

EFFECTS OF FOOD ADDITION ON A POPULATION OF GREY JAYS

by

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Abstract

Grey jays (*Perisoreus canadensis*) in the southwest Yukon were provided with supplemental food on three study areas to study the effects of food on territoriality and foraging strategies. Territory sizes and overlap were measured in 1993 and 1994. Territories of food addition grids were 30% smaller than those on grids without access to added food. There was only slightly more overlap between territories on food addition grids compared to controls, and the difference was not statistically significant.

Time spent foraging, the rate at which jays made caches, and the weights of jays were measured. These data were used to test four hypotheses about the factors that limit overwinter body masses of jays. Birds on food addition grids made three times as many caches as control birds in a similar amount of time spent foraging. In winter, grey jays with added food spent less time foraging, yet they were able to maintain higher body condition than control birds. These results were consistent with the hypothesis that overwinter weights are limited by both a food shortage and by costs associated with increasing weight.

Seasonal trends in body condition differed between birds on food addition grids and those without supplemental food. Birds with added food were in better condition year round, and were able to increase in weight between summer

and fall. Control birds lost weight between summer and fall, but then increased dramatically in winter. These different weight trends may represent different caching or cache retrieval strategies.

Table of Contents

| | |
|---|-----|
| Abstract..... | ii |
| Table of Contents..... | iv |
| List of Tables..... | v |
| List of Figures..... | vi |
| Acknowledgments..... | vii |
| Chapter One General Introduction..... | 1 |
| The Kluane Food Addition..... | 2 |
| Chapter Two Factors Limiting Overwinter Body Mass in Grey Jays..... | 7 |
| Introduction..... | 7 |
| Methods..... | 10 |
| Study Site..... | 10 |
| Trapping..... | 11 |
| Condition Index..... | 13 |
| Time Budgets..... | 13 |
| Statistical Treatment..... | 15 |
| Results..... | 18 |
| Condition..... | 18 |
| Time Budgets..... | 22 |
| Discussion..... | 22 |
| Regulation of Winter Fat Reserves... | 22 |
| Trends in Body Condition..... | 31 |
| Chapter Three Effects of Food Addition on Grey Jay Territories..... | 35 |
| Introduction..... | 35 |
| Methods..... | 37 |
| Study Site..... | 37 |
| Territory Mapping..... | 37 |
| Results..... | 40 |
| Discussion..... | 45 |
| Methodology..... | 45 |
| Territory Size..... | 46 |
| Territory Overlap..... | 50 |
| Number of Territories per Grid..... | 52 |
| Summary..... | 55 |
| Chapter Four General Discussion..... | 56 |
| Overwinter Condition..... | 56 |
| Territoriality..... | 58 |
| Conclusion..... | 60 |
| Literature Cited..... | 62 |

List of Tables

| | |
|--|----|
| Table 1. List of foods used by grey jays in the Kluane area..... | 4 |
| Table 2. Predicted direction of change in response to food addition for the four hypotheses..... | 9 |
| Table 3. Significance tests from ANOVA's comparing the variance in condition between social groups to the variance within social groups..... | 17 |
| Table 4. Significance tests of t-tests between mean condition of food and control birds in all trapping..... | 20 |
| Table 5. Agreement of results with predictions of the four hypotheses..... | 28 |
| Table 6. Observed and predicted number of territories per 36-ha grid..... | 43 |

List of Figures

| | |
|---|----|
| Figure 1. Map of the study site showing the locations of treatment and control grids..... | 12 |
| Figure 2. Mean condition indices for birds on food addition control birds in all trapping sessions..... | 19 |
| Figure 3. Seasonal trends in (a) body condition and (b) weights for individual birds on food addition (solid lines) and control (dashed lines) grids..... | 21 |
| Figure 4. Summer caching rates of food addition and control birds..... | 23 |
| Figure 5. Proportion of time spent in various activities during summer..... | 24 |
| Figure 6. Proportion of time spent in various activities during winter..... | 25 |
| Figure 7. Predicted weight trends according to two models of cache use during periods of food scarcity..... | 33 |
| Figure 8. Examples of territory maps for control (a) and food addition (b) groups..... | 39 |
| Figure 9. Diagrams showing approximate boundaries between territories..... | 42 |
| Figure 10. Percent overlap between territories with 95% confidence intervals..... | 44 |

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Chapter 1: General Introduction

The experimental addition of food has been used to study how food supply influences a range of response variables from individual behaviour to community structure (e.g. Ewald and Carpenter 1978, Ewald and Rohwer 1982, Krebs *et al.* 1992, Waite 1990). In Boutin's (1990) review of food supplementation experiments, he concludes that knowledge in several areas is still lacking despite the extensive literature already available. This is due, in part, to advances in theory that require increasingly sophisticated experiments. An example is the role of food supply in territory size.

Increased food density is often correlated with smaller territory sizes in birds (e.g. Stenger 1958, Enoksson and Nilsson 1983) but as the theory of optimal territory size advanced from the early conceptual model of economic defendability (Brown 1964) to more explicit mathematical models (Hixon 1980, Schoener 1983), the importance of intruder pressure was recognized and incorporated into experimental food additions, and non-experimental studies (e.g. Mares *et al.* 1982, Myers *et al.* 1979).

Shortcomings in methodology have also been recognized. For example, the role of food supply in demography has long been of interest (see review in Boutin 1990). As Boutin (1990) observed, food additions have generally resulted in twofold increases in density, but the real increase in

density may be less if animals are commuting from off the censusing area for food but are not truly residents (i.e. the effective censusing area is larger than control areas). This problem arises when inadequate attention has been paid to the spatial scale of the study system. The concept of ecological neighborhoods (Addicott et al. 1987) and recognizing the need to incorporate multiple scales in studies (Kotliar and Wiens 1990) have arisen from the methodological shortcomings of past studies. By incorporating relevant spatial scales into the designs of food additions, a shift from measuring qualitative to quantitative changes can be made, allowing more predictive power and testing of more explicit hypotheses.

The Kluane Food Addition

Since 1987, three 36-ha areas in white spruce (*Picea glauca*) boreal forest have had commercial rabbit chow added year-round (Krebs et al. 1992). The food is supplied by spreading pellets along four rows of a 20 x 20 grid. Numerous animals make use of this food addition: snowshoe hares (*Lepus americanus*); red squirrels (*Tamiasciurus hudsonicus*); arctic ground squirrels (*Spermophilus parryi*); moose (*Alces alces*); grizzly bears (*Ursus arctos*); chickadees (*Parus atricapillus*, and *P. hudsonicus*); dark-eyed juncos (*Junco hyemalis*); magpies (*Pica pica*); and grey jays (*Perisoreus canadensis*). The juncos, chickadees, and jays have been observed selecting the grain component of the

pellets, whereas the other animals appear to use the entire pellets (personal observation). I used the Kluane food addition to study the response of grey jays to the food addition.

Grey jays are common birds throughout boreal forest in North America. Because they are relatively tame, they are easily observed at most times, and readily adapt to the presence of human observers. They live in social groups comprised of a mating pair and usually one or two non-breeding birds (Rutter 1969, Waite and Reeve 1992). On occasion a group is made up only of males (Waite and Reeve 1992). The group defends an all-purpose territory which is held year-round.

Throughout the summer and into the fall, jays scatterhoard saliva coated boli of food in bark crevices and conifer branches (Rutter 1969); a list of the foods I have observed birds using in the Kluane area is presented in Table 1. The diverse nature of their diet leads to use of many habitat types. I have observed birds using mossy bogs, meadows, dense willow (*Salix* spp.) shrubs, and aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) forests at various times throughout the summer.

Jays will also cache opportunistically in the winter, for example when there is carrion (Rutter 1969, Waite and Reeve 1992) or, as in this study, when food is supplied year-round. The caches are used throughout the winter, and the birds observed in this study appeared to rely almost

Table 1. List of foods used by grey jays in the Kluane area. This is only a partial list based on items that I was able to identify.

| | Organism | Notes |
|--------------|--------------------------------|------------------------|
| Plant | <i>Arctostaphylos uva-ursi</i> | Flowers |
| | <i>A. rubra</i> | Berries |
| | Mushrooms | |
| Invertebrate | Moths/Butterflies | |
| | Unidentified Beetle Larvae | Found on willow leaves |
| | Ants | |
| | Dragonflies | |
| | Spider egg masses | |
| Vertebrate | Carrion, variety of species | |
| | <i>Dendroica coronata</i> | Nestlings |
| | <i>Turdus migratorius</i> | Eggs |

entirely on caches (see chapter 2). This study took place during the low of the snowshoe hare cycle (Krebs et al. 1992). Increased availability of carrion during the period of high hare numbers may result in very different observations.

Scatterhoarded caches are susceptible to theft, decay, and being forgotten (Vander Wall 1990). Theft of caches in the Kluane area is presumably due to other grey jays and magpies (see Waite 1988), and red squirrels have been observed stealing caches (J. Delehanty, pers. comm.). One method to mitigate the risks of losing caches over the winter is to store energy as fat reserves. There is, however, a complex system of tradeoffs between the relative costs and benefits of caches and fat reserves (Vander Wall 1990) which appears to limit the extent to which grey jays accumulate fat reserves (Waite 1992).

In chapter two I discuss these tradeoffs and test several hypotheses to determine whether food shortage and/or costs associated with increasing weight limit winter fat reserves. Also in chapter two I present the weight trends of birds on food addition and control grids, and discuss the different patterns in terms of the factors limiting overwinter weights.

I go on in chapter three to discuss the response of grey jay territoriality to food addition. I measured territory size, percent overlap between adjacent territories, and the arrangement of territories around food

addition and control grids. Using these results I then discuss the relationship between territory sizes and apparent population densities on the study areas.

Chapter 2:

Factors Limiting Overwinter Body Mass in Grey Jays

Introduction

Animals overwintering in temperate and sub-arctic regions can experience food shortage during times when maintaining adequate energy reserves is particularly important. Because winter in northern boreal forest brings short days, extreme cold, and reduced availability of food, animals must be able to store enough energy in either fat reserves or food caches to last the period of food shortage.

Although different energy storage strategies have been identified, little research has been done on the factors influencing the adaptive value of a particular strategy. Vander Wall (1990, p. 26) suggests that because fat deposition is a function of body mass and food storage is not, small animals can store more energy through food hoarding. In small birds, this explanation alone is insufficient as they have an extraordinarily high ability to store energy as fat (Blem 1976) yet actual winter fat mass is generally less than what is possible (King 1972).

In this study, I tested four hypotheses concerning the factors limit overwinter body mass in grey jays (*Perisoreus canadensis*). I first describe patterns of weight change in control birds and those with added food. I then compare time budgets of birds with added food to control birds.

These hypotheses and their predictions are described below and are summarized in Table 2. I also discuss the observed weight trends in the context of these findings.

Hypothesis 1: Winter fat reserves are not limited by food or weight-related costs. If this is the case, food addition should not affect body condition, nor should birds with extra food spend more time foraging in the winter, nor should they cache more food in the summer or fall.

Hypothesis 2: Food alone limits grey jay fat reserves. If jays are food limited, jays with added food should maintain better body condition over winter by spending more time foraging, and cache more in the summer or fall. This hypothesis allows some cost to added weight, but it is always less than the cost associated with storing the same amount of energy as caches.

Hypothesis 3: Costs associated with increasing weight are the sole limiting factors. The costs of added weight are in the form of predation risk while foraging or in the metabolic expense of transporting and maintaining the extra weight. In this case, birds with added food will maintain higher winter body condition than control birds (Lima 1986), but not because they have cached more in the summer; since food is not limited. Rather, birds are able to reduce their foraging time in winter because the food addition provides

Table 2. Predicted direction of change in response to food addition for the four hypotheses being tested. An increase is denoted by +, decrease by -, and no difference between food and control animals is =.

| Hypothesis | Condition | Winter | Summer |
|----------------------------|-----------|---------------------|---------------|
| | | Time Spent Foraging | Amount Cached |
| 1: Not Limited | = | = | = |
| 2: Food Limited | + | + | + |
| 3: Weight Limited | + | - | = |
| 4: Food and Weight Limited | + | - | + |

food with less search time involved. Since foraging time and the associated costs have been reduced, birds with added food can maintain higher weights than control birds without incurring a higher total cost.

