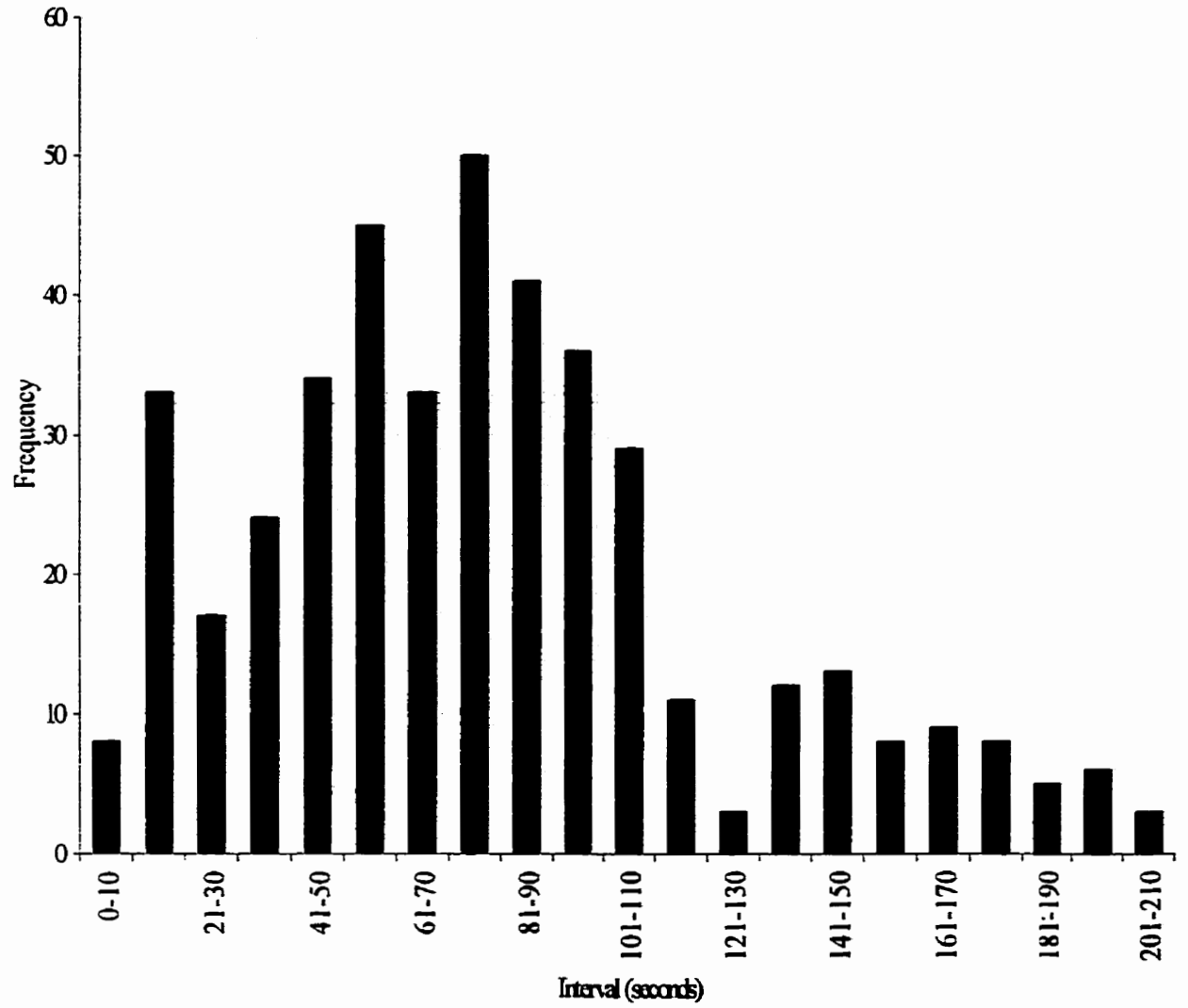


Figure 7. Distribution of unobserved feeder intervals during February for GR (β -bird).

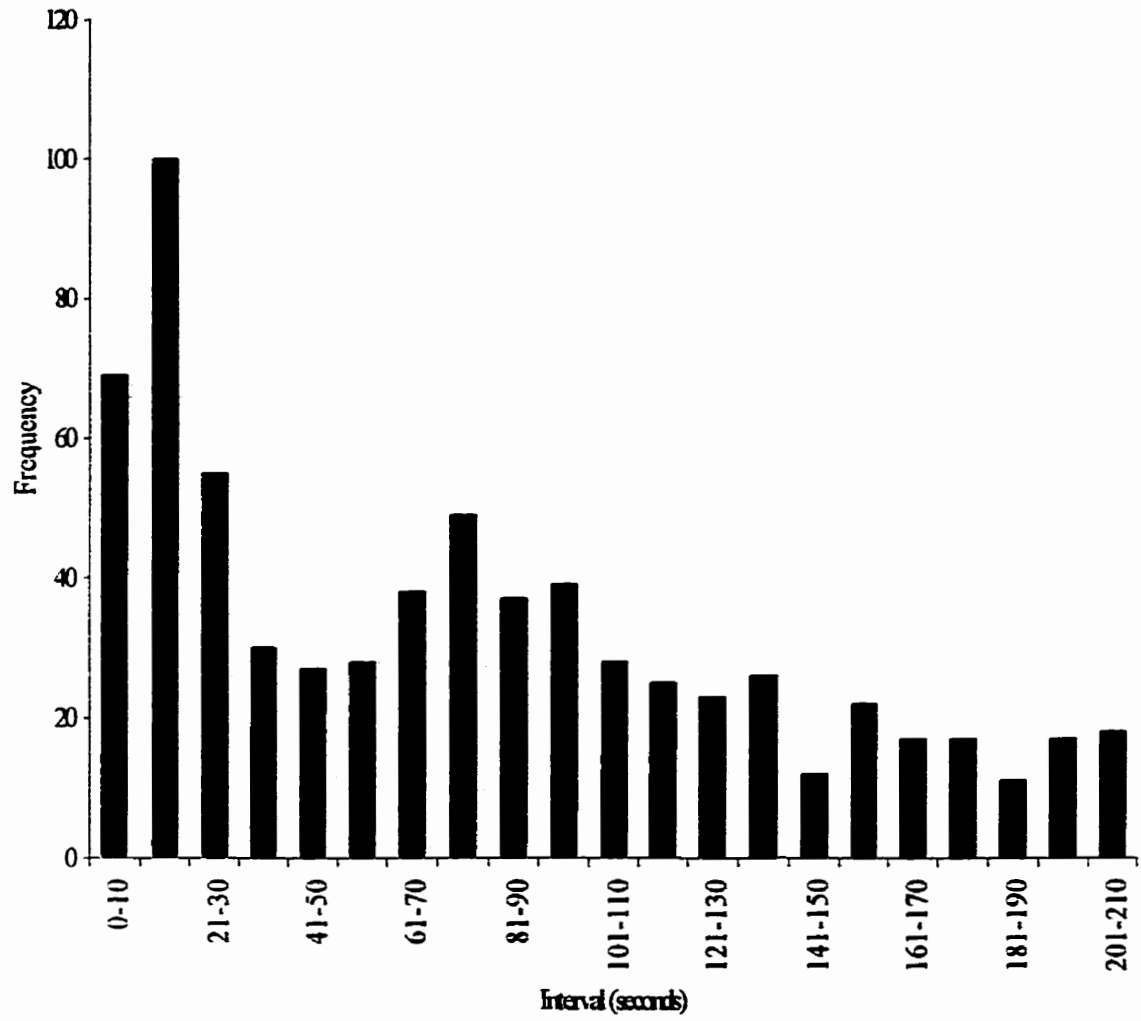


Figure 8. Distribution of unobserved feeder intervals during February for GY (γ -bird).

of hours between sunrise and sunset. For each bird two stepwise linear regressions were performed, one with total daily caches as the dependent variable and the three environmental variables as independent variables and the other with the same set of independent variables and total daily eats as the dependent variable.

