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The role of naturally stored food supplies in the winter diet of the boreal Willow Tit *Parus montanus*

ANDERS BRODIN

Abstract

The average amount of food that was stored during an autumn by Willow Tits *Parus montanus* was estimated by sampling hoarding intensities and analysing the energetic contents of the stored items. Measurements of retrieval and losses of the stored food made it possible to calculate how much of the stored food that actually was used by the hoarder. Also the chemical composition of the stored food was analysed, and a comparison of the energy contents of the food eaten with the energy requirements of the birds made it possible to assess the importance of hoarded food in the winter diet. According to the calculations, hoarded food can be assumed to account for almost all food that was consumed during December, whereas it was estimated to constitute around 24 % of the food eaten from January to March. During colder winters, with higher energetical stress, it is possible that stored supplies could be more important during this part of the winter, perhaps of the magnitude of 45 % of the total food consumed.

Anders Brodin, Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden

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Introduction

Boreal tit species, such as the Willow Tit *Parus montanus*, scatter hoard large quantities of seeds and larvae during the autumn (Haftorn 1956, 1959, Pravosudov 1985, Brodin 1994b). The seeds most frequently stored are those of spruce *Picea abies*, pine *Pinus silvestris*, juniper *Juniperus communis*, and hemp nettle *Galeopsis* spp., nuts and different kinds of larvae and other animal matter (Haftorn 1956, Brodin 1994b). Estimates of the total amount of seeds stored by one individual during the course of one autumn range between 50,000 to 80,000 (Haftorn 1959) and 150,000 items (Pravosudov 1985). Both of these estimates are from spruce peak mast years, when hoarding intensity may be very high. It is difficult to assess the acccuracy of these estimates for several reasons. Both are calculated on the means of all observations, not mean values for individuals. This makes it possible that "tame, high intensity hoarders" are overrepresented. Further, the lack of predetermined sampling periods may lead to periods of high hoarding intensity (which are easy to observe) being overrepresented, resulting in over-estimation of the number of hoarded items. It is also probable that hoarders do not cache from dawn to dusk at an equally high rate. Instead intensive hoarding bouts are often followed by periods of lower hoarding rates (own observations). Finally, different kinds of food require different search, handling and storing times (Haftorn 1956).

In order to get an idea of how important stored food is in the Willow Tit winter diet, measurements of when it is retrieved and how much of it that is lost before consumption are crucial. It is difficult to observe retrieval directly in nature, but I have assessed the longevity of stored food in my study area by monitoring 100 caches at regular intervals for 150 days (Brodin 1994a). Also, loss of caches due to pilfering and weather could decrease the supply of stored food. I have assessed the background loss of stored food in the area by rebaiting already retrieved caches and then monitor them for 126 days (Brodin 1994c). This is, however, long-term loss and there is also a possibilty of "immediate pilfering" directly after a food item is stored (Baker et al. 1990, Hitchcock 1992). I have observed this in the field, with theft both by conspecific Willow Tits and by great tits *P. major*.

Rehoarding, i.e. when stored items are retrieved and then stored again in new locations, has been suggested to be frequent in the Willow Tit (Haftorn 1956, Pravosudov 1985, Nakamura & Wako 1988), although it may not be easy to separate rehoarding of own caches from pilfering of those of others. Rehoarding could be a way of maintaining control over stored food the locations of which would otherwise have been forgotten (Brodin 1992). If rehoarding is frequent, consumption of cached food could occur considerably later than predicted by the disappearance of the caches I monitored (Brodin 1994a).

Seeds are more durable and remain longer in the caches than larvae, the main animal component among stored food (Brodin 1994b). Cached seeds had a minimum (many seeds still remained in their caching locations at the end of the study) mean longevity of 70.6 days , whereas larvae had a mean longevity of only 20.1 days (Brodin 1994b). Thus, stored seeds are probably more important than stored larvae in the winter diet of the Willow Tit.

The aim of this study was to estimate the amount of food that Willow Tits store in the autumn and to calculate how important this food is energetically during the winter.

Methods

I collected data on the hoarding behaviour by individually colour marked Willow Tits during five consecutive autumns, from 1989 to 1993, south of Stockholm, south-central Sweden (Brodin 1992). From 1989 to 1991 I focused on the caching acts, and did not record hoarding intensities (Brodin 1992, 1994a,b).

During 1993 (Brodin et al. unpubl.) we measured hoarding intensities of free-roaming Willow Tits using a standardized sampling technique, to compare simultaneous observations from different geographical areas. Foraging birds were followed for at least 20 60-s bouts from 6 September to 7 November, and data were collected from 09.30 to 15.30 hours almost daily (Brodin et al. unpubl.). Less extensively I also collected data with the same observation technique during other times of the day and earlier and later in the season. Normally observations of one individual were collected during one month, but twelve individuals were sampled both in September and October. The recorded intensities of these are included in the means of both months. This is conservative since any individual tendencies will decrease differences between months. In all other comparisons each individual is represented by one value.