Hypothesis 4: A limited food supply in winter and a cost of increasing weight combine to limit winter fat reserves. In summer, food addition allows jays to cache more food than control birds which, in turn, allows them to maintain higher weights in winter. Once again, though, because there is a cost to increased weight, the jays with added food must be able to balance those costs by decreasing the costs of foraging in the winter (Lima 1986). As with the weight-only hypothesis this gain can be had by using the added food available on the ground in the winter. In contrast to the weight only hypothesis, foraging time can also be reduced by having more caches from the summer.

Methods

Study Site

This study was conducted near Kluane Lake, in the southwest Yukon (61°N, 138°W) between May 1993 and November 1994. Grey jays are found throughout the study site which is dominated by white spruce (*Picea glauca*) overstory and a shrub willow understory (*Salix* spp.). A more complete description of the site is found in Krebs et al. (1986). Commercial rabbit chow (16% crude protein, 2% fat, 18%

fibre) is added year-round to three 36-ha grids as part of the Kluane Boreal Forest Ecosystem Project (Krebs et al. 1992). Grey jays use the grain component of this food, which often separates from the pellets (personal observation). Jays on the food addition grids and in other areas of similar habitat but with no access to food addition were used in the study (Figure 1).

Trapping

Jays were caught throughout the study in Tomahawk live traps during hare (*Lepus americanus*) and squirrel (*Tamiasciurus hudsonicus* and *Spermophilus parryi*) trapping sessions of other projects, and also when these traps were set explicitly for jays. Depending on the nature of the trapping session, traps were baited with either peanut butter, apple, raisins, or rabbit chow. The birds were banded with numbered aluminum bands and with one to three coloured plastic bands in unique combinations to make birds individually recognizable.

Jays were weighed to the nearest gram using a 300 g spring scale and their tarsus length was measured to the nearest 0.1 mm from the joint with the tibiotarsus to the last undivided scute at the distal end of the tarsus. The average tarsus measurement over all trapping sessions for each bird was then used with its average weight over a single trapping session to calculate a condition index (see below).

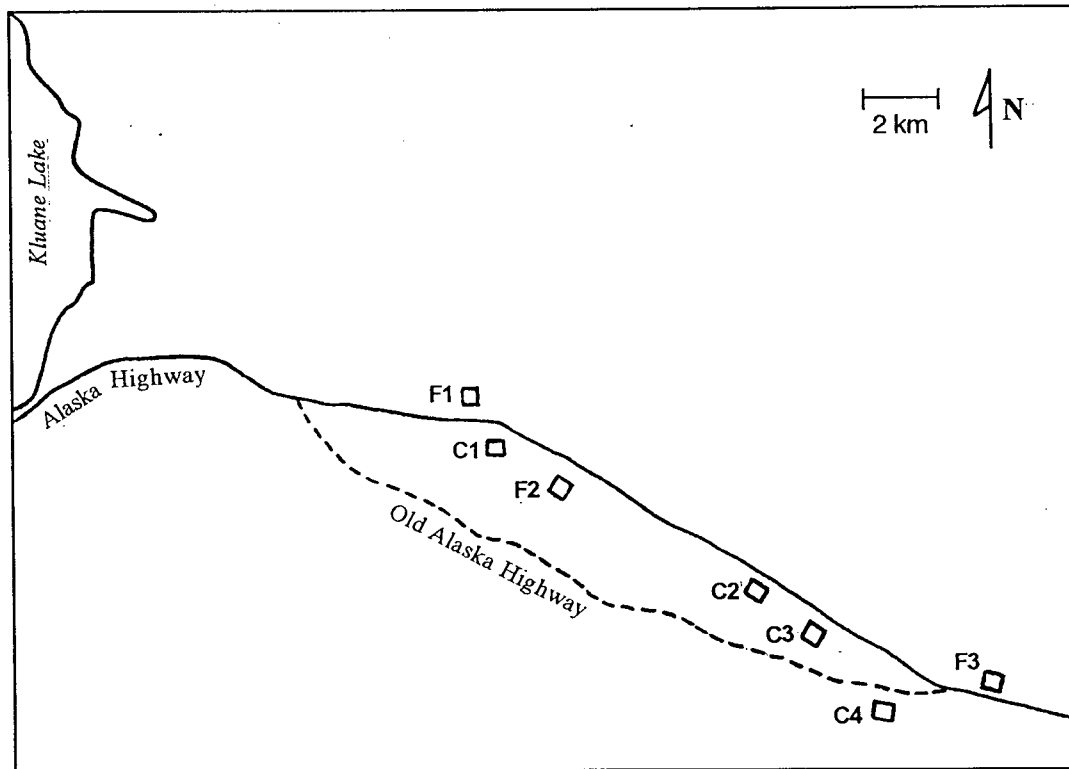


Figure 1. Map of the study site showing the location of food addition (F1 - F3) and control grids (C1 - C4). The three food addition grids and three of the control grids were used to estimate the number of territories per grid. Control grid 2 was not used due to incomplete information.

Condition Index

To estimate relative amounts of fat reserves a condition index based on weight and body size (as represented by tarsus length) was used (see Krebs and Singleton 1993 for a discussion of this technique). The first step in generating a condition index was to use weights and mean tarsus lengths of all control jays caught in trapping sessions in May and early June, 1993 and 1994. Because the relationship was linear and there were measurement errors in both weight and tarsus, the Geometric Mean Regression was calculated (Krebs 1989 p. 462) from this data. The resulting regression equation ($WEIGHT = 3.86TARSUS - 50.51$) was used to calculate a predicted weight for a bird with a given tarsus length. I then used the ratio of observed weight to predicted weight as a condition index. This condition index assumes that changes in mass are due to changes in fat reserves, and that this in turn represents an increase in body condition.

Time Budgets

To estimate the proportion of time spent foraging in winter, time budgets were conducted between January 17, 1994 and March 11, 1994. A total of 36 sessions were recorded involving 5 control groups and 7 food addition groups. Once a focal bird was selected, a watch and a hand held tape recorder were used to record time of day (to the nearest second), and whether the bird was perched, foraging,

caching, or flying. Flights less than two seconds were not included in the flight time as such short events were impractical to record. If birds were lost for more than 30 s the session was ended. In practice, however, when birds were lost, they were always lost for much more than 30 s. Originally, sessions between 5 min and 30 min were to be used, but to increase sample size, the lower limit was set at 4 min. An effort was made to sample each group at evenly distributed times of day.

To estimate the amount of food cached in the summer I collected 55 time budget sessions between June 19, 1994 and August 6, 1994 (using 3 food addition groups and 3 control groups). Summer time budgets were similar to the winter sessions, except that distinguishing between food gathering and food caching was more difficult than in winter. These two activities were therefore grouped together as foraging. I also recorded the number of caches made. To avoid counting "false" caches, only cases where the jay was seen manipulating the bolus in its beak before making caching motions were counted. As a result, the actual caching rate is probably slightly higher than reported here, but there is no reason to suspect that an unequal proportion of food and control birds' caches were recorded. Sessions less than 5 min were discarded, as were sessions where the bird was lost for more than 30 s. Based on winter results, the maximum session length was reduced to 20 min.

Statistical Treatment

1. General Procedures and Conventions:

All tests are one-tailed for hypotheses two through four where directional predictions are made. The tests for hypothesis one, although using the same data, are two-tailed because differences between food and control birds in either direction will lead to rejection of the hypothesis. The significance level for all tests was set at 0.05.

In tests where data were transformed, the results are presented as back transformed means with 95% confidence intervals since the standard error has no meaning if back transformed (Sokal and Rohlf 1981, p. 421; Krebs 1989, p. 447). Non-transformed data are presented as means with standard errors.

2. Condition Index:

Because jays live in social groups, there is the question whether individual condition measurements are independent, and that using them as such would be pseudoreplication. To test the independence of individual birds, an F-ratio was calculated using the mean square between social groups over the mean square within social groups. If the ANOVA is significant, then individuals are not independent and group means should be used in future analyses. There was no significant effect for either for food or control birds in any of the sessions (Table 3). Based on this, the effect of group membership appears to be

small, so the condition analysis was done using individuals as independent measurements.

3. Time Budget Analysis:

In winter, leg bands were rarely visible because the birds usually kept their legs tucked up in their feathers. Based on trapping, occasional confirmation of a bird's identity, and the location and behaviour of the birds, I am certain that I was able to accurately infer the group a bird belonged to although individuals within groups were not distinguished. For this reason, one-way ANOVA's were calculated using group means of the arcsine transformed proportion time spent in each behaviour during a session.

In the summer, the proportion of time spent in each activity was calculated, and then arcsine transformed. Because individuals could be recognized in the summer sessions this data was analyzed using a nested ANOVA, where multiple observations of individuals were nested within social groups within treatments. The caching rates were calculated for each session, square root transformed (because the rates were based on counts of observed caches; Sokal and Rohlf 1981, p. 421), and then analyzed with a nested ANOVA.

Table 3: Significance tests from ANOVA's comparing the variance in condition between social groups to the variance within social groups for both treatments in each trapping session. Non-significant results indicate that individual birds can be used as the experimental units in the condition analyses.

| Trapping Session | Treatment | Test Statistics |
|---------------------------------|-----------|------------------------------|
| Spring 93 (May 11-June 8) | Food | $F_{7,8} = 0.680$ $p=0.688$ |
| | Control | $F_{6,4} = 0.898$ $p=0.569$ |
| Summer 93 (Aug. 14 - Aug 26) | Food | $F_{6,13} = 1.86$ $p=0.164$ |
| | Control | $F_{4,8} = 0.142$ $p=0.962$ |
| Fall 93 (Oct. 16 - Nov. 13) | Food | $F_{9,9} = 2.62$ $p=0.084$ |
| | Control | $F_{1,2} = 1.02$ $p=0.419$ |
| Winter 94 (Jan. 1 - Mar. 30) | Food | $F_{13,15} = 1.46$ $p=0.241$ |
| | Control | $F_{2,7} = 0.27$ $p=0.771$ |
| Spring 94 (May 6 - June 9) | Food | $F_{7,6} = 0.713$ $p=0.668$ |
| | Control | $F_{9,10} = 1.30$ $p=0.342$ |
| Summer 94 (Aug. 8 - Aug 23) | Food | $F_{10,12} = 1.33$ $p=0.314$ |
| | Control | $F_{8,10} = 0.481$ $p=0.841$ |

Results

Condition

Mean tarsus lengths were similar between food addition and control grids (Control mean (SE)=32.0 mm (0.22); Food Addition mean (SE)= 31.8 mm (0.14); t-test $t=0.60$, $df=86$, $p=0.55$). Jays with added food were in significantly better condition than control birds in all trapping sessions (Figure 2, Table 4). The differences in condition indices between food addition and control birds ranged between 3% in the winter session, and 15% in the fall session, although there were only four birds in the control group for that session. In both 1993 and 1994 Spring and Summer sessions, the difference in condition was consistently between 5% and 7% higher on food addition grids.

The mean condition of control birds fell sharply between the Summer 1993 and Fall 1993 sessions, whereas the mean condition of birds on food additions rose during that period. This pattern was mirrored by trends of individual birds. I caught ten birds in all three sessions from Summer 1993 through Winter 1994. Of these, three were control birds. All control birds were in poorer condition in the fall session than in either the previous summer session or the following winter session (Figure 3a). All the birds on food addition grids increased from the summer session to the fall session (Figure 3a). For comparison with other work (see Discussion), the weight trends of these individual birds are also presented (Figure 3b).