Food-caching. There was no statistical relationship between total daily caches and any of the environmental variables for the α -bird. For the β -bird, the regression analyses produced an equation in which two variables, daylength and mean overnight temperature, were associated with daily caching. The multiple correlation between these two predictors and daily caches was significant ($R = .71$; $F(2, 48) = 24.37$, $p < .01$). Together these two variables accounted for 50.4% of the variance in total daily caches; however, most of this variance (44.2%) was accounted for by daylength alone. Increases in daylength and mean overnight temperature were associated with decreases in the number of caches made each day. The simple correlations between daily caches and daylength ($r = -.67$) and daily caches and overnight temperature ($r = -.48$) were both significant ($p < .01$). Figures 9 and 10 show scatterplots of daily caching and daylength and mean overnight temperature for the β -bird. For the γ -bird, daylength and mean daily temperature were significantly associated with total daily caches ($R = .58$; $F(2, 48) = 12.28$, $p < .01$). Together these two variables accounted for 33.9% of the variation in total daily caches, however most of this variation (27.8%) was accounted for by daylength alone. Although the best regression equation included mean daily temperature, there was no relationship between total daily caches and this variable alone ($r = .01$, $p > .4$). As was the case for the β -bird, daylength was most strongly associated with food caching; however, for the γ -bird this relationship

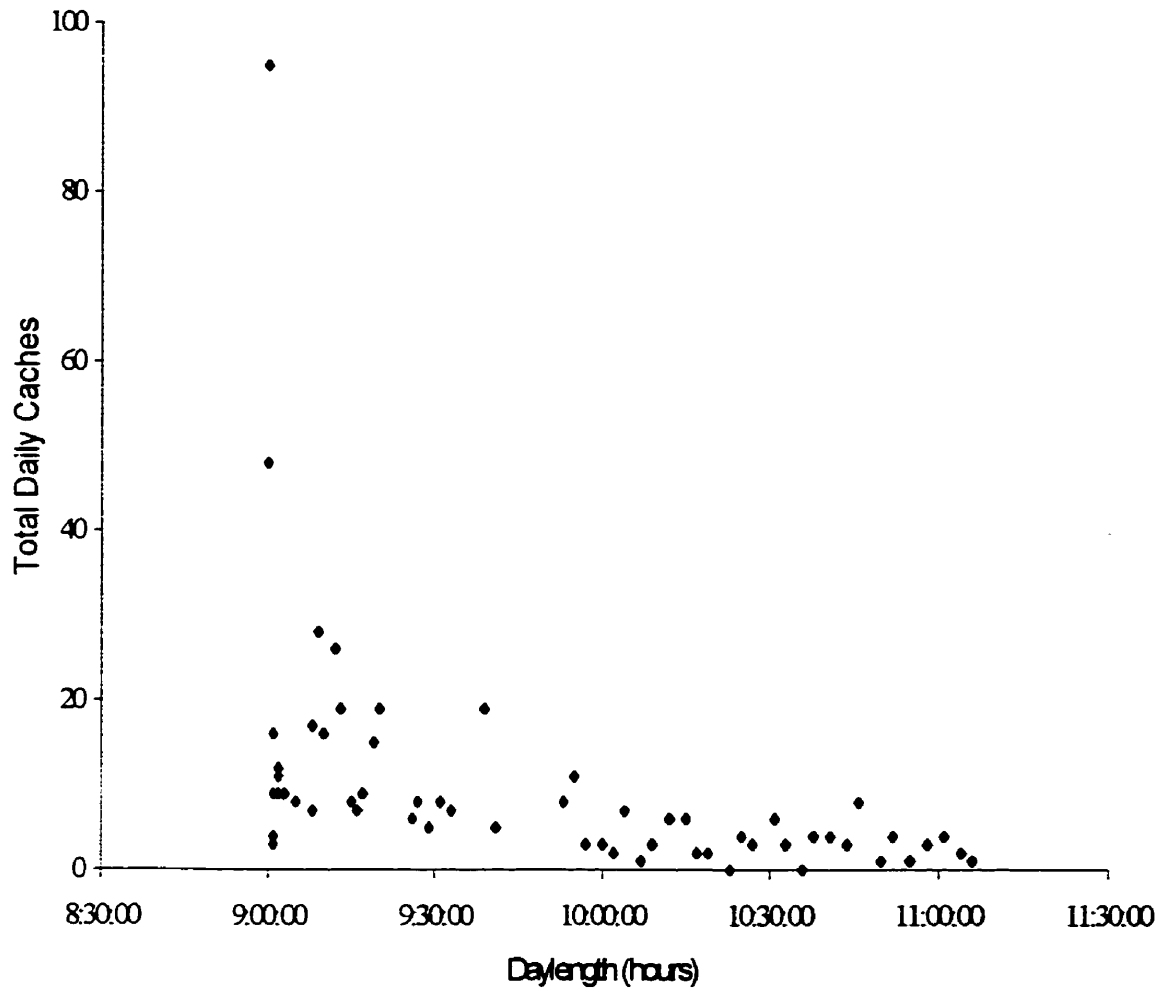


Figure 9. Scatterplot of total caching per day relative to daylength for the β -bird.

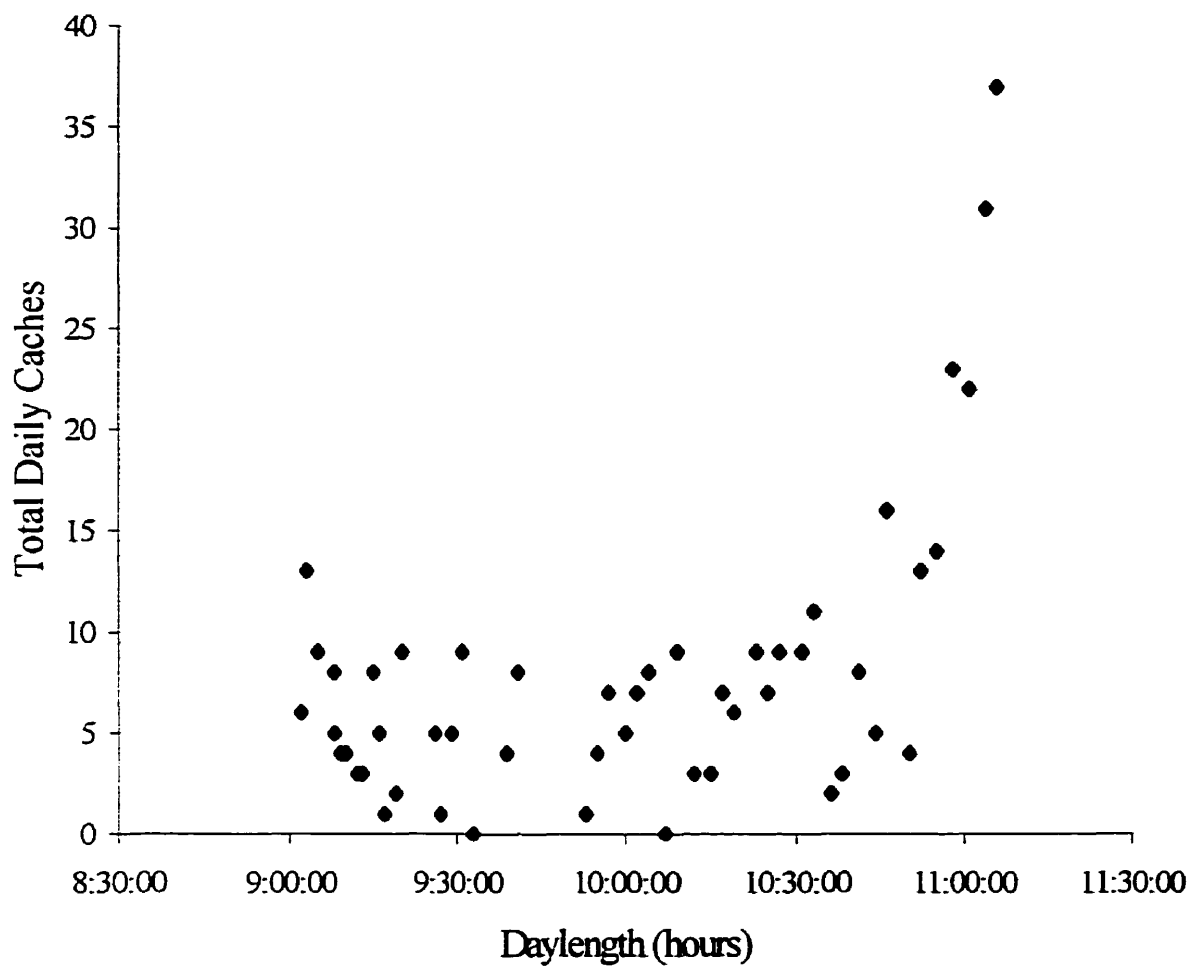


Figure 11. Scatterplot of total caching per day relative to daylength for the γ -bird.

was positive ($r = .53, p < .01$). Figure 11 shows a scatterplot of food-caching and daylength for the γ -bird. The scatterplot suggests that the direction and significance of the relationship is probably due to the last 7 days of the period when this bird cached most intensively. These last seven days are the longest days of the period, as daylength gradually increased through the study period.