The autumn 1992 I recorded hoarding intensities in a less systematic way. I observed foraging (individually marked) Willow Tits as long as they were visible, typically for periods from 30 s up to five minutes. This technique will probably overestimate periods of intensive hoarding because this activity is easy to observe. Still, these observations may serve as a control to intensities measured during 1993. Also, from 1992 I have more data from early mornings and late afternoons, and before 6 September and after 7 November. All statistical tests are two-tailed. To indicate the precision of my calculations I give the standard error for variables that I have measured, and denote this ±. In the calculations, I use the variables (hoarding intensities, type of food, etc.) measured during the autumn of 1993.

When a Willow Tit hoards a food item it is carried in the beak, typically to a nearby tree. I refer to these transports as "hoarding trips" and they are identical to Haftorns (1956) "long-distance transports". The number of food items stored is not equal to the number of flight trips from the food source to the storing positions since Willow Tits normally carry several seeds in the beak. These seeds are first deposited in a temporary site "the left luggage technique" (Haftorn 1956), after which they are positioned out in separate locations in the vicinity. Because I did not record this regularly, I estimate minimum figures, in order not to overestimate the amount of hoarded food. Willow Tits remove the fleshy pulp of the juniper berries and then store the seeds. I peeled a large number of juniper berries from the study area before having their contents analysed (Table 3), and almost all contained three seeds. A few contained only two, so 2.5 juniper seeds carried per hoarding trip should be a fair estimate. Hemp nettle normally contains four seeds in each fruit, and I have observed Willow Tits storing one to four seeds and use Haftorns (1956) minimum average estimate of 2.3 seeds per trip. For conifer seeds I rely on Haftorns (1956) estimate of "at least two seeds per trip". Except for aphids, animals are normally stored singly, and some large specimens may even be split in several caches (own observations).

Seeds are frequently stored in intensive bouts from very obvious sources, and hence normally easy to identify. For food that is more difficult to identify, like lepidopteran larvae, I collected some specimens for examination in the laboratory, and then tried to determine the rest through binoculars using the former as a reference. This will probably give a fair picture of the stored species, since a particular species typically will appear in large numbers for a short period e.g. when *Bupalus piniarius* leave the coniferous needles to pupate in the ground (Hedqvist et al. 1975).

When the energy contents of food could not be found in the literature it was analysed with traditional methods (Jennische & Larsson 1990) at the Swedish National Laboratory for Agricultural Chemistry. I assume that carbohydrats (except fibers) and fat are metabolised as energy sources. It is not clear if proteins are used for energy generation on a regular basis. To obtain an energy value when also proteins are included, one can multiply the presented values with 1.21. Birds may metabolise proteins more efficiently than mammals (Hazelwood 1972, Bairlein 1985) and according to Martin (1968) and Fisher (1972) small birds probably need less than 10 % protein in their diet for body maintenance. It is probable that the high proportion of invertebrates in the diet (Jansson 1982) will cover this.

Results

Hoarding intensities

The mean hoarding intensity per individual during the hoarding period (see below) was 0.50±0.08 (n=42) trips / minute, measured on a mean of 29 observations per individual. During 1992 the mean intensity was 0.63±0.06 trips / minute (n=31). No significant year effect could be found (t-test, t=1.64, p=0.106) suggesting that 1993 was not an aberrant year.

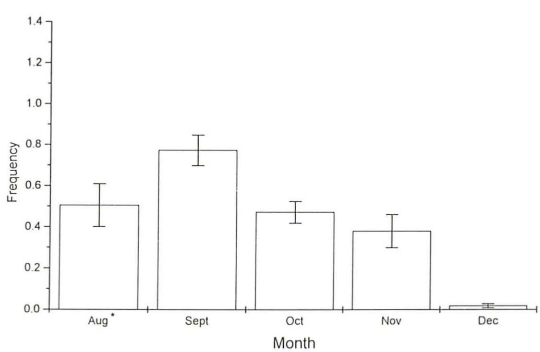

Fig. 1. Hoarding intensities during five months. Even if December is excluded, the difference is significant (Kruskal-Wallis ANOVA, H=13.8, df=3, p=0.003).
* Most August records are from the last week of the month.

Hamstringintensiteter under fem månader. Även om december inte tas med, är skillnaden signifikant.
** De flesta observationerna i augusti är från månadens sista vecka.*

Table 1. Hoarding intensities during the day.
Hamstringsintensiteter under dagen.