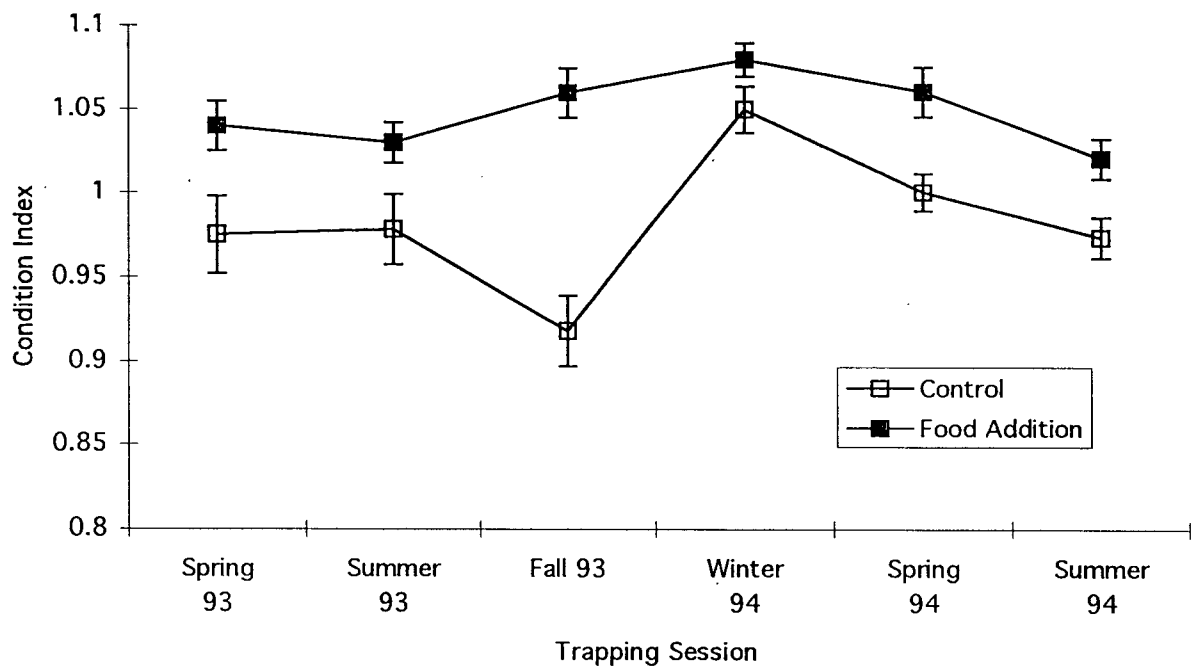


Figure 2. Mean (\pm SE) condition indices for birds on food addition and control grids in all trapping sessions. Results of significance tests are in Table 4.

Table 4: Significance tests of t-tests between mean condition of food and control birds in all trapping sessions. Asterisks indicate significant differences ($p < 0.05$)

| Session | Treatment | Mean (SE) | n | t-statistic |
|-----------|-----------|---------------|----|-------------|
| Spring 93 | Food | 1.04(0.015) | 16 | 2.66* |
| | Control | 0.975 (0.023) | 11 | |
| Summer 93 | Food | 1.03(0.012) | 21 | 2.13* |
| | Control | 0.978(0.021) | 13 | |
| Fall 93 | Food | 1.06(0.015) | 20 | 4.03* |
| | Control | 0.918(0.021) | 4 | |
| Winter 94 | Food | 1.09(0.010) | 30 | 2.66* |
| | Control | 1.05(0.013) | 11 | |
| Spring 94 | Food | 1.06(0.015) | 15 | 3.51* |
| | Control | 1.00(0.011) | 20 | |
| Summer 94 | Food | 1.02(0.012) | 23 | 2.45* |
| | Control | 0.973(0.012) | 17 | |

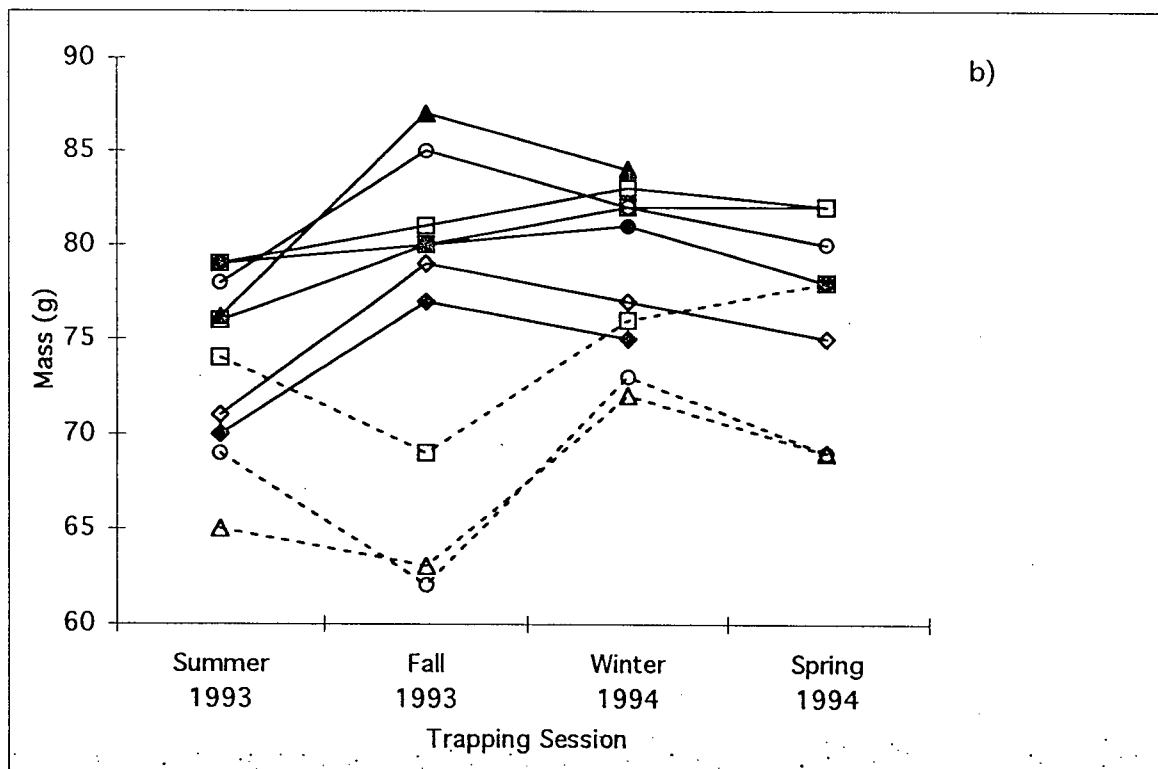
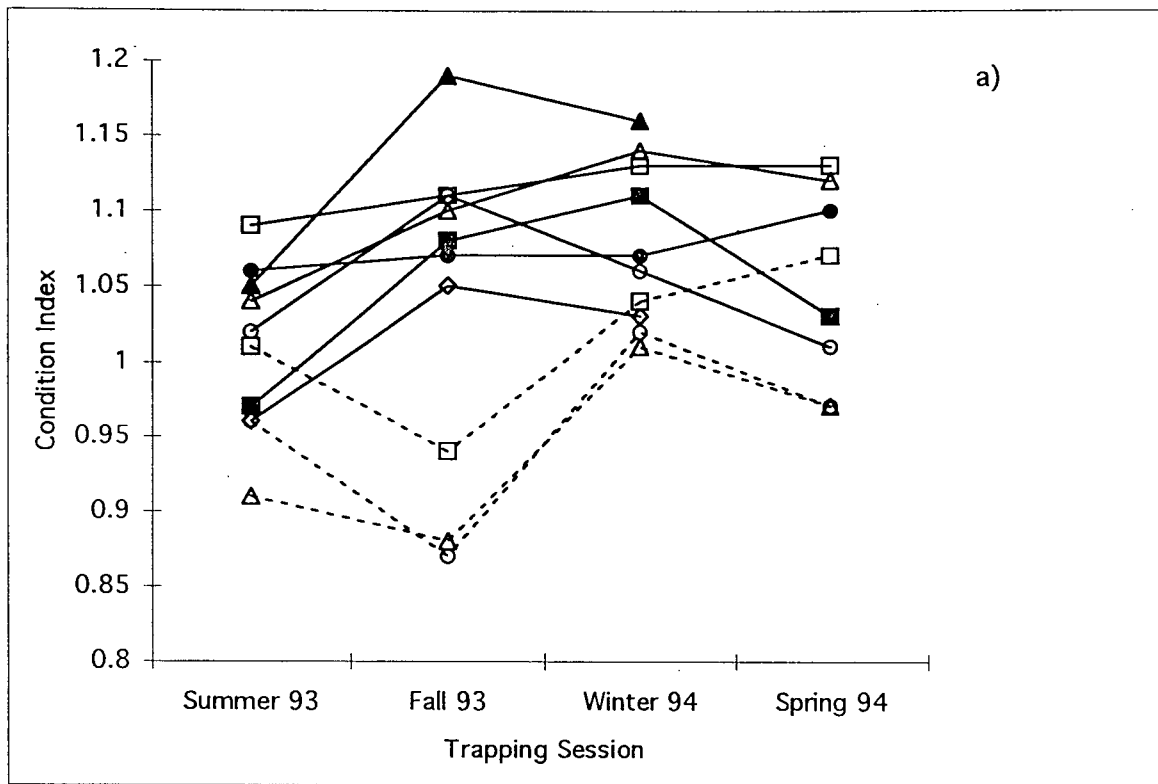


Figure 3. Seasonal trends in (a) body condition and (b) weights for individual birds on food addition (solid lines) and control (dashed lines) grids.

Time Budgets

Jays with added food made three times as many caches per hour in the summer as control birds (Nested ANOVA, $F_{1,4}=25.54$, $p=0.01$; Figure 4). Analysis of summer time budgets showed that there was no effect of food addition on time spent foraging, perching, or flying (Figure 5).

In winter, birds on food grids spent less of their time foraging than control birds (Figure 6). The difference was significant for the one-tailed test (ANOVA $F_{1,10}=4.88$, $p=.026$, one-tailed). No significant differences were found in the proportion of time spent perching (ANOVA $F_{1,10}=1.92$, $p=.20$) or flying (ANOVA $F_{1,10}=.11$, $p=.75$). Birds on food grids would regularly, though infrequently, cache the rabbit chow, whereas no control birds were ever seen making new caches (Figure 6).

Discussion

Regulation of Winter Fat Reserves

Energy storage strategies can be represented on a continuum ranging from pure food caching to pure fat storage. While food caches and fat reserves are analogous, evolutionary and ecological factors may make a particular storage strategy optimal (McNamara et al. 1990; Vander Wall 1990, p. 27). Wrazen and Wrazen (1982; see also Panuska 1959) found that individual eastern chipmunks (*Tamias striatus*) could either gain no mass before winter and subsist on stored food, or gain mass at the onset of winter,

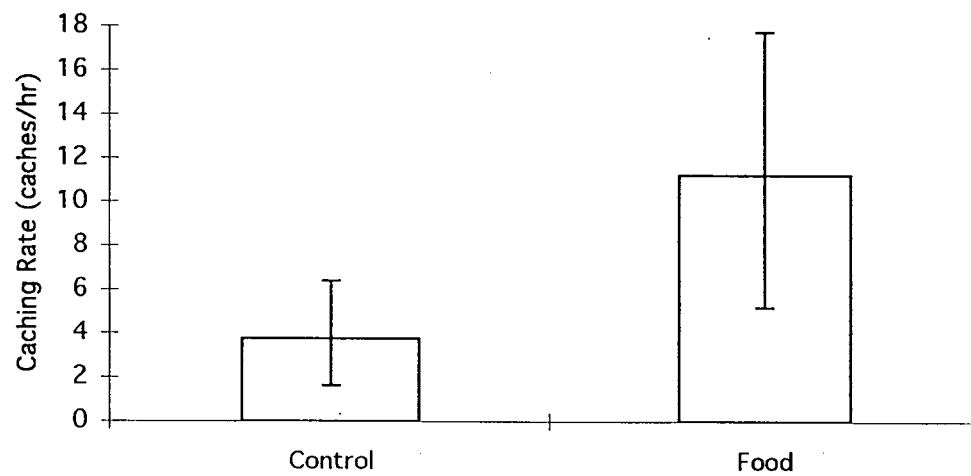


Figure 4. Summer caching rates of food addition and control birds. Means, shown with 95% confidence intervals, are significantly different (Nested ANOVA $F_{1,4}=25.54$, $p=0.01$).