The influence of environmental factors on food-caching differed according to social rank. For the α -bird, there was no statistical relationship between these variables. Both subordinate birds were influenced primarily by daylength, but the nature of this influence differed between birds. Increases in daylength were associated with decreases in food-caching by the β -bird, but were associated with increases in food-caching by the γ -bird. However, in the case of the γ -bird, for the majority of the study period there seemed to be no clear relationship between food-caching and daylength (Figure 11).

Eating. For the α -bird, the best regression equation included only mean daily temperature as a significant predictor of total daily eats ($R = .37; F(1,49) = 7.70, p < .01$). This variable was negatively correlated with eating ($r = -.37$) and accounted for 13.6% of the variance in eating. For the β -bird, only daylength was significantly associated with total daily eats ($R = .43; F(1,49) = 10.92, p < .01$). Daylength was negatively correlated with daily eating ($r = -.43$) and accounted for 18.2% of the variance. There was no significant relationship between total daily eats and any of the predictor variables for the γ -bird. Figures 12 and 13 show scatterplots for the α -, and β -birds.

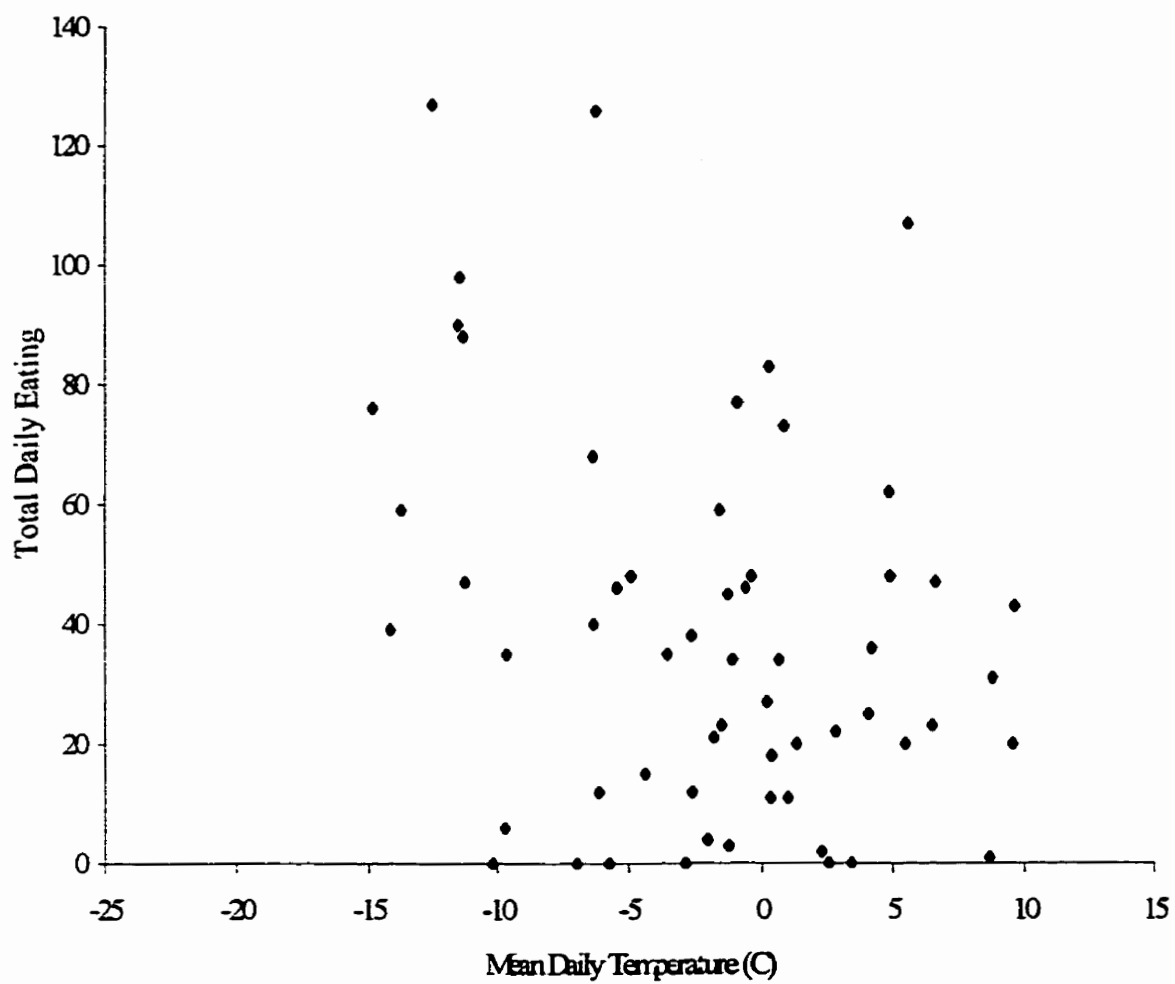


Figure 12. Scatterplot of total eating per day relative to mean daily temperature for the α -bird.

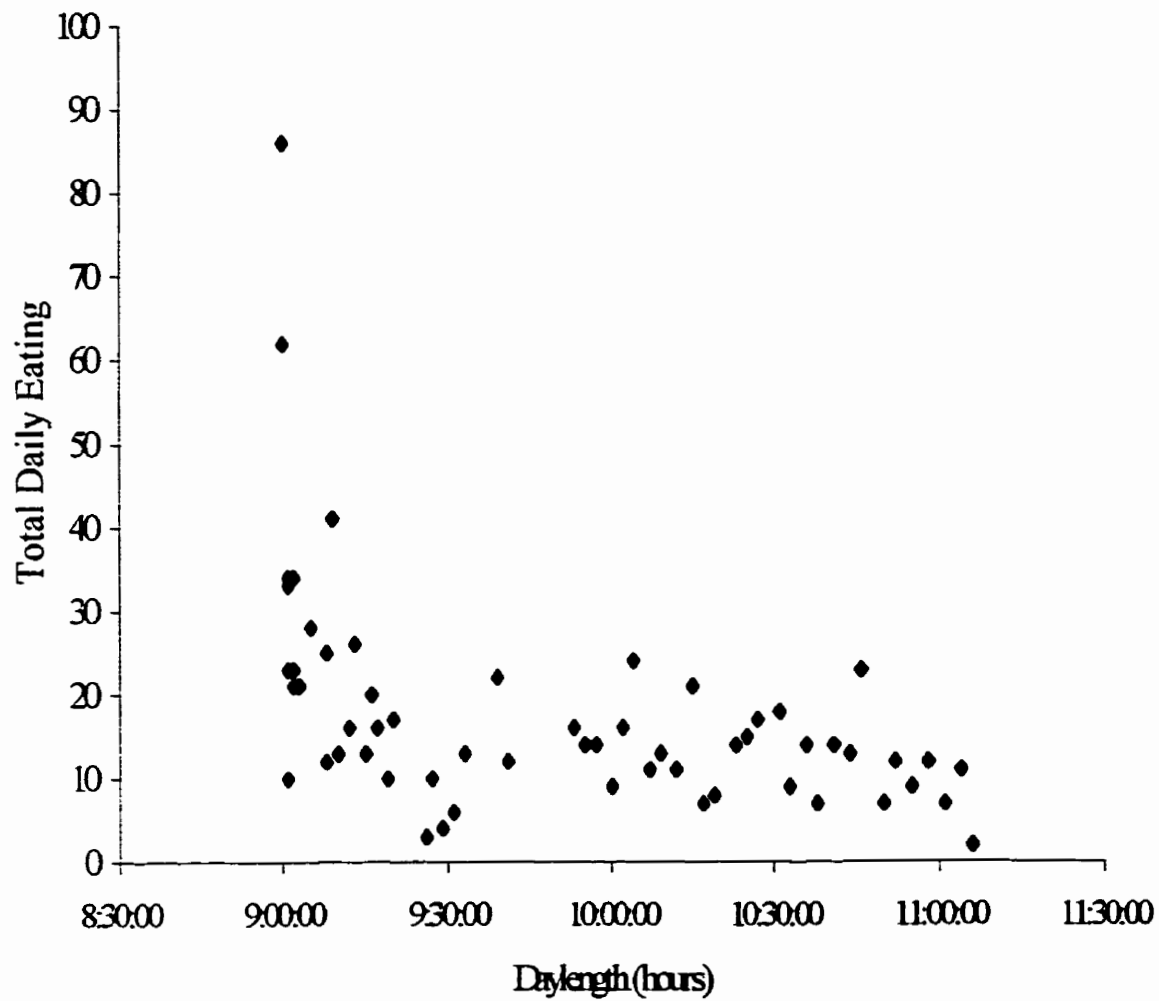


Figure 13. Scatterplot of total eating per day relative to daylength for the β -bird.