Time	<09.30	09.30–12.00	12.00–15.30	>15.30
Mean	0.55	0.57	0.61	0.57
SE	0.08	0.04	0.05	0.11
n*	29	59	60	13

* Number of individuals in pooled data from 1992 and 1993.

** Antalet individer i sammanslagna data från 1992 och 1993.*

I only observed occasional hoarding acts in late July and early August. Later in August (most August observations in Fig. 1 are from the last days of the month), the hoarding intensity increased to reach a peak in September, whereafter it declined during October and almost ceased around 20 November when a lasting snowcover arrived (Fig. 1). I therefore consider the hoarding period to last from 15 August to 20 November. During August and September, the Willow Tits seemed to store more hemp nettle and juniper seeds than later during the autumn when they predominantly stored larvae. Using data from 1989–1993, the proportion of seeds of the stored food in August and September (0.78±0.01, n=55) was significantly higher (U=518, p>0.001) than in October and November (0.24±0.01, n=57), when the tits stored more larvae (U=521, p<0.001, both tests Mann-Whitney U-test).

To increase sample sizes on the daily variation in hoarding intensities, I pooled data from the years when I recorded hoarding intensities, i.e. 1992 and 1993. Intensities were similar over the day (Table 1), although it should be noted that I observed no storing during the first hour after sunrise at two dawn visits in mid September.

In early winter, rehoarding should be at its peak and most easy to observe, since there is still much stored food around, and hoarding from other sources has almost ceased (Haftorn 1956, Pravosudov 1985). The hoarding intensity in December was 1.8 (±1) trips / h (Fig. 1), which can be considered a maximum estimate of the rehoarding intensity. The tits' activity period is seven hours in both November and December, because Willow Tits are active a larger part of the day when days get shorter (Haftorn 1989). This intensity corresponds to a maximum of 13 seeds rehoarded per day during both months, or 390 seeds in November and 403 seeds in December.

Table 2. Proportions of different food types observed to be stored during five years. Means (for individuals, not years) are shown with standard errors.

Proportionerna av de oftast hamstrade födoslagen under fem år. Medelvärden (som är för individer, inte år) ges med standardfel eftersom de sedan används i vidare beräkningar.

Year *År* Food *Föda*	1989	1990	1991	1992	1993	Mean±SE
Hemp nettle *Dån*	0.07	0.34	0.20	0	0.09	0.18±0.04
Juniper *En*	0.21	0.02	0.46	0.46	0.27	0.24±0.01
Conifer seeds* *Barrträdsfrön*	0.52	0.10	0.05	0	0.05	0.16±0.01
***Seeds total** Frön totalt*	***0.80***	***0.48***	***0.72***	***0.46***	***0.41***	***0.58***±0.01
Larvae *Larver*	0.11	0.47	0.23	0.54	0.35	0.34±0.01
***Animal total** Djur totalt*	***0.20***	***0.52***	***0.28***	***0.54***	***0.59***	***0.42***±0.01
n**	15	17	17	8	22	79 –

* Pine and spruce seeds together.
** Individuals observed to store at least four identified food items, some individuals may be included in two different years.

** Tall och gran tillsammans.*
*** individer som observerats hamstra minst fyra artbestämda födoslag, några av individerna kan förekomma två år.*

If the kinds of seed are rehoarded in the same proportions as they are stored, 400 seeds correspond to 40–50 kJ. Larvae are decapitated and often "glued" to the substrate when they are stored, and therefore they are probably not rehoarded (own observations). I have no estimates of rehoarding rates from January to March, but since the amount of stored food is then lower (Brodin 1994), it will have little influence.

Types of food stored

The most frequently stored food items varied much (Kruskal-Wallis ANOVA, H=13 to 44, p=0.01 or less for all types of food tested separately) during 1989 to 1993 (Table 2), probably depending on access. The seeds stored were juniper, hemp nettle, and, depending on year, spruce or pine. Spruce and pine seeds were hoarded in alternative years, and since these seeds have similar masses I pool them as conifer seeds. Spruce seeds were stored much more frequently than pine seeds and I therefore use the energy values from spruce although they are slightly higher than for pine (Turcek 1960). The chemical composition of the seeds preferred for storing is listed in Table 3. Because proportions of the various food components varied much between years, the

Table 3. The chemical contents in % of the most frequently stored seeds, analysed at the National Laboratory for Agricultural Chemistry of Sweden. Estimates used are: 1 g fat=39.4 kJ, 1 g carbohydrate =17,6 kJ, 1 g protein=18.0 kJ (Schmidt-Nielssen 1980).

Innehållet i % i de oftast hamstrade fröna, enligt analys vid Statens Lantbrukskemiska Laboratorium. Uppskattningarna som använts är 1g fett=39,4 kJ, 1g kolhydrat=17,6 kJ och1g protein=18.0 kJ (Schmidt-Nielssen 1980).