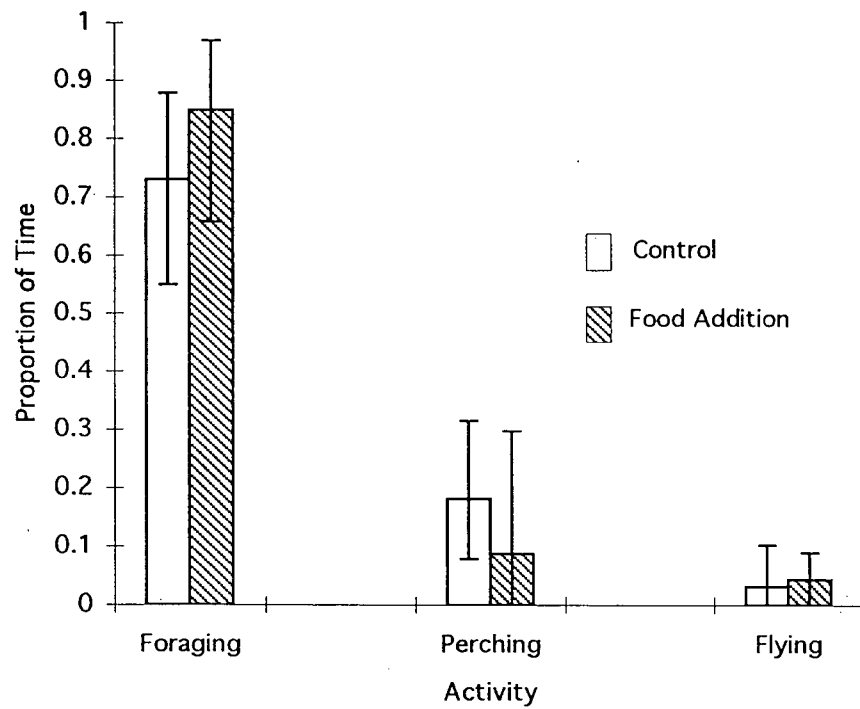


Figure 5. Proportion of time spent in various activities during summer. Means are shown with 95% confidence intervals. Two-tailed p-values of treatment effects from nested ANOVA's are as follows: Foraging $p=0.086$; Perching $p=0.12$; Flying $p=0.36$.

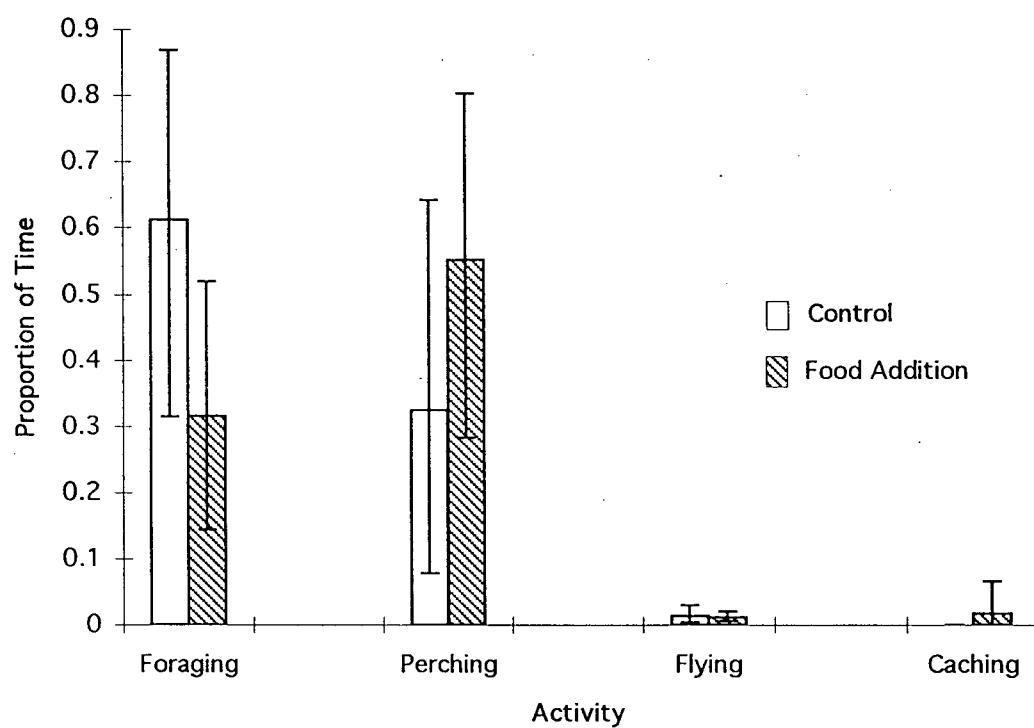


Figure 6. Proportion of time spent in various activities during winter. Means are shown with 95% confidence intervals.

become semitorpid, and rely less on stored food. Similarly, adult beavers (*Castor canadensis*) rely on fat storage for overwinter survival (Novakowski 1967, Aleksuk 1970) while the kits and yearlings rely more on cached food in order to gain weight over the winter (Novakowski 1967). In birds, Rogers (1987) found the amount of fat reserves was inversely related to the reliability of food supply. Nilsson et al. (1993) found that nuthatches relied less on caches in good weather when other sources of food were available. They also found that the number of caches consumed was inversely proportional to ambient temperature. Evans (1969) found that fat reserves of Yellow Buntings (*Emberiza citrinella*) were negatively correlated with the long term minimum temperature for the day of capture.

Although there is evidence of some system of benefits and costs to storing energy as either fat or caches (McNamara et al. 1990, Vander Wall 1990 p. 26, Lucas 1994), few studies have tested the nature of these tradeoffs. Waite (1992) studied grey jays in central Alaska and found evidence that jays increase their fat reserves as midwinter approaches. He suggested that this is evidence that the birds are regulating body mass in a way that balances higher predation risk and lower risk of starvation. Similar trends in other species (Rogers 1987, Rogers and Smith 1993, Blem 1976, Blem and Pagels 1984) have likewise been ascribed to a tradeoff between fat reserves and predation risk (Blem 1975,

Lima 1986, McNamara and Houston 1990) or increased metabolic expense (Blem 1975, 1976).

While Rogers (1987) and Waite (1992) provide supportive evidence for the predation risk hypothesis, experimental work is lacking. Moreover, alternative hypotheses of what limits overwinter weights (or even if they are limited at all) have not been tested. This study was able to test the predictions of several hypotheses on the factors that may limit winter body mass in grey jays.

My results support hypothesis four, that the overwinter weights of the jays I studied are limited both by costs associated with increasing weight, and by a shortage of food (Table 5). Food limitation for the grey jays appears to have its root in the summer, since birds on food grids did not spend a significantly larger proportion of time foraging but made three times as many caches. This suggests that control jays cache as much as they can through the summer, but birds with added food cache more because of the greater abundance of food in their territories.

This result is consistent with Waite and Ydenberg's (1994) finding that jays maximize the rate at which they store recoverable energy. Rate maximization is expected when animals are time constrained, rather than constrained by an energy-expenditure ceiling (Ydenberg et al. 1994). It appears that control birds are limited by their capacity to cache rather than by the availability of food. Birds with

Table 5. Agreement of results with predictions of the four hypotheses. An asterisk by the prediction indicates the results met the prediction. No asterisk indicates that the data did not fit the prediction statistically. Where directional predictions were made, tests were one-tailed.

| Hypothesis | Winter | | Summer |
|----------------------------|-----------|---------------------|---------------|
| | Condition | Time Spent Foraging | Amount Cached |
| 1: Not Limited | = | =* | = |
| 2: Food Limited | +* | + | +* |
| 3: Weight Limited | +* | -* | = |
| 4: Food and Weight Limited | +* | -* | +* |

added food, however, are able to cache at a higher rate because of the greater food density.

In territories with added food, the shortage of food was further reduced by regular winter caching. Control birds may get the opportunity to cache in winter when carrion is found, but in this study no such events were observed (Figure 6). Also in winter, birds on food addition grids were able to reduce the amount of time spent foraging for food. This could reflect both the increased density of caches from the summer, and the availability of rabbit chow on the ground.

This study was not able to describe the nature of the food shortage. The value of added food could be due to either an absolute scarcity of food or a strong incentive to keeping as many caches as possible until the end of winter. Such incentives may include reproductive benefits (Jansson *et al.* 1981) or the uncertain length of winter. The allocation of caches to present and future needs, and the fitness consequences of such decisions are interesting problems for modelling and field experiments, and which have not been explored in detail to my knowledge (but see Nilsson *et al.* 1993).

The trend in condition indices shows that birds on food addition grids were in better condition in all trapping sessions. The winter time budgets show that control birds spent more time foraging than birds with added food. Higher

condition and lower foraging times in winter were predicted in hypotheses three and four and are evidence of weight-related limits to winter fat reserves.

To explain why many temperate bird species do not maintain maximum fat reserves, Lima (1986) and McNamara and Houston (1990) have proposed models where the survival value of fat reserves (i.e. the ability to survive periods of food inaccessibility) is balanced by increasing risk of predation because of increased foraging time or by decreased agility in escaping predators. Three of four predictions made by Lima's model have been confirmed: Rogers (1987) found that fat reserves increase as the frequency or harshness of food shortage increases; Waite (1992) found that fat reserves increase with decreasing temperatures; and this study shows that winter weights increase with increasing food resources (Table 4).

Rogers' (1987) and Waite's (1992) results are also consistent with McNamara and Houston's model, but the increase in body condition in response to increased food abundance found in this study are opposite to the predictions in McNamara and Houston (1990). As the authors of this model point out, the disagreement between their model and Lima's (1986) is due to different assumptions about the nature of environmental variability. In Lima's model a day was either good or bad, whereas in McNamara and Houston's model foraging success was a continuous, stochastic function. Under the conditions that each model

was run, this difference led to opposite predictions. Because grey jays are retrieving caches from tree branches, foraging success is likely to be dependable (Rogers 1987) except on days with extreme weather, and more accurately represented by Lima's model. For this reason, I based my predictions on Lima's model, rather than McNamara and Houston's model.

Although Lima (1986) argues against the relevance of costs to added weight other than predation risk, and McNamara and Houston (1990) do not address alternate costs, in this study I have not excluded the possibility that the weight-related costs to increasing fat reserves are due to transport or maintenance costs. Rogers (1987) also recognizes that his results are equally consistent with other models that involve costs to winter fattening. Measuring the relative importance of predation risk and transport or maintenance costs will be a useful next step in understanding body mass regulation in wintering birds.

Trends in Body Condition

Although the Fall 1993 trapping session included only four control birds, the trends of individual birds matched the population condition trends implying reliability in the pattern (Figures 2, 3a, and 3b). While birds with access to food addition were able to maintain or even increase their weights between the Summer and Fall 1993 trapping session, the control birds' weights declined. Despite this decline,

control birds were able to raise their weights in the Winter session such that the weights were closer to food addition birds than in any other trapping session. Between these two sessions caches would likely be the only food available to control birds.