Within-Day Patterns in Food-caching and Eating

Each day was divided into five equal time periods, which began at sunrise and ended at sunset. The five periods were labeled early morning, late morning, midday, early afternoon, and late afternoon. Every day for each bird the proportion of the bird's total caches and eats that occurred in each division was calculated. This provided an indication of the relative amount of caching and eating that occurred in each division in the daily foraging routines of the birds. To determine whether there were differences across birds in the proportions cached and eaten at different times of day, a repeated measures ANOVA was conducted with division of the day as the factor.

Food-caching. There was no overall effect of division of the day on caching ($F(4,8) = 1.48, p > .3$). Inspection of Figure 14 reveals some striking differences between birds in their daily patterns of food-caching. The α -bird cached, on average, a roughly uniform proportion (20-24%) of the day's total caches in the first four divisions of the day. Caching, however, dropped dramatically in the late afternoon, such that less than 10% of its days caches were made in this division. The β -bird displayed two daily minima in caching, one during the late morning and another in late afternoon. Maximal caching occurred in the early morning, when 29% of its daily caches were stored. The γ -bird stored most seeds during the afternoon, particularly during the early afternoon (26%). Minimal caching occurred during the late morning (13%).

Comparing birds, differences in the late morning and late afternoon are most noticeable. In the former division, the β -bird and to a lesser extent the γ -bird, reduced caching from the previous division, while the α -bird actually cached a slightly greater proportion of seeds in late morning than in the previous division. In the last division

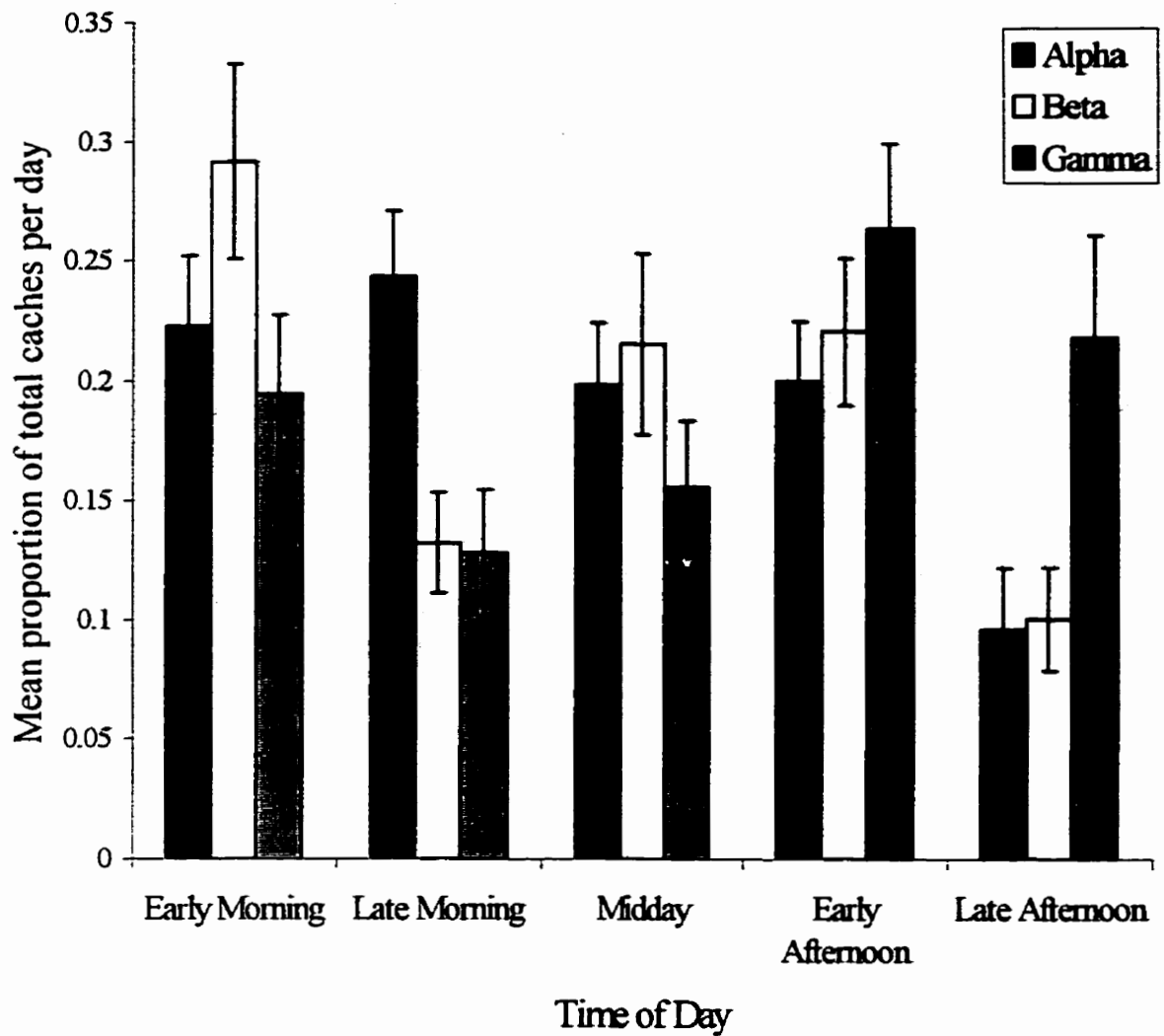


Figure 14. Within-day patterns in food-caching by the α -, β -, and γ -birds. Each bar shows the proportion of a bird's total daily caches that were made in each division. The solid bars show the α -bird's daily pattern, the empty bars show the β -bird's daily pattern, and the hatched bars show the γ -bird's daily pattern. Error bars show the standard error of measurement.