Food item *Födoslag* Contents *Innehåll*	Hemp nettle nuts *Galeopsis frön*	Juniper seeds *Enbärs-frön*	Spruce seeds* *Gran-frön*
Carbohydrats total *Kolhydrater totalt*	59.8	71.4	37.5
Ditto excl. fibers *Dito exkl. fibrer*	6.5	36.4	6.2
Fat *Fett*	9.0	9.0	32.6
Protein	20.7	7.6	20.4
Ashes *Aska*	4.6	2.8	3.5
Water *Vatten*	5.9	9.2	6.0
kJ x g-1**	4.7	10.0	13.9
kJ x g-1***	8.4	11.3	17.6

* Spruce seeds analysed by Haftorn (1959).
** Avaliable energy is calculated on fat + carbohydrats (–fibers).
*** If also proteins are metabolised as energy.

** Granfrön analyserade av Haftorn (1959).*
*** Tillgänglig energi har beräknats på fett + kolhydrater (–fibrer).*
**** Om också protein förbränns som energi.*

most meaningful figure to use in the calculations is the mean for all individuals.

Only in 1993 did Willow Tits store clumps of aphids (24 % of the stored food!), a frequent behaviour in coal tits *P. ater*. The birds collected a mean of 20.2±2.3 aphids (n=26) in each stored ball. Normally larvae are by far the most frequently stored animal matter (Table 2), and therefore I treat the animal food as if it only consisted of larvae. Each year I collected a few larvae, which were identified by entomologists. Several of these were *Bupalus piniarius* which, by far, appeared to be the most frequently stored larva as judged from observations through binoculars. In October this species leaves its protected sites in the pine needles to pupate in the ground (Hedqvist et al. 1975) and may then be easy to find for foraging tits. Besides *B. piniarius*, I also found various other types of lepidopteran larvae, fly larvae *Diptera* sp, and several pine wasp larvae, probably *Neodiprion sertifer*. The hard cocoons of the latter were frequently opened and the pupa eaten. I did not analyse the energetic contents of the different invertebrates, but Larsson & Tenow (1979) estimated it to 6710 J per 10 individuals of *N. sertifer*. *N. sertifer* is of similar size to *B. piniarius*, 25 mm, and both live on a pine needle diet, which makes it probable that they are similar in contents.

Accuracy of the estimates

The main source of error in my calculations is the hoarding frequencies. Since I sampled hoarding intensities with a stricter technique during 1993 than 1992, I prefer to use only the former. This will decrease sample size but will probably give more correct means. The mean standard error calculated from Table 4 (weighted for number of days in each month) is 14.8 %. The rehoarding intensity is so low that a standard error of 10 % will mean about 1 seed a day, so I disregard this possible error. Proportions of the different food types and the proportion of animal to plant matter are based on large samples as I can pool them over years. Thus, these will generally have standard errors below 1 % which I consider as negligible.

For two variables, the weight of the food items and their energy contents, I have no dispersion measurement, but the means should be the best available. The energy contents of the seeds were analysed by professional chemists using a few of hundred ground seeds (which I provided). For weight, I give no dispersion, only means for spruce seeds taken from Haftorn (1959), hemp nettle from Grime et al. (1988) and juniper seeds from Snow & Snow (1988). There is of course some variation between individual seeds, but the mean will probably be the same.

Table 4. Calculated mean number of hoarding trips during 1993.
Den genomsnittliga mängden hamstringstillfällen under 1993.

	Daylight hours *Timmar dagsljus*		Intensity *Intensitet*	Number of hoarding trips *Antal hamstringstransporter*
Month *Månad*	per day* *per dag**	per month** *per månad***	trips/h *turer/h*	
August	15.0	224	30.3±7.4	6787
September	13.0	360	46.3±4.5	16668
October	10.2	285	28.3±3.2	8066
November	7.0	140	22.8±4.8	3192
Total	–	1009	–	**34713**

* Daylength from Beck (1980, Table 1). Since I did not observe any hoarding acts during two dawn visits in September, and Haftorn (1989) reports shorter daily activity than daylength during the autumn, I have subtracted one hour each day during August through October.
** I consider the hoarding period to last from 15 August to 20 November (see text).

**Dagslängden från Beck (1980, Tabell 1). Jag har dragit av en timme per dag från augusti till slutet av oktober, eftersom aktivitetsperioden är kortare än dagen under hösten (Haftorn 1989).*
*** Hamstringsperioden varade från 15 augusti till 20 november (se texten för förklaring).*

Table 5. Calculated mean number of stored items.
Beräknat antal hamstringar.