In general, there are few studies of birds that have recorded series of weights; more information is available for mammals. Fattening at the onset of winter and gradually declining until spring has been observed in chipmunks (*Tamias striatus*; Panuska 1959) and in beaver (*Castor canadensis*; Aleksuk 1970). My results and those in Waite (1992) suggest that grey jays, like other small birds (Blem 1976, Blem and Pagels 1984), increase mass in mid-winter rather than building up reserves for the onset of winter. Furthermore, the differences I found in weight and condition trends between birds with and without access to food addition suggest that food addition may alter the strategy used.

There are currently no models of overwinter cache use that have considered a bird subsisting entirely off caches as grey jays seem to do, but there are at least two models that consider caching and cache use. The acorn woodpecker (*Melanerpes formicivorus*) caches acorns for use in the winter when other food sources are less abundant. In a model of caching in this woodpecker, Hitchcock and Houston (1994) predict a constant rate of cache use resulting in stable body weights (Figure 7a). In a model of caching

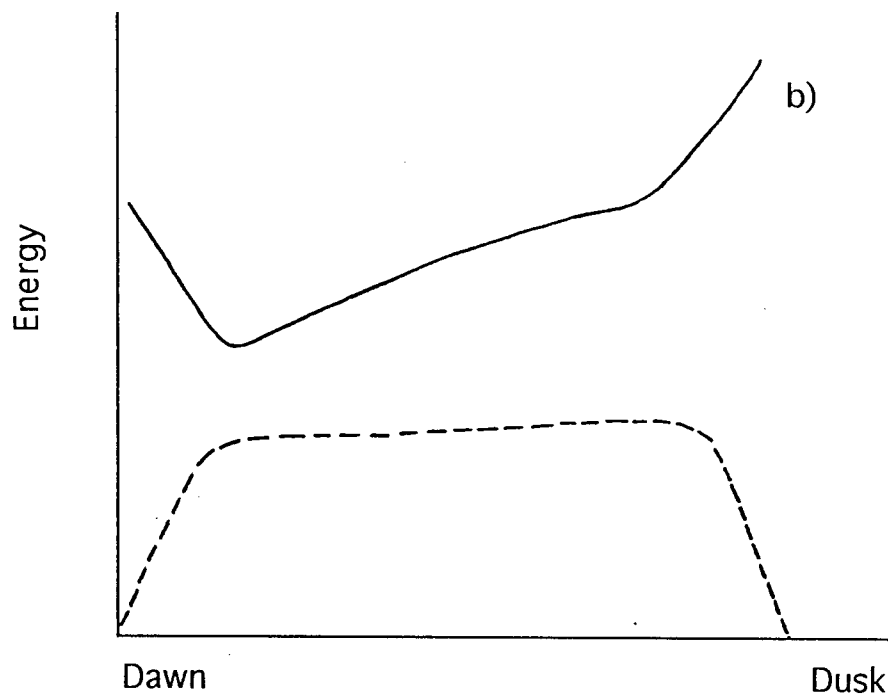
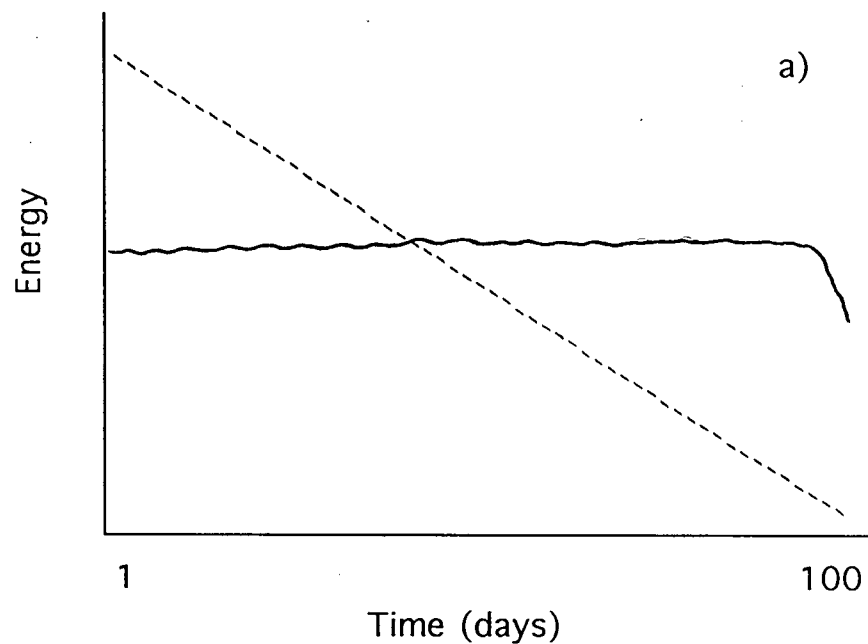


Figure 7. Predicted weight trends according to two models of cache use during periods of food scarcity: a) a model of a small bird in winter from McNamara et al (1990); b) a model of acorn woodpecker cache use from Hitchcock and Houston (1994). Solid lines represent body reserves, dashed lines are caches.

behaviour, McNamara et al (1990) consider a bird that forages and makes short-term caches during the non-breeding season. The predicted daily pattern of fat storage (Figure 7b) resembles the seasonal pattern of control jays from Summer 1993 through Winter 1994. A modification of one of these models could be used to model overwinter cache use by grey jays. By incorporating both the control conditions and the food addition into such a model, a preliminary test of the model exists. The weight series predicted by the model under control and supplemental food conditions should resemble the patterns I observed for treatment and control birds (Figure 2). Perhaps more important than another model of caching, is that experiments catch up with theory and begin to test the models and assumptions of how animals use their caches during periods of food shortage. One way this could be done is by monitoring the caches of individuals with and without supplemental food. Nilsson et al. (1993) have observed that European nuthatches (*Sitta europaea*) used caches of supplemented food more often in poor weather, but they did not collect data on cache use by control birds. This study has observed very different weight trends between fed birds and controls, but this falls far short of understanding how differences in cache use has resulted in these patterns. This is likely a fruitful area for future research.

Chapter 3:

Effects of Food Addition on Grey Jay Territories

Introduction

Interest in territoriality has led to a great deal of research into the economics of maintaining an exclusive territory and the optimal size of such a territory (e.g. Brown 1964, Davies 1978, McNab 1963, Ebersole 1980, Hixon 1980, Schoener 1983). Theory suggests that territory size of animals holding food territories (*sensu* Hinde 1956) is regulated by food availability and intruder pressure (Ebersole 1980, Hixon 1980, Schoener 1983).

Food additions have been the most common experimental manipulation to test this model of territoriality (for a review see Boutin 1990), although there have been a few attempts to look more explicitly at the effect of intruder pressure (Mares *et al.* 1982, Price *et al.* 1986). Results from food addition studies have proved to be variable depending on the species studied. Enoksson and Nilsson (1983) found that the European nuthatch (*Sitta europaea*) decreased territory size in response to food addition, while the rufous-sided towhee (*Pipilo erythrophthalmus*) did not change home range size (Franzblau and Collins 1980), and the reef fish (*Eupomacentrus leucostictus*) increased territory size (Ebersole 1980).

Schoener (1983) examined a number of models of territory size and, by clarifying the underlying assumptions, was able to unify them into a comprehensive

model. By defining three types of territory holders (time minimizers, and two types of energy maximizers) and four types of environmental variation (i.e. the relationship between food availability and intruder pressure) Schoener's model shows how these factors determine the optimal territory size. A more detailed description of the model as it applies to this study is given in the discussion below.

Fewer studies have examined the effect of food addition on overlap between territories (see Boutin 1990). Overlap should increase as the net benefit of defending an exclusive area decreases. Territorial economics predicts that an animal should defend an exclusive foraging area when the benefits of exclusiveness outweigh the costs of defense (Brown 1964). When food is scarce, the energy spent guarding it exceeds the energy gained from the territory, and when competition for food is reduced, the benefits of exclusive access are negated. Carpenter and MacMillen (1976) found that a species of Hawaiian honeycreepers (*Vestiaria coccinea*) altered their level of defense such that intermediate densities of flowers were defended more than low or high densities. Other studies show that some animals will maintain territories or not depending on the level of food resources (see review in Davies 1978).

This study used the long term, year round food addition of the Kluane Boreal Forest Ecosystem Project (Krebs et al. 1992) to examine the effect of food availability on the territory characteristics of grey jays (*Perisoreus*

canadensis). My objectives were to examine the effects of food addition on territory size, overlap, and spatial arrangement.

Methods

Study Site

The study was conducted near Kluane Lake in southwest Yukon (61°N, 138°W) May through August, 1993 and 1994. As part of the Kluane Boreal Ecosystem Project, three 36-ha grids have had commercial rabbit chow (16% crude protein, 2% fat, 18% fibre) added year-round since 1987. Among the species that use the food are grey jays - year-round residents of the boreal forest, which maintain all-purpose group territories (Rutter 1969).

Territory Mapping

To map territories my assistant and I found groups of colour banded jays (see chapter 2) on food addition grids and on other grids of similar habitat but without access to the food addition (Figure 1). We followed the birds between 0600h and 1400h from June 9, 1993 to August 13, 1993, and from July 10, 1994 to August 15, 1994. We recorded their location to the nearest 15 m on grids with stakes spaced at 30 m. When the birds travelled off the grid we used 1:10 000 aerial photos of the area to estimate their locations using identifiable landmarks. Accuracy and precision of locations off the grid varied depending on the

nature of the landmarks in the area. At best, we were able to locate the exact tree on the photo while at worst we could only estimate the location to the nearest 30 m.

In the territory maps we included locations where birds made repeated vocalizations, foraged, cached food, perched for more than one minute, or interacted with neighbours at a border. It soon became clear that intrusions onto neighbouring territories were occurring, but these were not seen to extend more than 100 m into the neighbouring territory. At these times the behaviour of intruding birds changed from being highly visible and audible, to being very quiet and inconspicuous. The focal birds were sometimes chased away by other birds (either the owners or assumed owners of the neighbouring territory). We noted this behaviour and did not include these areas in the territory maps. Areas where two groups tolerated each other (i.e. were plainly visible to one another, but were not aggressive) were recorded as areas of overlap (Figure 8).