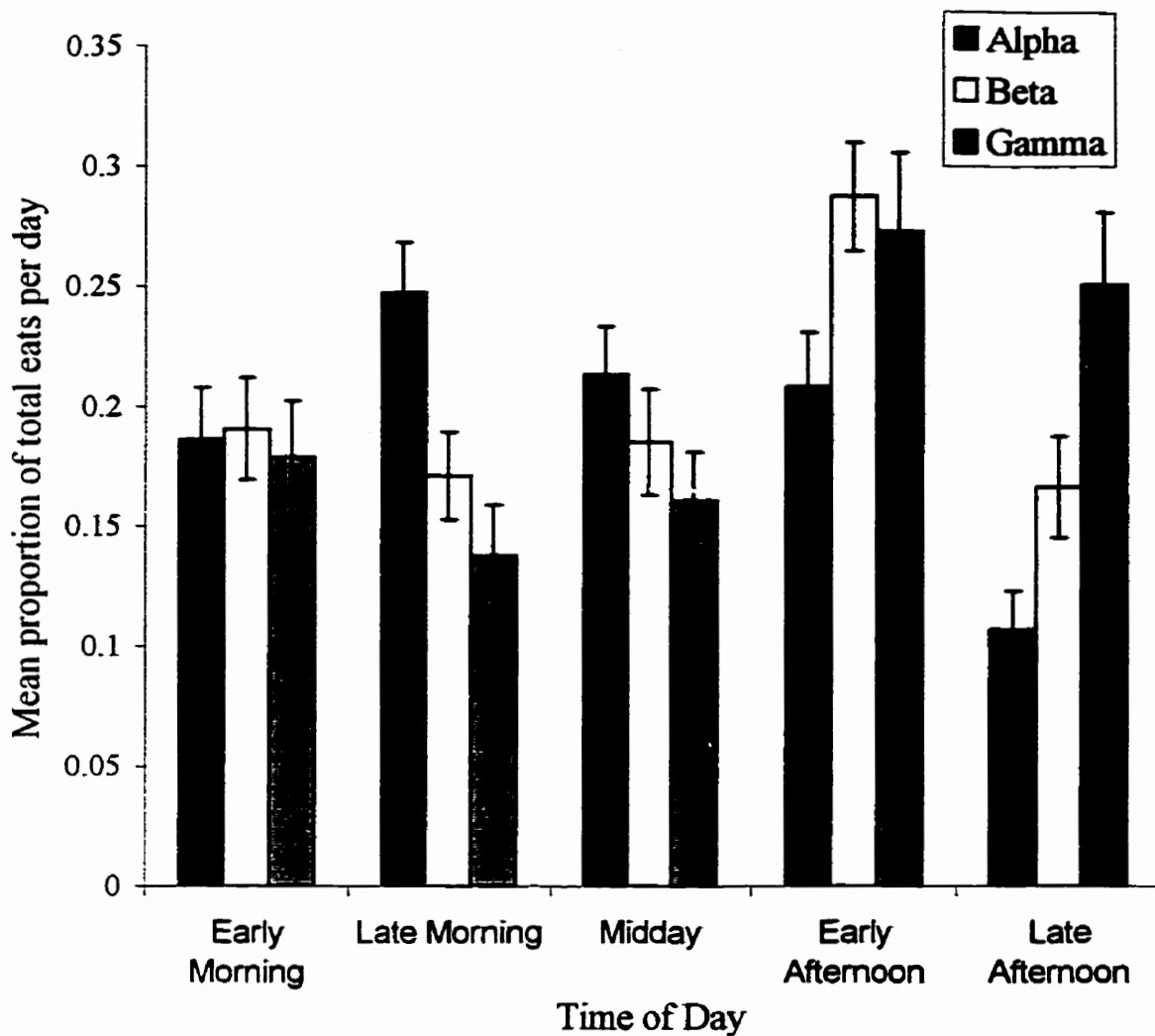


Figure 15. Within-day patterns in eating by the α -, β -, and γ -birds. Each bar shows the proportion of a bird's total daily eats that were made in each division. The solid bars show the α -bird's daily pattern, the empty bars show the β -bird's daily pattern, and the hatched bars show the γ -bird's daily pattern. Error bars show the standard error of measurement.

before sunset, the α - and β -birds cached many fewer seeds than in the previous division.

However, the γ -bird more or less maintained its high levels of caching.

Eating. As with caching, there was no overall effect of division on eating ($F(4,8) = 1.22$, $p > .3$). Each bird's pattern of eating is shown in Figure 15. The α -bird distributed eating through the day in much the same way it distributed caching: roughly equal proportions of total eats occurred in all but the last division of the day, when little eating occurred. In both cases, the daily peak occurred in the late morning. The β -bird ate in equal proportions in the first three divisions of the day, but ate the greatest proportion of its days seeds in the early afternoon. A large drop in eating in the last division followed this peak. An early afternoon peak in eating is also striking in the behavior of the γ -bird whose daily pattern of eating mirrored its pattern of caching: little in the early morning, late morning, and midday periods, followed by increased eating and caching during the afternoon divisions.

Body Weight

Owing to the behavior of the bird on the perch, not all body weight records were usable. For instance, the β -bird rarely sat on the perch, opting instead to hop down on the floor of the feeder to reach up for seeds. As a result, too few body weights were recorded for this bird to permit analysis. Similarly, few usable body weight readings are available for the γ -bird during the month of January. Together, several hundred usable body weight records were obtained for the γ -bird during February and for the α -bird during both January and February. Thus, direct comparisons between these birds were possible during February.

Overall Body Weight and Daily Weight Gain.

The α - and γ - birds maintained the same body weights through February (12.03 g, $SD = .32$; 11.99 g, $SD = .23$). An independent samples t-test confirmed that no differences existed between birds ($t(45) = .43$, $p > .6$). Interestingly, despite the differences in eating and caching between birds, they showed essentially the same pattern of weight gain through the day (Figure 16).

Temperature and Daylength.

To investigate the relationship, if any, between body weight and environmental conditions stepwise linear regressions were performed. For the α -bird there were 46 days in the study period for which sufficient data existed (at least 1 weight record in each division) to calculate mean daily body weight. For the γ -bird 22 such days existed in February. Thus, an analysis of the regression of mean daily body weight on mean overnight temperature, mean daily temperature and daylength was conducted separately for each of these birds.

For the α -bird, only daylength was significantly related to body weight ($R = .64$; $F(1,44) = 29.66$, $p < .01$). This variable accounted for 40.3% of the variance in mean daily body weight and the two variables were negatively correlated ($r = -.64$). For the γ -bird daylength and mean overnight temperature were both significantly related to mean daily body weight ($R = .86$; $F(2,21) = 26.55$, $p < .01$). Individually, daylength and mean overnight temperature accounted for 25.8% and 47.8% of the variance in body weight. The simple correlations of mean daily body weight with daylength and overnight temperature were $-.51$ and $.47$, respectively.

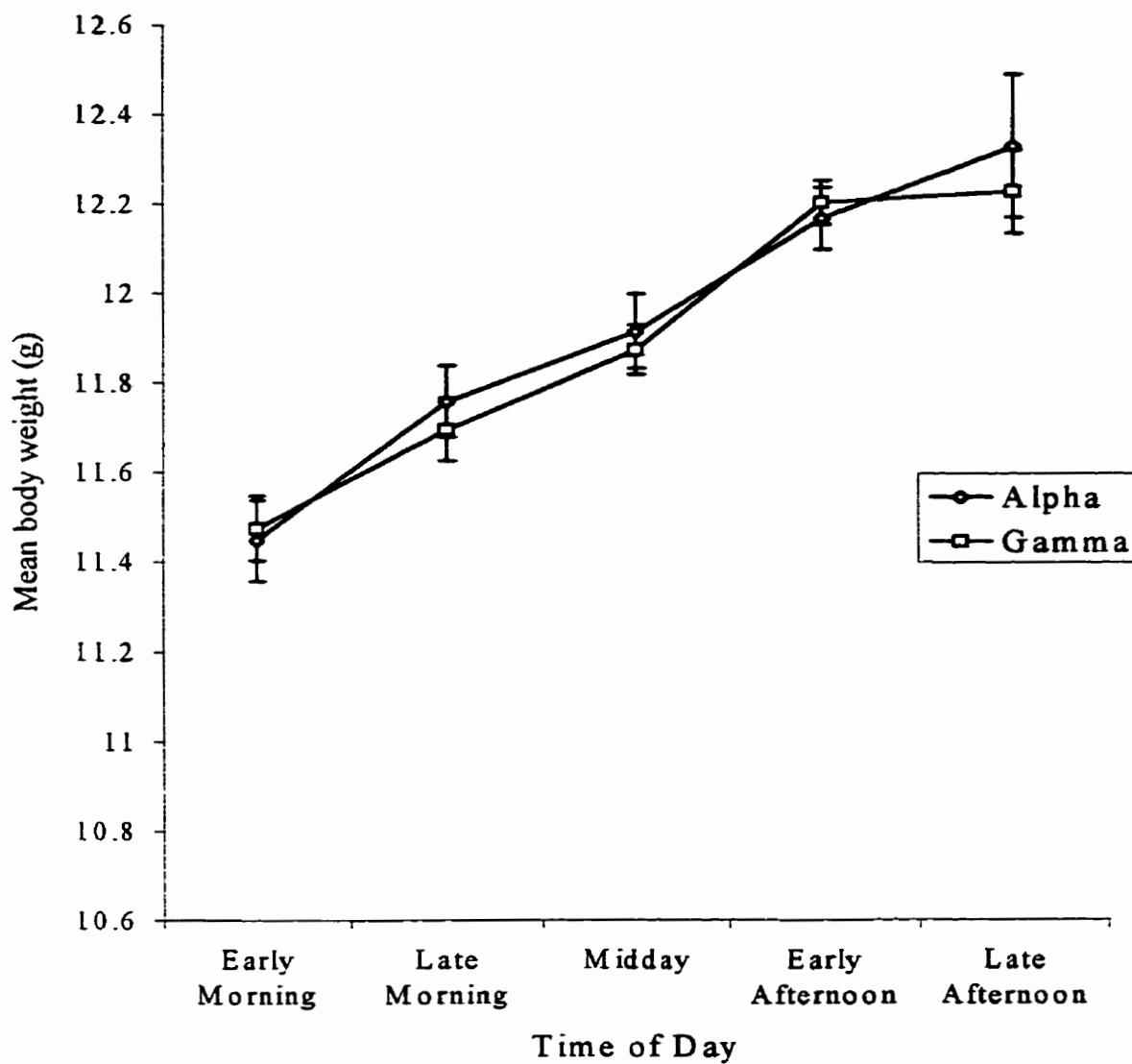


Figure 16. Mean daily gain in body weight for α - and γ -birds during February. Each point represents the mean body weight for that division of the day. Error bars show the standard error of measurement.