Food item *Födoslag*	No. of hoarding trips* *Antal hamstringsturer**	No. of itemns *Antal objekt*	Total amount stored (g)** *Total mängd hamstrad (g)***	Energy content (kJ) *Energiinnehåll (kJ)*
Hemp nettle *Dån*	6248	14371	69	324
Juniper *En*	8331	20828	333	3332
Conifer seeds *Barrträdsfrön*	5554	11108	79	1096
Total seeds *Summa frön*	**20736**	**46307**	**481**	**4752**
Animals *Djur*	14579	14579	–	9783

* No of trips from Table 4 times mean proportions in Table 2.
** Weights are: hemp nettle 4.8 mg (Grime et a. 1988), Juniper 16 mg (Snow and Snow 1988) and spruce 7.1 mg (Haftorn 1959).

**Antalet transporter enl. Tabell 4 multiplicerat med proportionerna i Tabell 2.*
*** Vikter: Galeopsis 4,8 mg, Enbärsfrö 16 mg och granfrö 7,1 mg.*

The retrieval and loss curves which I use were calculated on data from 100 food caches each, during two consecutive years, and are therefore probably as accurate as they can get (Brodin 1994a,c). The main problem with these disappearance measurements is that they were made during two extremely mild winters, with temperatures seldom below zero. During cold winters retrieval could be higher. The immediate loss (pilfering directly after storing) was 5 % in a laboratory study of the closely related black-capped chickadee *P. atricapillus* (Hitchcock 1992). Pilfering is probably higher in a small aviary than under natural conditions. On the other hand, only two individuals were present in the aviary during that experiment, and during natural storing there are many more potential observers around. Since I have observed "immediate pilfering" several times in the field, 5 % could be a reasonable estimate in order to not overestimate the amount of stored food available for retrieval.

Calculated amount of food stored

The mean total number of hoarding trips per individual can be calculated from the storing intensities during the different months (Fig.1). Knowing the proportions of the various food items stored (Table 2), the number of storing trips for each of these can be calculated (Table 4). The mean number of seeds carried on each trip will then give the total amount stored per individual (Table 5).

From the intensities recorded during 1993, an individual Willow Tit can be estimated to have hoarded on average 46,300±6900 seeds, with a total weight of c. 480±71 g. These seeds would have an energy value of 4750±703 kJ.

Under conditions of food shortage, proteins may also be used as an energy source. The energy contents of the stored food including proteins can be obtained by multiplying my values with 1.21. Since most seeds were stored in September, I regard this estimate as valid from 15 October. Calculated in the same way, the stored animal matter should have had an energetic value of about 9800±1450 kJ.

The daily long-term loss due to factors like pilfering and weather, etc. would have been around 1 % x day^{-1} (Brodin 1994c). Here calculations are more complicated, because this loss should be subtracted from a supply that is already decreasing because of retrieval. To facilitate calculations I subtract this loss over longer periods. The daily percentage has then to be lowered, since it will be working on a gradually smaller suppy, as food is recovered. I therefore approximate it to 0.5 % per day, by the equation $Y= e^{-0.005x}$. With an immediate loss of 5 % because of pilfering at hoarding, and 20 % of the remaining seeds being lost during the following 45 days, 3763 kJ will remain on 1 December, with 50 kJ added from rehoarding. I refer to these 3820 kJ as the "available" supply. In an attempt to determine the pattern of consumption of the stored food, I calculate the disappearance rate of seeds using the data in Fig 2. According to this 43 % of the available supply of seeds disappeared the first month after storing. How-

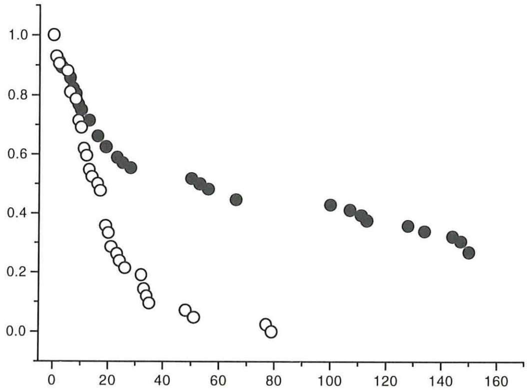

Fig. 2. Disappearance rate of caches stored by naturally foraging Willow Tits during the autumns of 1991 and 1992. Filled symbols represent seeds and open symbols animal matter. Calculated from Brodin (1994a).

Försvinnande av hamstrad föda från höstarna 1992 och 1993. Fyllda symboler är frön och öppna symboler animalisk föda. Data är beräknade ur Brodin (1994a).

ever, the 5 % immediate pilfering should also be included, meaning that the hoarder could have retrieved about 38 % of the seeds, corresponding to 1452 kJ. If seeds corresponding to 50 kJ were rehoarded, and the loss during December was 0.5 % a day before consumption, the hoarder could have consumed around 1205 kJ this month.