My assistant and I mapped a total of nine territories over the two summers (Figure 1). Mapping was labour intensive; it required about one month, mapping three territories at a time, to be satisfied that very little area was missing or wrongly included. This is largely a function of territory size: the bigger the territory, the more time the birds spend in the interior of the territory, and the longer the perimeter that is needed to define the territory

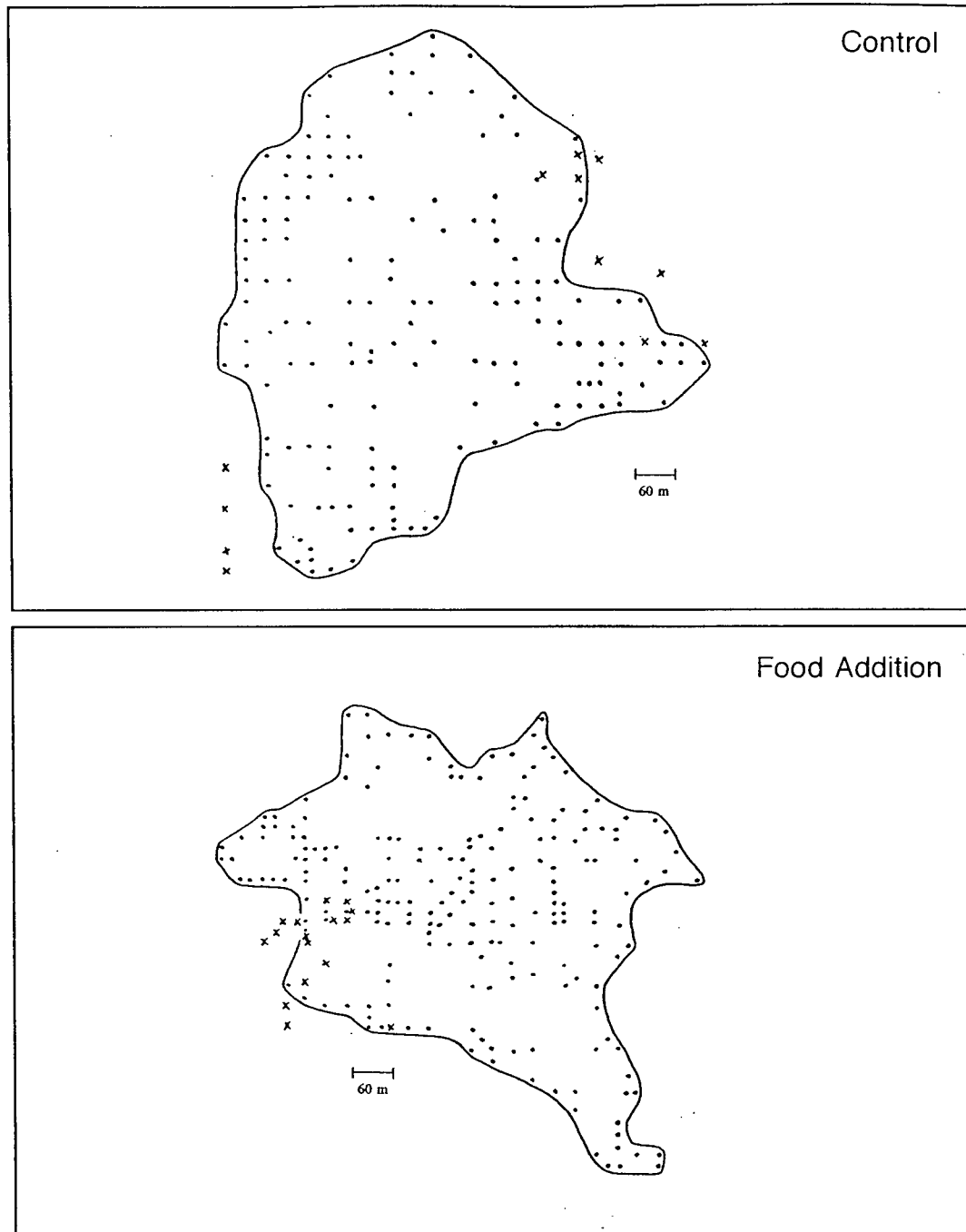


Figure 8. Examples of territory maps for control (a) and food addition (b) groups. Each point represents at least one observation of one or more birds from the group. Locations where birds were judged to be intruding on other territories were not included in the maps. Dots represent members of the owner group, crosses represent neighbouring groups. Areas where there are crosses inside the territory borders drawn were used to calculate overlap.

boundary. Limited visibility in many of the habitat types also contributed to the difficulty of territory mapping.

From trapping records and observations, my assistant and I noted the approximate borders of other territories on the grids where we worked. Most of the groups that included part of a grid in their territories had at least some members colour banded, so we are confident that we were able to accurately distinguish between groups. This allowed us to determine the number of territories that were entirely or partially within the boundaries of three food addition and three control grids.

Results

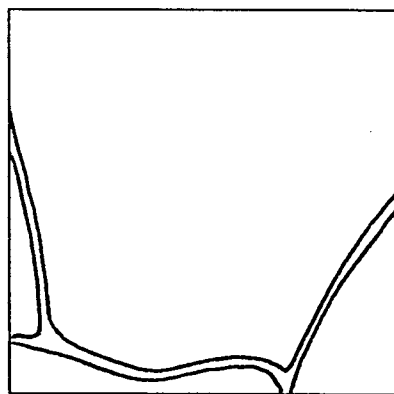
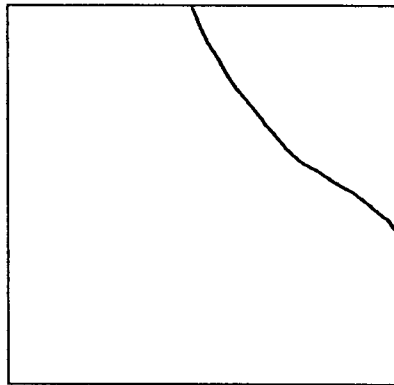
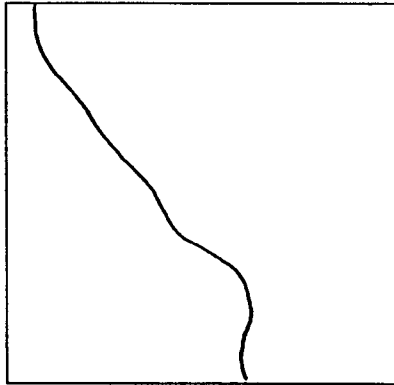
Territory maps consisted of an average of over 220 points as well as points from neighbouring groups that helped to define borders (Figure 8). These points were often concentrated near the edges of the territories since we were interested in defining the territory borders rather than recording proportional usage of the area. The mean size of territories on food addition grids was approximately 30% smaller than control territories. The mean size of five control territories was 23.2 ha (SE = 1.4) compared to a mean area of 15.8 ha (SE = 1.9) for the four territories on food addition grids (t-test, $t=3.19$, $p=0.02$). Based on these results, if the number of territories per grid is strictly proportional to mean territory size (which assumes there is no unoccupied space), there should be more territories on

food addition grids. On the three control grids there were an average of 2.67 territories per grid, and on the three food addition grids studied, there was an average of 4.67 territories (Figure 9). To determine whether this increase is more or less than expected based only on territory size, I used a simple Monte Carlo simulation.

In the simulations, territories were approximated as squares with an area equal to the mean territory size I observed for the respective treatment. A 36-ha grid was placed at random on the landscape of contiguous territories 1000 times, and the mean number of territories per grid calculated. There was no significant difference between the mean number of territories on control grids and the mean number the model predicted (Table 6). There were 1.7 times more territories on food addition grids than expected based on the model (Table 6).

Because some of the nine mapped territories were adjacent to each other, only six territories were used in the overlap analysis to keep each measurement independent. All but one of the six territories used in this analysis had at least some overlap with other territories. The amount of overlap between territories on control grids was consistently low, while that on food grids was 4.7 times higher compared to control grids. The lack of a statistically significant difference (Figure 10) despite the magnitude of the difference is due to the low power of the test (estimated to be 0.3).

Control Grids



Food Addition Grids

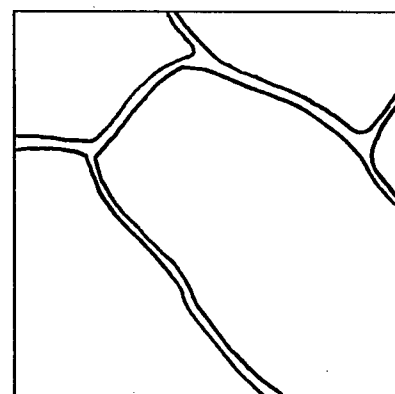
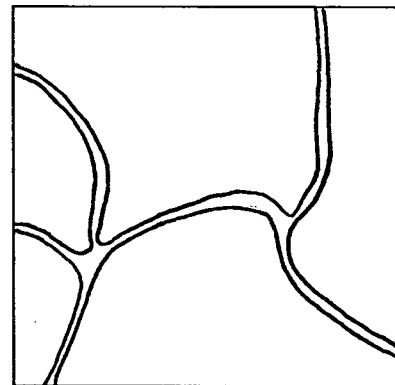
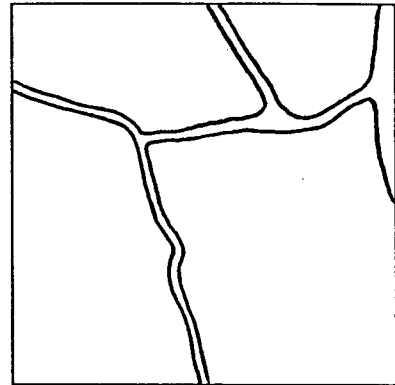


Figure 9. Diagrams showing approximate boundaries between all the territories that had access to three food addition and three control grids. Each square is 600 m by 600 m, representing the borders of the grid.

Table 6. Observed and predicted number of territories per 36-ha grid. Predicted numbers are from a Monte Carlo simulation as described in chapter two. The p-values shown are from t-tests between observed and predicted mean number of territories per grid.

| | Observed | Model | |
|---------------|-------------|--------------|---------|
| Control | | | |
| mean (SE) | 2.67 (0.66) | 2.35 (0.047) | p>0.5 |
| n | 3 | 1000 | |
| Food Addition | | | |
| mean (SE) | 4.67 (0.33) | 2.77 (0.043) | p=0.016 |
| n | 3 | 1000 | |

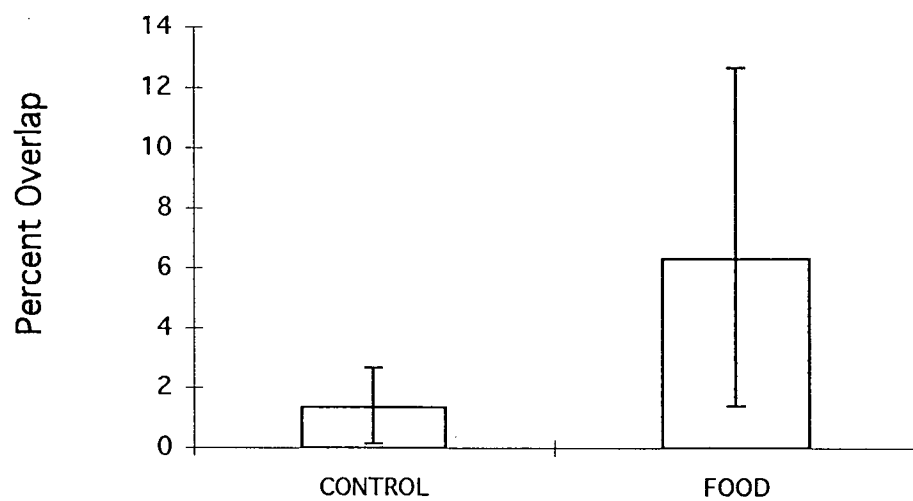


Figure 10. Percent overlap between territories with 95% confidence intervals. The data were arcsine transformed; the values presented are back-transformed. T-test: $t=2.16$, $df=5$, two-tailed $p=0.084$.

The mean number of adult birds per group was identical for food addition and control areas. We were confident of our estimates of the number of members in each group for five control and five food addition groups. Four groups had four members, and one had three on both supplemented and control grids (mean=3.8, SE=0.2). To be confident of our counts, all or all but one bird had to be colour banded, and we had to see them regularly enough that we were able to verify our counts.

Discussion

Methodology

In general the methods used to map territories were successful, but some difficulties arose. Because the territories are large, neighbouring groups are not seen together frequently at territorial borders. Woolfenden and Fitzpatrick (1984) were able to use very conspicuous territorial displays at borders to map Florida scrub jay territories. The scrub jays they studied are also strongly territorial. Although grey jays do not generally tolerate other jays on their territories, border displays are not as frequent or as visible as described in Woolfenden and Fitzpatrick (1984). Another factor that makes territory mapping easier is areas that are not used by the animals. In scrub jays, Woolfenden and Fitzpatrick (1984) found that the birds never used low-lying and open areas; consequently

these areas often formed a large part of the territorial boundaries.

Grey jays use such a diversity of habitats, that no such natural features were consistently useful in mapping territories. The use of radio telemetry might be useful for quickly locating groups, but triangulation is unlikely to be precise enough to map the relatively complex borders of grey jay territories. Nonetheless, the use of grid stakes and aerial photos appears to be a reliable method for mapping territories.