DISCUSSION

The purpose of the present study was to investigate the influence of social dominance on the simultaneous expression of food-caching and body weight in black-capped chickadees exposed to winter conditions. This study has an obvious limitation: sample size is small. Despite this limitation, the methods reported here produced a great deal of data, and the method itself is a novel approach to collecting this type of data.

Food-caching and eating.

A strongly linear dominance hierarchy characterized the flock and the data clearly show that the most dominant bird had priority of access to the feeder. That high dominance status confers this benefit is well supported in field and laboratory studies of social dominance: dominant individuals have been shown to feed before subordinates, to consume food at higher rates than subordinates, to spend more time feeding than subordinates, and to exclude subordinates from the best foraging microhabitats (Ekman & Lilliendahl, 1993; Koivula & Orell, 1988; Lahti et al., 1998; Piper, 1997). The α -bird also cached more seeds than the lower ranking birds. Lahti et al. (1998) have shown that among free-ranging willow tits, dominant individuals store food more intensively during the winter than do subordinates. That these results are in agreement with behavior in the wild suggests that the protocol used here succeeded in capturing elements of the natural environment.

Interestingly, the differences in overall caching and eating between the two subordinate birds were not large. The β -bird ate slightly more than the γ -bird, but this pattern was reversed slightly with respect to caching. If dominance status was perfectly related to these foraging behaviors greater separation between these two birds would be

expected. One explanation for this finding is that in the relatively small space of the aviary the α -bird could easily control the feeder.

While the quantitative differences between birds are striking, the relative ratios of caches:eats for each bird are also informative. For instance, for every seed eaten the α -, β -, and γ -birds cached .45, .51, and .61 seeds respectively. This suggests that caching may have been more important for the lower rank birds, and especially the γ -bird, than it was for the α -bird. The β and γ birds may have been balancing two different tactics: taking seeds to be consumed immediately because the α -bird limited their use of the feeder for eating, and caching seeds that they could retrieve when access to the feeder was denied by the α -bird.

The daily patterns of food-caching and eating suggest that the birds were using different strategies of accumulating energy. The α -bird used the feeder for eating and caching consistently from sunrise to early afternoon. It was particularly active during the late morning and used the feeder sparingly during the late afternoon. The subordinate birds' reliance on the feeder was much more variable with time of day. Both birds reduced their use of the feeder during the late morning, and increased their use of the feeder in the last two divisions of the day. The obvious exception to this is the early morning peak in food-caching exhibited by the β -bird. These patterns make some sense if the proportions shown in Figures 14 and 15 are translated into actual seeds eaten and cached. For instance by midday during the winter the α -, β -, and γ -birds had eaten approximately 65%, 54%, and 48% of the seeds they would eat by the end of the day. However, these proportions represent very different amounts of food (about 31, 8, and 6 seeds

respectively). Not surprisingly then, the low rank birds relied on the feeder most heavily as sunset approached. Interestingly, the β -bird cached most heavily in the early morning, perhaps to secure food to consume in the early part of the day when the dominant controlled the feeder. The results of several studies of daily caching patterns have been equivocal. Some species have demonstrated peak caching in the morning (Waite & Grubb, 1988) but others have shown peaks at midday (Lucas & Walter, 1991), in the afternoon (Pravosudov & Grubb, 1997b) or inconsistent patterns (Hurly, 1992). Such disparate results may reflect differences in experimental design and whether birds were held indoors or in outdoor aviaries. The present results show that social dominance can influence within-day patterns of caching. This suggests that dominance rank may be a factor influencing the patterns observed in other studies.

The notion that the birds used different strategies to acquire sufficient reserves is further supported by the quantitative differences in food-caching and eating: subordinate birds must have relied on food outside of the automated feeder. Because, the maintenance diet provided in bowls in the aviary was rarely used, low rank birds must have relied on cache pilferage to obtain food. Because the dominant bird created the majority of caches it is likely that it was the main victim of pilferage. Cache pilferage could not be quantified in the present study, but, individuals were observed to steal food stored by other birds and given the size of the aviary, pilferage was probably quite high. In the wild, caches are always at risk due to the presence of diurnal and nocturnal animals. Experimental investigations of cache pilferage have demonstrated that animals compensate for loss of caches. For instance, Hampton and Sherry (1992) showed that Black-capped chickadees could learn to avoid storing food in areas of an aviary where stored food was always

removed by the experimenters. Perhaps more relevant to the present study is the finding that Carolina chickadees increased caching intensity under conditions of pilferage as compared to no pilferage (Lucas & Zielinski, 1998). This finding begs the question whether the dominant bird in the present study responded to cache pilferage in a similar manner. In other words, was the high caching intensity of the dominant bird, in part, a response to high rates of cache loss? This cannot be answered by the present data, but it would clearly be important to determine whether the high levels of caching demonstrated by the α -bird were influenced by high rates of cache loss.

The influence of environmental conditions on food-caching and eating was inconsistent. Overall, the β -bird seemed to be most influenced by environmental factors because both its caching and eating were negatively related to daylength and there was a slight effect of overnight temperature on eating. Although, the γ -bird's caching behavior was related to daylength, this was probably due to an increase in caching during the last week in February. Thus, for the majority of the winter period the γ -bird did not respond to changes in environmental conditions in terms of eating and caching behavior. The α -bird's eating, but not caching was influenced by daily temperature. These findings suggest that the α - and β -birds were able to adjust their behavior in response to environmental conditions. The γ -bird did not make such adjustments, at least through the use of the automated feeder, and may have been most influenced by what the other birds were doing.

Body Weight.

Together the analyses of food-caching and eating suggest that the birds in the present study adopted different behavioral strategies to obtain sufficient reserves. What is clear from Figure 16, however, is that these strategies did not result in differences in the

levels of body weight obtained or in the daily gain of body weight. Considering only the differences in food-caching and eating between the α - and γ -birds, it might be expected that the γ -bird would have maintained lower body weight and a slower rate of daily weight gain than the α -bird.

The relationship between social status and body weight in small passerine birds is not clear in the literature. Some authors have found subordinates weigh less than dominants (Koivula et al., 1995; Piper & Wiley, 1990; Verhulst & Hogstad, 1996), but others have found the reverse to be true (Ekman & Lilliendahl, 1993; Hake, 1996; Witter & Swaddle, 1995). Despite differences in body weight between dominants and subordinates, some studies have shown equivalent rates of daily weight gain between dominance classes in free-ranging birds (Ekman & Lilliendahl, 1993). A common prediction in the literature is that subordinates will maintain higher reserves than dominants because, owing to the competitive ability of dominants, resources are more variable or unpredictable for subordinates (Clark & Ekman, 1995; Ekman & Lilliendahl, 1993; Witter & Swaddle, 1995). Since the behavioral data here certainly suggest that food availability was at least more variable for the lower ranking birds, what factors might explain the similarity in body weight?

Cache pilferage is the most plausible explanation for the absence of body weight differences in the present study: by obtaining food away from the feeder, low rank birds were able to maintain similar body weights and similar weight gains through the day. In fact, in a sense, to the low rank birds food availability may have been less unpredictable than the daily foraging routines suggest. That is, if day after day the α -bird controlled the feeder in the early parts of the day and used it sparingly in the final few hours before

sunset, the γ - and β -birds may have simply adopted a strategy of foraging away from the feeder until late in the day. To the extent that the α -bird's feeder use or defense was consistent, unpredictability may have been reduced for the subordinate birds.