Because 27 % of the available supply remained cached at the end of the winter (Brodin 1994a), 30 % or 1146 kJ must have disappeared during January through March (Fig.2). It is not easy to predict the shape of the disappearance curve, and here I simply assume that, after initially being high in December, disappearance rate will remain rather constant during the rest of the winter. With daily losses of 0.5% (14 % per month) excluded, this means that the hoarder could have consumed a total of c. 986 kJ during these three months.

Almost 90% of the stored animal matter disappeared within a month after storing (Fig. 2). Since most of it was stored in October, very little would have remained at the beginning of December. Thus, there may still be some effect of stored animal matter in December, but probably not later.

Discussion

After being high during December, the disappearance rate may seem very low during the rest of the winter. This low disappearance rate, however, was measured during two very mild winters, when 27 % of the stored seeds still were present at the end of the study (Fig.2). During mild winters there is plenty of the preferred invertebrate food (Gibb 1960) and Willow Tits probably rely less on stored seeds. The winter 1993/94 was very cold, and it is possible that much less, perhaps around 10%, was left at the end of the winter if the Willow Tits foraged more intensively for hoarded seeds. If so, after losses around 1834 kJ or 48 % of the available supply, could have been consumed from January to March.

Assuming that 90 % of the nutrients in the food are metabolized (Bairlein 1985), a Willow Tit needs an energy intake of about 46±1.6 kJ daily during the winter (calculated on from Moreno et al. 1988). This corresponds to 1420 kJ during December, and 4094 kJ during January through March. The consumed hoarded seeds would then cover 85 % of the tit's energy requirements during December. If stored animal matter would still be available, the whole need during the month could actually have been covered by hoarded food. During the rest of the winter, hoarded food would cover 24 % of the requirements. If, however, more caches are retrieved during cold than mild winters, then hoarded food might constitute a higher proportion, around 45 %, of the energy needed from January to March.

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Sammanfattning

Betydelsen av naturligt hamstrade födoförråd i vinterdieten hos den boreala talltitan

Under hösten hamstrar nordliga mesar såsom talltitan *Parus montanus* stora mängder föda (Haftorn 1956, 1959, Pravosudov 1985, Brodin 1994b). De vanligaste födosorterna är då frön av gran *Picea abies*, tall *Pinus silvestris*, en *Juniperus communis*, olika typer av dån *Galeopsis* spp. samt insektslarver (Haftorn 1956, Brodin 1994b). Uppskattningar av den den totala mängden frön som hamstrats per individ under en höst varierar från 50.000 till 80.000 (Haftorn 1959) och upp till 150.000 (Pravosudov 1985). Det är dock något osäkert hur tillförlitliga dessa uppskattningar är, då de ej är beräknade som medelvärden för individuella fåglar eller med förutbestämda observationsperioder.

Jag har sedan tidigare uppskattningar på i vilken takt naturligt hamstrad föda försvinner (Brodin 1994a) samt hur mycket av den som går förlorad (Brodin 1994c). Till detta kommer också ett "ögonblickligt snattande", när exempelvis talgoxar *P. major* och andra talltitor observerar en hamstring och direkt tar maten. Omhamstring, dvs när redan hamstrad föda tas fram och hamstras igen i ett nytt gömställe, skulle dock kunna göra att hamstrade förråd egentligen äts senare än vad som framgår av mina skattningar.

Frön är hållbarare och finns kvar längre i gömställena än larver, och är därför troligen viktigare som föda under vintern. Gömda frön hade en kortaste "medellivslängd" av 70,6 dagar, medan larver hade en "medellivslängd" på 20,1 dagar (Brodin 1994b).

Metoder

Jag har samlat hamstringsdata på färgringsmärkta talltitor under fem höstar, från 1989 till 1993, i ett område söder om Stockholm (se Brodin 1992 för en beskrivning). Hamstringsintensiteter har jag endast mätt under två år, 1992 och 1993. Under 1992 följde jag hamstrande individer under så långa perioder som möjligt, från 30 sekunder upp till fem minuter. En sådan teknik kommer troligen att överskatta mängden hamstrad föda, eftersom talltitorna är lättare att följa under intensiva hamstringsperioder än under förflyttning. Pg av detta använder jag uppskattningarna från 1992 endast som en kontroll av att intensiteterna under 1993 inte är avvikande.

Under 1993 har Brodin m.fl. (opubl.) observerat hamstringsintensiteter i stor omfattning på ett mer

metodiskt sätt. Varje individ följdes i minst 20 st 60 sekunders perioder, lika fördelade på för- och eftermiddag. Denna undersökning pågick från den sjätte september till den sjunde november. I mindre omfattning har jag även samlat data på samma sätt på tider som ej ingick i denna studie. För att möjliggöra en bedömning av hur rimliga mina skattningar är, anger jag standardfelet som ±. Alla statistiska test är tvåsidiga.