Territory Size

To apply Schoener's (1983) model, we first must be able to classify the territory holder as either a time minimizer, or an energy maximizer (Schoener 1971). A time minimizer meets a minimum feeding requirement to meet its needs, whereas an energy maximizer tries to gain as much energy as possible. Energy maximizers can be constrained by either the time available to forage, or by a processing constraint.

Because jays store food in the summer for use over winter and into the breeding season (Rutter 1969, personal observation) it seems likely that they should be energy maximizers (Pianka 1976). Waite and Ydenberg (1994) found that caching by jays was accurately modeled as net rate maximizing (where the ratio of energy stored, less the cost of transport, to time spent caching is maximized) .

Ydenberg et al. (1994) show that this currency is expected

when foraging is limited by time. This is consistent with grey jays being an example of Schoener's first type of energy maximizer, which is constrained by time available for foraging rather than by a capacity constraint (Schoener 1983).

Moreover, in summer there was no significant difference in the proportion of time spent foraging by birds with added food and those on control areas. As was discussed in chapter 2, this suggests that both groups of birds were spending as much time as possible in foraging activities. This, and the fact that jays are foraging to make caches and not just for immediate consumption, is good evidence that grey jays are constrained by time rather than processing constraints in summer. In summary, of the three types of territory holder defined by Schoener, grey jays meet the criteria for being classed as energy maximizers with time constraints.

The next consideration in applying Schoener's model of optimal territory size is what he describes as the type of environmental variation. More explicitly, this refers to the relationship between food density and intruder pressure. The four types are as follows:

1. a change in food density does not change intruder pressure;
2. a change in intruder pressure independent of changes in food abundance;

3. an increase in food density increases intruder pressure; and

4. an increase in intruder pressure decreases food density in the territory.

For grey jays, intruders can have two effects: intruders can steal caches food resources, or they can steal uncached food. There is also the cost of expelling intruders. Although there may be arguments for not simply dismissing this latter cost, I believe that the energy spent in flight during chases and vocalizations is minimal relative to the energy lost when food or caches are stolen (personal observations). Although this assumption seems reasonable, it remains to be confirmed.

First I consider the relationship between cache density and intruder pressure. Waite (1988) found the rate of loss of simulated grey jay caches was density dependent. Density dependent survival of caches seems to be common in scatterhoarders: Stapanian and Smith (1984) found such a relationship for simulated fox squirrel (*Sciurus niger*) caches, and Clarkson *et al.* (1986) found that the distribution of magpie (*Pica pica*) caches was consistent with density dependent cache loss. Thus, food addition, by increasing the number of caches made (chapter 2, Figure 4) should result in proportionally greater losses due to intruders.

Second, I consider the relationship between uncached food density and intruder pressure. This interaction is

less clear. Presumably the same mechanism that allows thieves to steal a greater proportion of caches as cache density increases, would result in a similar density dependent rate of loss of uncached food. If this assumption is valid, then food addition should result in an increased effect of intruders. In summary, there is evidence (Waite 1988) that increasing food density in grey jay territories results in increased costs of intruders.

The final piece of information needed in Schoener's (1983) model is how the costs of intruders change with the area of the territory. As grey jay territory size increases cache density should decrease and the cost of theft by intruders should therefore decrease. As territory size increases the density of uncached food will not change, but the proportion of total food resources stolen by intruders will decrease. Thus the net cost of intruders should decrease with increasing territory size.

In summary, grey jays are time constrained energy maximizers, increasing food density results in an increase in intruder pressure (i.e. an increased effect of intruders if not an increase in the number of intruders), and the cost of intruders is likely to decrease as territory size increases. With this information, the optimal territory size for jays on food addition grids is predicted to be smaller than on control grids by Schoener's (1983) model. My results show that grey jay territories do respond in this way to food addition.

Territory Overlap

As food density increases, defense is expected to at first increase, and then to decrease as food becomes very abundant (e.g. Carpenter and MacMillen 1976). In this study the position of grey jays on control grids along this continuum was unknown, which is why the t-test comparing overlap was two-tailed. Food addition could either increase the value of exclusiveness and therefore reduce the amount of overlap, or it could increase the food density to the point where the benefits of exclusiveness begin to fade, which would lead to more overlap on food addition grids. In the extreme case, if the Kluane food addition increases food density to the point where defense is no longer economical, territoriality should break down. However, because jays are dependent on their caches in winter, and winter is such an energetically stressful period (Waite 1991), such an extreme case would be unlikely. These responses depend on the territorial behaviour of jays being plastic enough to respond to the food addition.

Although my sample size of territories was small, there appears to be a slight increase in overlap between grey jay territories on food addition grids compared to control grids. The difference was not statistically significant, but the power of the t-test was estimated to be 0.3, signifying a 70% chance of making a type II error. The available data is not sufficient to draw conclusions, but

does suggest that more research is warranted. Stamps and Tanaka (1981) measured percent overlap in juvenile *Anolis aeneus* home ranges. These juveniles are normally territorial, but these territories sometimes overlap with those of neighbours. Stamps and Tanaka (1981) found that overlap increased when food was added uniformly through the study area during the dry (reduced food) season. This situation is similar to the food addition to grey jays in the summer. In both cases the animals are experiencing food shortages: the density of food for the lizards is reduced in the dry season (Stamps and Tanaka 1981), and the jays are food limited by time constraints. In both cases there appears to be an increase in the amount of overlap.

In this study I did not measure territory size and overlap in winter. Also, this study took place during the low of the "10 year cycle" of snowshoe hare (*Lepus americanus*) when there is little carrion available to supplement grey jay caches. Measuring territory size and overlap in winter and when natural food is more abundant may lead to more insight into how these features of territories vary in response to environmental conditions. Stamps and Tanaka (1981) found home range overlap in *A. aeneus* did not increase when food was added to an already food-rich environment in the wet season, and in control areas, there was more overlap in the dry season than in the wet season.

An alternative explanation for the overlap observed is that the neighbouring groups that had the greatest overlap

had familial ties, and so greater overlap was permitted. In Florida scrub jays, new territories are sometimes formed by the helpers of one group (usually offspring of the mated pair) defending part of the home and/or neighbouring territories (Woolfenden and Fitzpatrick 1984). If a similar process occurs in grey jays, the relatedness explanation may be valid (although no such overlap was noted in scrub jay territories). More will have to be learned about how grey jay territories are formed and how juveniles disperse before these explanations can be distinguished.

Number of Territories per Grid

There were more territories on food addition grids than expected based on a simple simulation model. The model used a simplified landscape of territories and generated the expected distribution by laying 1000 36-ha grids at random on this landscape and counting the number of territories on each grid. When simulating control and food addition grids, the model used the observed mean territory size for the respective treatments (23.2 ha for control, and 15.8 ha for food addition grids). The observed mean number of territories per 36-ha control grid was not significantly different from the model's expected mean. This suggests that control territories are randomly distributed with respect to the Kluane grids as the model assumes.

When the model was run to simulate food addition grids the expected mean number of territories was less than the

observed mean. This suggests that the increase in number of territories on food addition grids is not solely due to the smaller mean size of territories on these grids, and that the food addition has attracted territories. Similar responses have been found in other studies. Boutin (1984) found that some snowshoe hares that were attracted to a food addition area became residents, but others commuted to and from their home ranges off the site. In the territorial red squirrel (*Tamiasciurus hudsonicus*), Klenner and Krebs (1991) found increased densities on food addition sites, and some of the immigrants seemed to become resident. In their study the pulse food addition ended in the fall, at which time densities on supplemented sites fell to control levels over the next six months (Klenner and Krebs 1991). Boutin (1990) raises the possibility that apparent increases in population densities may be partly due to an increase in the effective censusing area caused by the attraction of animals to the supplemental food. My results support this hypothesis in the case of grey jays.

Based on the number of territories per grid and average group size, 75% more groups had access to the food addition grids compared to control grids. Since food addition had no effect on the number of birds per group, the number of birds per grid is also 75% higher. In a census of the population on the grid without knowledge about territory sizes, this would likely translate into an estimate of densities being 75% higher on food addition grids. Based on mean territory

size, densities on food addition grids were only 47% higher than on control grids, representing a considerably smaller response to food addition than would be estimated with less labour intensive methods.

In the case of grey jays and other territorial animals, comparing territory sizes and overlaps will avoid the problem of attracting individuals to the treatment areas. It is more difficult when a population includes floaters (non-territorial individuals) or when the animal is non-territorial. In such cases several individuals may be using the same areas, making it harder to distinguish commuters from residents. As Boutin (1990) suggests, increasing the spatial and temporal scales of food supplementation experiments (which tend to be very small in most studies) could resolve these problems. Food additions should be made to areas large enough that the census area in the interior is not affected by commuting individuals, and they should be long enough that territorial borders, and home range conflicts are resolved before the censusing is done.

The problem of attracting individuals, although it may never change the qualitative results of a study, will make comparing the responses of different organisms and different environments unreliable. Explicit study of this phenomenon is needed to understand how it may bias studies using food additions.

Summary

I found that grey jays on food addition grids had smaller territories than control birds. This result is consistent with Schoener's (1983) model of optimal feeding territory size. I also found that there was a slight increase in the amount of overlap between territories, but a larger sample size is needed to determine if the observed differences are real, or are just artefacts of small sample size. Finally, there were more territories on food addition grids than on control grids. This difference was not solely attributable to smaller territory sizes on food addition grids, and likely represents the increased value of the habitat due to the food addition.

Chapter 4: General Discussion

In this study I examined the response of grey jays (*Perisoreus canadensis*) to a long term food addition. The two areas I examined were winter body mass regulation and territoriality.

Overwinter Condition

In chapter two I tested four hypotheses about the factors that limit overwinter body mass in grey jays. I found evidence that winter weights of grey jays were limited by food supply and by costs associated with extra weight. Birds that had supplemental food year-round made more caches in the summer than control birds did. As a result, these birds maintained higher body condition through the winter and yet were able to spend less time foraging for food than control birds.

From these results, three areas for future work become apparent. First, the nature of food limitation is not clear. The value of extra food can be either in aiding daily survival through the winter, or as extra fuel for breeding in early spring (Jansson et al. 1981). The relative importance of these components can be explored by supplementing food at different times of the year and comparing the responses of jays.

A second area for future research is the nature of the costs of weight. Two previous correlational studies (Rogers

1987, Waite 1992) found patterns consistent with costs to weight as in Lima's (1986) and McNamara and Houston's (1990) models of winter body mass. My results provide experimental evidence for these costs. Lima (1986) assumed the cost was the risk of predation, and that predation risk increased at an increasing rate with mass. McNamara and Houston (1990) modeled both mass-independent and mass-dependent predation risk as the costs of foraging. The assumption that predation risk is the ultimate cost of added weight remains untested; the cost may simply be the weight in and of itself. The heavier the bird, the greater its transport and body maintenance requirements will be (Blem 1975, 1976). A physiological study would reveal the relationship between weight and metabolic expense. A study of the impact of predation on the birds might also lead to some insights into whether predation risk is a likely cost.

The third area requiring more study is the pattern of seasonal weight trends. I found in one year of study that under natural conditions grey jay weights declined between summer and fall, and then increased from fall to winter again. When provided with supplemental food, however, the jays I monitored increased from summer to fall and maintained high weights through the winter. This difference suggests that food addition may change the way caches are made and used.

The grey jays appeared to rely entirely on the caches they made in the summer and fall for overwinter food. When

foraging in the summer, the birds can either consume the food and store the energy as fat reserves, or they can cache the food and store the energy in that way. As my results show, there is some cost to carrying weight, although the exact form or magnitude of that cost remains uncertain. At the same time, storing energy as caches can be risky if they rot, are forgotten, or are stolen by other animals or conspecifics. Furthermore, the relative importance of these costs will change throughout the year, resulting in a complex system of relative costs and benefits to fat storage versus caching.