In addition, one of the key factors hypothesized to affect internal energy levels was absent here. Because subordinates are often forced to forage in less safe habitats (Lahti et al., 1998; Piper, 1997), it has been suggested that the increased risk of predation associated with activity in these habitats (Koivula et al., 1994; Lahti et al., 1997) may cause birds to reduce their body weight below the level of dominants. Such reductions may result from delays in foraging time caused by the presence of predators (McNamara, Houston, & Lima, 1994) or may reflect the fact that being lean may improve a bird's chances of escaping a predator (Witter & Cuthill, 1993). In the present study, however, there were no differential risks of predation between habitats within the aviary; in fact, there was no risk of predation. That subordinates did not pay a price for foraging away from the central food source in terms of predation may have eliminated this downward pressure on body weight.

Both the α - and γ -bird showed changes in body weight that were associated with changes in environmental conditions. Both birds maintained smaller weights on longer days, a finding that has been shown with some European tits (Haftorn, 1989). One difference between the birds was in the relative importance of temperature. The average daily body weight of the α -bird was not associated with daily or overnight temperature, however, overnight temperature predicted the mean daily body weight of the γ -bird. This suggests that although on average the α - and γ -birds maintained similar body weights, the γ -bird was more affected by changes in overnight temperature than was the α -bird. Given

that this regression was based on only twenty-two data points these data should be interpreted cautiously.

Integrating Food-caching and Body Weight.

As noted earlier, recent interest in the expression of food-caching and body weight has been driven in part by a number of theoretical models that predict patterns of energy regulation in winter birds (e.g. Brodin & Clark, 1997; Clark & Ekman, 1995; Lucas & Walter, 1991; McNamara et al., 1990). Most of these models consider the simultaneous expression of food-caching and body weight under the influence of many factors, including weather conditions, food availability, predation risk, cache pilferage, and longevity of memory for caches. One prediction that has seldom been addressed empirically is that during the winter, food-storing birds will cache maximally at intermediate body weight (see Introduction). Lucas and Walter (1991) predict that intermediate body weight will be achieved at midday, but McNamara et al. (1990) predict birds will be at intermediate weights during the morning. Three of four Carolina chickadees that Lucas and Walter tested supported their prediction and cached maximally at midday. Some studies have shown peak caching in the morning (Waite & Grubb, 1988) supporting McNamara et al. (1990), but the prediction that birds will be at intermediate body weight during the morning has not been supported (Grubb & Pravosudov, 1994; Haftorn, 1989; Lehikoinen, 1987; Pravosudov & Grubb, 1997b). In the present study, the α - and γ -bird each displayed daily body weight gains as predicted by Lucas and Walter, but, each bird displayed a different diurnal pattern in caching and neither showed a clear peak in caching when they were at an intermediate body weight. This suggests that social dominance may

influence diurnal caching patterns. Future models should address the influence of social dominance in determining daily caching patterns.

Future Research.

Clearly additional data on a larger number of birds are required. In addition, cache pilferage needs to be quantified in order to shed light on how dominant and subordinate birds maintained similar internal reserves in this study. Ultimately, of course, it is natural variation in behavior that is of most interest. The protocol used here is novel and produced a very large sample of data for each individual. The utility of this method in the field depends most critically on whether the differences in time required to eat and to cache seeds by free-ranging animals are large enough to produce distributions similar to those obtained here. Preliminary data on Black-capped chickadees, collected in a local forest, suggest that this approach will transfer well to a field setting. Thus, this time-interval based approach may ultimately provide data on the influence of social dominance on energy regulation in free-ranging animals.

References

- Balda, R. P., & Kamil, A. C. (1992). Long-term spatial memory in Clark's nutcrackers, *Nucifraga columbiana*. *Animal Behaviour*, *44*, 761-769.
- Bednekoff, P. A., Biebach, H., & Krebs, J. (1994). Great tit fat reserves under unpredictable temperatures. *Journal of Avian Biology*, *25*, 156-160.
- Bednekoff, P. A., & Krebs, J. R. (1995). Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology*, *9*, 457-462.
- Blem, C. R. (1976). Patterns of lipid storage and utilization in birds. *American Zoologist*, *16*, 671-684.
- Blem, C. R. (1990). Avian energy storage. *Current Ornithology*, *7*, 59-113.
- Brodbeck, D. R. (1994). Memory for spatial and local cues: A comparison of a storing and a non-storing species. *Animal Learning & Behavior*, *22*, 119-133.
- Brodbeck, D. R., & Shettleworth, S. J. (1995). Matching location and color of a compound stimulus: Comparison of a food-storing and a non-storing bird species. *Journal of Experimental Psychology: Animal Behavior Processes*, *21*, 64-77.
- Brodin, A. (1993). Low rate of loss of willow tit caches may increase adaptiveness of long-term hoarding. *Auk*, *110*, 642-645.
- Brodin, A. (1994). The disappearance of caches that have been stored by naturally foraging willow tits. *Animal Behaviour*, *47*, 730-732.
- Brodin, A., & Clark, C. W. (1997). Long-term hoarding in the Paridae: A dynamic model. *Behavioral Ecology*, *8*, 178-185.
- Brodin, A., & Kunz, C. (1997). An experimental study of cache recovery by hoarding willow tits after different retention intervals. *Behaviour*, *134*, 881-890.

- Brown, M. E. (1996). Assessing body condition in birds. Current Ornithology, *13*, 67-135.
- Carrascal, L. M., & Moreno, E. (1993). Food caching versus immediate consumption in the nuthatch: The effect of social context. Ardea, *81*, 135-141.
- Carrascal, L. M., & Polo, V. (1999). Coal tits, *Parus ater*, lose weight in response to chases by predators. Animal Behaviour, *58*, 281-285.
- Chaplin, S. B. (1974). Daily energetics of the black-capped chickadee, *Parus atricapillus*, in winter. Journal of Comparative Physiology, *89*, 321-330.
- Clark, C. W. (1991). Modeling behavioral adaptations. Behavioral and Brain Sciences, *14*, 85-117.
- Cuthill, I. C., & Houston, A. I. (1997). Managing time and energy. In J. R. Krebs, & N. B. Davies (Eds.), Behavioural ecology: An evolutionary approach (pp. 97-120). Oxford, England: Blackwell Science Ltd.
- Ekman, J. B., & Clark, C. W. (1995). Dominant and subordinate fattening strategies: A dynamic game. Oikos, *72*, 205-212.
- Ekman, J. B., & Hake, M. K. (1990). Monitoring starvation risk: Adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behavioral Ecology, *1*, 62-67.
- Ekman, J. B., & Lilliendahl, K. (1993). Using priority to food access: Fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. Behavioral Ecology, *4*, 232-238.
- Enoksson, B. (1988). Age- and sex-related differences in dominance and foraging behavior of nuthatches *Sitta europaea*. Animal Behaviour, *36*, 231-238.

- Fagerstone, K. A., & Johns, B. E. (1986). Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife. Journal of Wildlife Management, *51*, 294-297.
- Gosler, A. G. (1996). Environmental and social determinants of winter fat storage in the great tit *Parus major*. Journal of Animal Ecology, *65*, 1-17.
- Grubb, T. C., & Pravosudov, V. V. (1994a). Ptilochronology: Follicle history fails to influence growth of an induced feather. Condor, *96*, 214-217.
- Grubb, T. C., & Pravosudov, V. V. (1994b). Toward a general theory of energy management in wintering birds. Journal of Avian Biology, *25*, 255-260.
- Haftorn, S. (1954). Contribution to the food biology of tits especially about storing of surplus food. Part I. The crested tit (*Parus c. cristatus* L.). Det Kgl Norske Videnskabers Selskabs Skrifter, *1953(4)*, 1-123.
- Haftorn, S. (1956a). Contribution to the food biology of tits especially about storing of surplus food. Part II. The coal-tit (*Parus a. ater* L.). Det Kgl Norske Videnskabers Selskabs Skrifter, *1956(2)*, 1-52.
- Haftorn, S. (1956b). Contribution to the food biology of tits especially about storing of surplus food. Part III. The willow-tit (*Parus atricapillus* L.). Det Kgl Norske Videnskabers Selskabs Skrifter, *1956(3)*, 1-79.
- Haftorn, S. (1956c). Contribution to the food biology of tits especially about storing of surplus food. Part IV. A comparative analysis of *Parus atricapillus* L., *P. cristatus* L. and *P. ater* L. Det Kgl Norske Videnskabers Selskabs Skrifter, *1956(4)*, 1-54.
- Haftorn, S. (1989). Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. Wilson Bulletin, *101*, 217-235.