Vid en hamstringstransport bär en talltita normalt flera frön samtidigt i näbben, vilka sedan placeras sedan ut på enskilda gömställen. Mina skattningar av antalet frön per transport är minimibedömningar, eftersom jag inte har mätt detta i större omfattning. Skattningarna kommer både från egna observationer, och från Haftorns (1956) iakttagelser: enbär: 2,5 frön, dån: 2,3 frön samt gran och tall: 2 frön per transport. Förutom bladlöss, har jag endast sett animalier hamstras var för sig.

Frön är oftast enkla att bestämma eftersom man ser var de tas. Fjärilslarver och dyl. är naturligtvis svårare att bestämma genom kikaren, men jag har varje år samlat några av de vanligaste, och fått hjälp av entomologer med bestämningen av dessa. Med utgångspunkt från detta har jag sedan försökt bestämma larver även genom kikaren.

Innehållet i födokomponenter som jag inte funnit i litteraturen har jag låtit analysera vid statens lantbrukskemiska laboratorium. Jag har antagit att kolhydrater (förutom fibrer) och fett är tillgängligt för förbränning. Det är inte klart om småfåglar regelbundet använder proteiner som energikälla, och för att få värdena med proteiner inräknade multiplicerar man de angivna energivärdena med 1,21.

Resultat

Hamstringsintensitet

Medelhamstringsintensiteten per individ under 1993 var 0,50±0,08 och under 1992 0,63±0,06 transporter per minut, så 1993 bör ha varit ett representativt år. Hamstringsintensiteten under olika månader framgår av Fig. 1. I början av augusti var intensiteten mycket låg och de flesta observationerna är från månadens sista dagar. Proportionen frön som hamstrats är högre under augusti–september (0,78±0,01, n=55) än senare (0,24±0,01, n=57, Mann-Whitney U-test, U=518, p<0,001). Intensiteterna varierade inte mycket under dagen, även om jag inte såg någon hamstring under två besök i gryningen under september. Omhamstringen verkade vara låg, högst 1.8 frön per timme, eller 13 frön om dagen. Detta uppsaktade jag under december, då den vanliga hamstringen nästan helt upphört. Troligen omhamstras endast frön, eftersom larver ofta "limmats fast" i underlaget (de hackas ofta sönder vid hamstringen).

Typ av föda som hamstrades

Variationen mellan åren var stor (Kruskal-Wallis ANOVA, H=13 till 44, p=0.01 eller mindre för alla typer av föda, Tabell 2). Nästan alla hamstrade frön var från en, dån och gran eller tall. Gran- och tallfrön hamstrades olika år, och eftersom som de är ungefär lika stora, behandlar jag dem tillsammans. Jag använder då energivärden från gran, som var vanligast förekommande av de två. Då variationerna i typ av hamstrad föda var mycket stora mellan åren, anser jag det mest meningsfullt att använda medelvärden för de fortsatta beräkningarna.

Under 1993 samlade talltitorna stora mängder bladlöss, en vana jag förut iakttagit hos svartmes, *P. ater*. Antalet bladlöss i varje hamstrad boll, var i genomsnitt 20,2±2,3 (n=26). Normalt är annars larver den oftast hamstrade animaliska födan (Tabell 2), och jag behandlar därför i fortsättningen alla hamstrade animalier som om de vore larver. Den vanligaste larven verkade vara tallmätare, *Bupalus piniarius*. Dessa lämnar i oktober tallbarren för att förpuppas (Hedqvist m. fl. 1975), och kan vara lätta att hitta under denna förflyttning. Jag hittade också ett flertal andra typer av larver, av vilken den vanligaste verkade vara röd tallstekel, *Neodiprion sertifer*. Jag analyserade inte energiinnehållet i de olika evertebraterna, men detta är uppskattat till 6710 J per 10 individer för den röda tallstekeln (Larsson and Tenow 1979). Eftersom denna är lika stor som tallmätaren och lever av en likartad föda (tallbarr), antar jag att detta energivärde är giltigt för alla animalier.

Giltigheten i mina uppskattningar

Den största felkällan i mina uppskattningar kommer av mätningarna av hamstringsintensitet. Standardfelet för dessa var i genomsnitt 14,8 %, beräknat från Tabell 5. Standardfelet i övriga variabler var mycket litet, under 0.01. Energiinnehållet i de olika frötyperna analyserades på ett par hundra malda frön av varje sort, varför medelvärdet bör vara mycket tillförlitligt. Vikten av fröerna är litteraturuppgifter givna utan spridningsmått (Haftorn 1959, Grime et al. 1988, Snow och Snow 1988) , och bör vara de bästa möjliga. Uppskattningarna av hur frön försvinner och hur många som förloras, är uppmätta på under lång tid på vardera 100 st frön och borde vara tillförlitliga. Ett problem med dessa uppskattningar kan dock vara att de gjordes under två mycket milda vintrar när letandet efter hamstrade frön kan ha varit mindre intensivt än under kalla vintrar.