A comparison of time budgets between food addition and control birds through the fall when the weight trends are so different is needed to clarify why the weight trends are so different (i.e. is this a transition period between making and consuming caches?). It should then be possible to model the tradeoffs between making caches and putting on fat in the summer, and retrieving caches and keeping caches in the winter.

Territoriality

Based on the results of other studies, I was able to fit grey jays into Schoener's (1986) model of territory size. To predict how territory size will respond to food addition, one must know whether the animal is a time minimizer or energy maximizer, and the nature of intruder pressure and defense costs must be clear. This information

is crucial if the mechanisms behind the response are to be understood. For grey jays, Schoener's model predicts that territory size should decrease as food density increases. In chapter three I showed that grey jays maintain smaller territories when provided with extra food, supporting this model. Schoener's model illustrates that simply observing how territory sizes respond to food addition is not intrinsically interesting. There are only three possible responses (increase, decrease, no change) but many slightly different mechanisms can lead to that change. In future work on territory size in response to food addition, an understanding of these mechanisms will be crucial.

Another finding of interest was that the food addition appears to have drawn in territories. The mean number of territorial groups that were entirely or partly within the borders of the 36-ha grids I was using, is not significantly different from the estimated mean of a Monte Carlo simulation that assumed territories were distributed randomly with respect to the grids. There were more territories on food addition grids than predicted by the model, even when the smaller mean size of territories was taken into account. This implies that the territories have changed shape in a way that more groups have access to at least part of the food addition. This has some implications for the use of food additions to study population density.

One of the most common goals of food addition experiments is to study population dynamics, and the

majority of these studies have found increased densities of the study animal (Boutin 1990). Although these results probably represent increases in density of the study animals, the data may be confounded by animals that are attracted to the food, but which are not actually residents of the food addition area. Boutin (1984) found that non-territorial snowshoe hares (*Lepus americanus*) commuted from their home ranges off the supplemented grid to forage on the added food. I found similar results for a territorial animal. The increase in density as measured by the inverse of the mean territory size is less than the increase in the number of jays that have access to the food addition grids. If useful comparisons are to be made between species and environments, or if the results of these studies are to be used in mathematical models, the distinction between real and apparent effects of food additions on population densities should be made.

Conclusion

This study examined some of the effects a long term food addition has had on a population of grey jays in the southwest Yukon. The birds are abundant, relatively tame, and habituate to human observers. In general they are quite trappable and easily observed. These factors combine to make grey jays good subjects for studying a variety of ecological questions.

Caching and cache use has received much recent attention (McNamara et al. 1990, Nilsson et al. 1993, Hitchcock and Houston 1994, Waite and Ydenberg 1994). By comparing grey jays, which rely heavily on caches made in the summer as overwinter food, to other birds that rely less on long term caches (e.g. European nuthatch, *Sitta europaea*; Nilsson et al. 1993) or birds that make short term caches (e.g. various tits, *Parus* spp.; McNamara et al. 1990) we may be able to get a more unified understanding of caching and foraging behaviour in birds.

Literature Cited

- Addicott, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340-346.
- Aleksiuk, M. 1970. The function of the tail as a fat storage depot in the beaver (*Castor canadensis*). *J. Mamm.* 51:145-148.
- Blem, C.R. 1975. Geographic variation in wing-loading of the house sparrow. *Wilson Bull.* 87:543-549.
- Blem, C.R. 1976. Patterns of lipid storage and utilization in birds. *Amer. Zool.* 16:671-684.
- Blem, C.R. and J.F. Pagels. 1984. Mid-winter lipid reserves of the golden-crowned kinglet. *Condor* 86:491-492.
- Boutin, S.A. 1984. Effects of late winter food addition on numbers and movements of snowshoe hares. *Oecologia* 62:393-400.
- Boutin, S.A. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* 68:203-220.
- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.
- Carpenter, F.L., and R.E. MacMillen. 1976. Threshold model of feeding territoriality and a test with a Hawaiian honey-creeper. *Science* 194:639-642.
- Clarkson, K., S.F. Eden, W.J. Sutherland, and A.I. Houston. 1986. Density dependence and magpie food hoarding. *J. Anim. Ecol.* 55:111-121.
- Davies N.B. 1978. Ecological questions about territorial behaviour in *Behavioural ecology: an evolutionary approach*. J.R. Krebs and N.B. Davies eds. Blackwell: Oxford.
- Ebersole, J.P. 1980. Food density and territory size: an alternative model and a test on the reef fish *Eupomacentrus leucostictus*. *Am. Nat.* 115:492-509.
- Enoksson, B., and S.G. Nilsson. 1983. Territory size and population density in relation to food supply in the nuthatch *Sitta europaea* (Aves). *J. Anim. Ecol.* 52:927-935.

- Ehrlich, P.R., D.S. Dobkin, and D. Wheye. 1988. The Birder's Handbook. Simon and Schuster: New York.
- Evans, P.R. 1969. Winter fat deposition and overnight survival of yellow buntings (*Emberiza citrinella* L.). J. Anim. Ecol. 38:415-423.
- Ewald, P.W., and F.L. Carpenter. 1978. Territorial response to energy manipulations in the Anna hummingbird. Oecologia 31:277-292.
- Ewald, P.W., and S. Rohwer. 1982. Effects of supplemental feeding on timing of breeding, clutch size, and polygyny in red-winged blackbirds *Agelaius phoeniceus*. J. Anim. Ecol. 51:429-450.
- Hainsworth, F.R., and L.L. Wolf. 1978. The economics of temperature regulation and torpor in nonmammalian organisms in Strategies in Cold, L.C.H. Wang and J.W. Hudson eds. Academic Press: New York.
- Hinde, R.A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.
- Hitchcock, C.L., and A.I. Houston. 1994. The value of a hoard: not just energy. Behav. Ecol. 5:202-205.
- Hixon, M.A. 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115:510-530.
- Hixon, M.A. 1982. Energy maximizers and time minimizers: theory and reality. Am. Nat. 119:596-599.
- Jansson, C., J. Ekman, and A. von Brömssen. 1981. Winter mortality and food supply in tits *Parus* spp. Oikos 37:313-322.
- King, J.R. 1972. Adaptive periodic fat storage in birds. pp. 200-217 in Proceedings of the Fifteenth International Ornithological Congress. K.H. Voous, ed. Brill, London, England.
- Klenner, W., and C.J. Krebs. 1991. Red squirrel population dynamics. I. The effect of supplemental food on demography. J. Anim. Ecology 60:961-978.
- Kotliar, N.B., and J.A. Wiens. 1987. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253-260.
- Krebs, C.J. 1989. Ecological Methodology. Harper and Row: New York.

- Krebs, C.J., B.S. Gilbert, S. Boutin, A.R.E. Sinclair, and J.N.M. Smith. 1986. Population biology of snowshoe hares I: Demography of food supplemented populations in the southern Yukon. *J. Anim. Ecol.* 55:963-982.
- Krebs, C.J. and G.R. Singleton. 1993. Indices of condition for small mammals. *Aust. J. Zool.* 41:317-323.
- Krebs, C.J., R. Boonstra, S. Boutin, M. Dale, S. Hannon, K. Martin, A.R.E. Sinclair, J.N.M. Smith, and R. Turkington. 1992. What drives the snowshoe hare cycle in Canada's Yukon? in *Wildlife 2001: Populations*, ed. D.M. McCullough and R. Barrett. 886-896.
- Lima, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377-385.
- Lucas, J.R. 1994. Regulation of cache stores and body mass in Carolina chickadees (*Parus carolinensis*). *Behav. Ecol.* 5:171-181.
- Mares, M.A., T.E. Lacher, Jr., M.R. Willig, and N.A. Bitar. 1982. An experimental analysis of social spacing in *Tamias striatus*. *Ecology* 63:267-273.
- McNab, B.K. 1963. Bioenergetics and the determination of home range size. *Am Nat* 97:133-140.
- McNamara, J.M., and A.I. Houston. 1990. The value of fat reserves and the tradeoff between starvation and predation. *Acta Biotheoretica* 38:37-61.
- McNamara, J.M., A.I. Houston, and J.R. Krebs. 1990. Why hoard? The economics of food storing in tits, *Parus* spp. *Behav. Ecol.* 1:12-23.
- Myers, J.P., P.G. Connors, and F.A. Pitelka. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *Auk* 96:551-561.
- Nilsson, J.-Å., H. Källander, and O. Persson. 1993. A prudent hoarder: effects of long-term hoarding in the European nuthatch, *Sitta europaea*. *Behav. Ecol.* 4:369-373.
- Novakowski, N.S. 1967. The winter bioenergetics of a beaver population in northern latitudes. *Can. J. Zool.* 45:1107-1118.
- Panuska, J.A. 1959. Weight patterns and hibernation in *Tamias striatus*. *J. Mamm.* 40:554-566.

- Pianka, E.R. 1976. Natural selection of optimal reproductive techniques. *Am. Zool.* 16:775-784.
- Price, K., K. Broughton, S. Boutin, and A.R.E. Sinclair. 1986. Territory size and ownership in red squirrels: response to removals. *Can. J. Zool.* 64:1144-1147.
- Rogers, C.M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* 68:1051-1061.
- Rogers, C.M., and J.N.M. Smith. 1993. Life-history theory in the non-breeding period: trade-offs in avian fat reserves. *Ecology* 74:419-426.
- Rutter, R.J. 1969. A contribution to the biology of the Gray Jay (*Perisoreus canadensis*). *Can. Field Nat.* 83:300-316.
- Schoener, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:370-404.
- Schoener, T.W. 1983. Simple models of optimal feeding-territory size: a reconciliation. *Am. Nat.* 121:608-629.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry*, 2nd ed. W.H. Freeman and Company: New York.
- Stamps, J.A., and S. Tanaka. 1981. The relationship between food and social behavior in juvenile lizards (*Anolis aeneus*). *Copeia* 1981:422-434.
- Stapanian, M.A., and C.C. Smith. 1984. Density dependent survival of scatterhoarded nuts: an experimental approach. *Ecology* 65:1387-1396.
- Stenger, J.A. 1958. Food habits and available food of ovenbirds in relation to territory size. *Auk* 75:335-346.
- Vander Wall, S. 1990. *Food Hoarding in animals*. University of Chicago Press.
- Waite, T.A. 1988. A field test of density-dependent survival of simulated gray jay caches. *Condor* 90:247-249.
- Waite, T.A. 1990. Effects of caching supplemental food on induced feather regeneration in wintering Gray Jays *Perisoreus canadensis*: a ptilochronology study. *Ornis Scand.* 21:122-128.
- Waite, T.A. 1991. Nocturnal hypothermia in gray jays *Perisoreus canadensis* wintering in interior Alaska. *Ornis Scandinavica* 22:107-110.

- Waite, T.A. 1992. Winter fattening in Gray Jays: seasonal, diurnal and climatic correlates. *Ornis Scand.* 23:499-503.
- Waite, T.A., and J.D. Reeve. 1992. Caching behaviour in the gray jay and the source-departure decision for rate-maximizing scatterhoarders. *Behaviour* 120:51-67.
- Waite, T.A., and R.C. Ydenberg. 1994. What currency do scatter-hoarding gray jays maximize? *Behav. Ecol. and Sociobiol.* 34:43-49.
- Woolfenden, G.E., and J.W. Fitzpatrick. 1984. The Florida scrub jay: Demography of a cooperative-breeding bird. Princeton University Press: Princeton.
- Wolff, J.O., and G.C. Bateman. 1978. Effects of food availability and ambient temperature on torpor cycles of *Perognathus flavus* (heteromyidae). *J. Mamm.* 59:707-716.
- Wrazen, J.A., and L.A. Wrazen. 1982. Hoarding, body mass dynamics, and torpor as components of the survival strategy of the eastern chipmunk. *J. Mamm.* 63:63-72.