- Haftorn, S. (1992). The diurnal body weight cycle in titmice *Parus* spp.. Ornis Scandinavica, 23, 435-443.
- Hake, M. (1996). Fattening strategies in dominance-structured greenfinch (*Carduelis chloris*) flocks in winter. Behavioral Ecology and Sociobiology, 39, 71-76.
- Hampton, R. R., & Sherry, D. F. (1994). The effects of cache loss on choice of cache sites in the black-capped chickadee. Behavioral Ecology, 5, 44-50.
- Hitchcock, C. L., & Sherry, D. F. (1990). Long-term memory for cache sites in the black-capped chickadee. Animal Behaviour, 40, 701-712.
- Hogstad, O. (1987). It is expensive to be dominant. Auk, 104, 333-336.
- Hurly, T. A. (1992). Energetic reserves of marsh tits (*Parus palustris*): Food and fat storage in response to variable food supply. Behavioral Ecology, 3, 181-188.
- Kallander, H., & Smith, H. G. (1990). Food-storing in birds: An evolutionary perspective. Current Ornithology, 7, 147-207.
- Koivula, K., Orell, M., Rytönen, S., & Lahti, K. (1995). Fatness, sex and dominance; seasonal and daily body weight changes in willow tits. Journal of Avian Biology, 26, 209-216.
- Koivula, K., Lahti, K., Rytönen, S., & Orell, M. (1994). Do subordinates expose themselves to predation? Field experiments on feeding site selection by willow tits. Journal of Avian Biology, 25, 178-183.
- Krebs, J. R., Healy S. D., & Shettleworth, S. J. (1990). Spatial memory of Paridae: Comparison of a storing and non-storing species, the coal tit, *Parus ater*, and the great tit, *Parus major*. Animal Behaviour, 39, 1127-1137.

- Lahti, K., Koivula, K., & Orell, M. (1997). Dominance, daily activity and winter survival in willow tits: Detrimental cost of long working hours? Behaviour, *134*, 921-939.
- Lahti, K., Koivula, K., Rytönen, S., Mustonen, T., Welling, P., Pravosudov, V. V., & Orell, M. (1998). Social influences on food caching in willow tits: A field experiment. Behavioral Ecology, *9*, 122-129.
- Lahti, K., & Rytönen, S. (1996). Presence of conspecifics, time of day and age affect willow tit food hoarding. Animal Behaviour, *52*, 631-636.
- Lehikoinen, E. (1987). Seasonality of the daily weight cycle in wintering passerines and its consequences. Ornis Scandinavica, *18*, 216-226.
- Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: Determinants of body weight in birds. Ecology, *67*, 377-385.
- Lima, S. L. (1988). Initiation and termination of daily feeding in dark-eyed juncos: Influences of predation risk and energy reserves. Oikos, *53*, 3-11.
- Lucas, J. R. (1994). Regulation of cache stores and body weight in carolina chickadees (*Parus carolinensis*). Behavioral Ecology, *5*, 171-181.
- Lucas, J. R., & Walter, L. R. (1991). When should chickadees hoard food? Theory and experimental results. Animal Behaviour, *41*, 579-601.
- Lucas, J. R., & Zielinski, D. L. (1998). Seasonal variation in the effect of cache pilferage on cache and body weight regulation in carolina chickadees: What are the trade-offs? Behavioral Ecology, *9*, 193-200.
- Ludescher, F. B. (1980). Fressen und verstecken von samereien bei der weidenmeise *Parus montanus* im jahreslauf under konstanten ernahrungsbedingungen. Okologie der Vogel, *2*, 135-144. [English translation]

- Mangel, M., & Clark, C. W. (1988). Dynamic modeling in behavioral ecology. NJ: Princeton University Press.
- Marascuilo, L. A., & Levin, J. R. (1983). Multivariate statistics in the social sciences: A researcher's guide. Belmont, CA: Wadsworth, Inc.
- McNamara, J. M., Houston, A. I., & Krebs, J. R. (1990). Why hoard? The economics of food storing in tits, *Parus* spp. Behavioral Ecology, *1*, 12-23.
- McNamara, J. M., Houston, A. I., & Lima, S. L. (1994). Foraging routines of small birds in winter: a theoretical investigation. Journal of Avian Biology, *25*, 287-302.
- Moreno, J., Lundberg, A., & Carlson, A. (1981). Hoarding of individual nuthatches *Sitta europaea* and marsh tits *Parus palustris*. Holarctic Ecology, *4*, 263-269.
- Piper, W. H. (1997). Social dominance in birds: Early findings and new horizons. Current Ornithology, *14*, 125-187.
- Piper, W. H., & Wiley, R. H. (1990). The relationship between social dominance, subcutaneous fat, and annual survival in wintering white-throated sparrows (*Zonotrichia albicollis*). Behavioral Ecology and Sociobiology, *26*, 201-208.
- Pravosudov, V. V. (1985). Search for and storage of food by *Parus cinctus lapponicus* and *P. montanus borealis* (Paridae). Zoologichesky Zhurnal Akademii Nauk SSSR, *64*, 1036-1043. [English translation]
- Pravosudov, V. V., & Grubb, T. C. (1997a). Energy management in passerine birds during the nonbreeding season: A review. Current Ornithology, *14*, 189-234.
- Pravosudov, V. V., & Grubb, T. C. (1997b). Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. Behavioral Ecology, *8*, 332-339.

- Pulliam, H. R., & Caraco, T. (1984). Living in groups: Is there an optimal group size? In J. R. Krebs, & N. B. Davies (Eds.), Behavioural ecology: An evolutionary approach (pp. 122-147). Oxford, England: Blackwell Science Ltd.
- Reinertsen, R. E., & Haftorn, S. (1986). Different metabolic strategies of northern birds for nocturnal survival. Journal of Comparative Physiology, B., 156, 655-663.
- Sherry, D. F. (1984). Food storage by black-capped chickadees – Memory for the location and contents of caches. Animal Behaviour, 32, 451-464.
- Sherry, D. F. (1985). Food storage by birds and mammals. Advances In The Study Of Behavior, 15, 153-188.
- Sherry, D. F. (1989). Food storing in the paridae. Wilson Bulletin, 101, 289-304.
- Sherry, D., Vaccarino, A. L., Buckenham, K., & Herz, R. S. (1989). The hippocampal complex of food-storing birds. Brain, Behavior and Evolution, 34, 308-317.
- Shettleworth, S. J., Hampton, R. R., & Westwood, R. P. (1995). Effects of season and photoperiod on food storing by black-capped chickadees, *Parus atricapillus*. Animal Behaviour, 49, 989-998.
- Smith, S. M. (1991). The black-capped chickadee: Behavioral ecology and natural history. Ithaca, NY: Cornell University Press.
- Stevens, T. A., & Krebs, J. R. (1986). Retrieval of stored seeds by marsh tits, *Parus palustris*, in the field. Ibis, 128, 513-525.
- Vander Wall, S. B. (1990). Food hoarding in animals. Chicago, IL: University of Chicago Press.
- Verhulst, S., & Hogstad, O. (1996). Social dominance and energy reserves in flocks of willow tits. Journal of Avian Biology, 27, 203-208.

- Waite, T. A., & Grubb, T. C. (1988). Diurnal caching rhythm in captive white-breasted nuthatches *Sitta carolinensis*. Ornis Scandinavica, 19, 68-70.
- Welty, J. C., & Baptista, L. (1990). The life of birds (4th ed.). Orlando, FL: Saunders College Publishing.
- Witter, M. S., & Cuthill, I. C. (1993). The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society of London, B., 340, 73-92.
- Witter, M. S., & Swaddle, J. P. (1995). Dominance, competition, and energetic reserves in the european starling, *Sturnus vulgaris*. Behavioral Ecology, 6, 343-348
- Woodrey, M. S. (1991). Caching behavior in free-ranging white-breasted nuthatches: The effects of social dominance. Ornis Scandinavica, 22, 160-166.