En del frön stjäls direkt vid hamstringstillfället. Hitchcock (1992) har i laboratorieförsök uppskattat detta till 5 % hos black-capped chickadee, *P. atricapillus*, den "amerikanska talltitan". Det stjäls troligen mer frön i ett litet aviarium än under naturligt furagerande, men å andra sidan hade hon bara två individer i aviariet. Under naturliga betingelser finns det betydligt fler individer som kan akttaga en hamstring. Jag räknar därför med 5 % för att inte överskatta mängden hamstrad mat.

Beräknad mängd hamstrad föda

Med utgångspunkt från intensiteterna under de olika månaderna (Fig. 1) kan det totala antalet hamstringstransporter beräknas. Om man sedan tar proportionerna av de olika komponenterna (Tabell 2) kan man få antalet transporter för vardera av dessa (Tabell 5). Slutligen ger antalet frön som hamstras per transport, den totala mängden hamstrad föda per individ (Tablell 5).

Om vi utgår från de under 1993 uppmätta intensiteterna, kommer en talltita att i medeltal ha hamstrat 46.300±6.900 frön med en vikt av ca 480±71 g. Dessa skulle då ha ett energiinnehåll av 4750±703 kJ. Möjligen skulle även proteiner kunna förbrännas som energikälla, och energiinnehållet med proteiner medräknade fås genom att multiplicera mina värden med 1,21. Då de flesta fröna hamstrades i september, antar jag att denna uppskattning gäller från 15 oktober. Den total energimängden i den hamstrade animaliska födan kan på motsvarande sätt beräknas till 9800 kJ.

Med en omedelbar förlust på 5 % vid hamstringstillfället, och sedan en fortsatt förlust på 0,5 % per dag, kommer ca 3763 kJ att finnas kvar i början av december. Till detta kan läggas 50 kJ från omhamstrade frön, och de resulterande 3820 kJ är då tillgängliga i förråd. Om försvinnandet av enbart frön extraheras ur Fig. 2, kommer ca 43 %, att försvinna under december. Av dessa måste de 5 % som stals vid hamstringstillfället ha tagits av andra än hamstraren som då får 38 % eller1452 kJ kvar. Om 50 kJ av det som försvann i december omhamstrades och 0,5 % om dagen gick förlorat, kan 1205 kJ ha konsumerats av hamstraren under denna månad.

Eftersom 27 % av födan fanns kvar i förråden vid vinterns slut (Brodin 1994a), måste omkring 30 %, eller 1146 kJ, ha försvunnit under januari till mars. Med 0,5 % per dag (14 % per månad) i förluster borträknade, skulle detta innebära att hamstraren skulle ha kunnat konsumera omkring 986 kJ under dessa tre månader.

Nästan 90% av animalierna försvinner inom en månad efter hamstringen (Fig. 2). Eftersom den största mängden av dessa hamstras i Oktober, kommer mycket lite att finnas kvar i början av december. Möjligen kan det fortfarande finnas en effekt av hamstrad animalisk föda i december, men knappast senare.

Diskussion

Efter den initialt höga konsumtionen under december, kan denna verka låg under resten av vinter. Försvinnandet jag använt som utgångspunkt för beräkningarna mättes dock under två mycket milda vintrar. Under sådana finns det rikligt av den evertebratfauna som mesar föredrar (Gibb 1960), och det är möjligt att talltitor då är mindre beroende av hamstrade frön. Vintern 1993/94 var mycket kall, och det är möjligt att en större del av förråden då konsumerades. Om 10 % av de ursprungliga förråden fanns kvar vid vinterns slut skulle, efter förluster, 48 %, eller 1834 kJ kunna ha konsumerats under januari till mars.

Om 90 % av näringsämnena tas upp (Bairlein 1985), behöver en talltita ca 46±1,6 kJ per dag under vintern (Moreno et al. 1988). Detta blir ca 1420 kJ under december och 4094 kJ under januari till mars. Det som konsumerats av hamstrad föda skulle då utgöra 85 % av energibehovet under december. Om hamstrad animalisk föda fortfarande finns tillgänglig skulle hela behovet under december kunna täckas av hamstrad föda. Under resten av vintern skulle ca 24 % av energibehovet kunna klaras av med hjälp av hamstrad föda. Om sökandet efter hamstrad föda är mer intensivt under kalla vintrar, skulle istället ca 45 % av behovet kunna täckas av konsumtionen av hamstrad föda.