



COMMENTARY

On seasonality in food-storing behaviour in parids: do we know the whole story?

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Avian food-caching species have been at the centre of many investigations into general biological questions concerning the evolution of memory and the hippocampus (Krebs et al. 1989; Sherry et al. 1989) as well as the relations between environment, memory and the hippocampus (Barnea & Nottebohm 1994; Smulders et al. 1995, 2000; Pravosudov & Clayton 2002). It has been well documented that food-caching birds rely, at least in part, on spatial memory to retrieve their food caches and that the hippocampus plays a key role in spatial memory (Sherry & Vaccarino 1989; Hampton & Shettleworth 1996). Food-caching parids (Aves, Paridae), in particular, have served as a key model for several important studies relating hippocampal processes (neurogenesis, changes in volume and neuron numbers) with spatial memory thought to be crucial during creation and recovery of numerous food caches (Barnea & Nottebohm 1994; Smulders et al. 1995, 2000) as well as for studies investigating the role of photoperiod in seasonal regulation of food-caching behaviour and hippocampal processes (Krebs et al. 1995; MacDougall-Shackleton et al. 2003; Karpouzou et al. 2005). Many of these conceptual studies relied heavily on an assumption that food-caching behaviour is seasonal with a single peak during autumn when food-caching parids store enormous amounts of food. For example, the groundbreaking study of Barnea & Nottebohm (1994) reported that neuronal recruitment into the hippocampus of black-capped chickadees, *Poecile atricapillus*, was highest in October and significantly lower during the rest of the year. Barnea & Nottebohm (1994) assumed that food-caching activity in black-capped chickadees was also highest specifically during just one month of the year, October, which allowed the authors to conclude that increased hippocampal neurogenesis is related to heightened demands for spatial memory during the time of most intense food

caching. Similarly, Smulders et al. (1995, 2000) reported that black-capped chickadees have the largest hippocampal volume and more hippocampal neurons only in October, and these authors also concluded that such an expansion of the hippocampus during October is related to increased memory demands caused by the most intensive food caching during that month. Finally, several studies attempted to investigate whether photoperiod is a factor affecting food-caching activity and hippocampal structure based on a premise that a single peak of food caching in the autumn always coincides with a decrease in daylength (Krebs et al. 1995; Clayton & Cristol 1996; MacDougall-Shackleton et al. 2003; Karpouzou et al. 2005).

It is clear that the assumption about a single seasonal peak in food caching in autumn (or in many studies even more narrowly just in October) is a cornerstone of these investigations and thus it is imperative that there are solid data supporting such assumption. Here, I review all available data on natural food caching in parids and show that data on seasonality of natural food caching in parids have often been oversimplified.

First, none of the conceptual studies investigating the relation between memory and the hippocampus or between photoperiod and food-caching behaviour had their own data on food-caching activity of their species during different seasons; instead, they all relied on previously reported data. There is, however, only a handful of field studies that have documented food-caching rates in parid species in natural conditions without using supplemental food (Haftorn 1954, 1956a, b, c; Pravosudov 1985; Nakamura & Wako 1988; Brodin 1994a, 2005). Of these few studies, only Haftorn (1954, 1956a, b, c), Pravosudov (1985) and Nakamura & Wako (1988) actually investigated food-caching activity throughout the entire year, whereas other studies were focused on late summer–autumn only. All these studies reported results of intensive direct observations of birds caching naturally available food in the wild. Pravosudov (1985) and Nakamura & Wako (1988) reported caching intensity as a percentage of cached

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food (items cached/items found), while all other studies reported caching rates (number of items cached per unit time). These two measures allow direct comparisons of food-caching activity across seasons, and in all these studies, similar observational methods were used that did not seem to create any biases in reported patterns. Even though all the research undoubtedly shows that there is indeed a strong peak in food-caching activity during autumn, it is also clear that October might not necessarily be the only month when parids cache the most.

Many studies cited Odum (1942) as evidence that food caching in black-capped chickadees is most intensive during the month of October (Barnea & Nottebohm 1994; Smulders et al. 1995, 2000). Odum (1942), however, did not report detailed observations of food caching in black-capped chickadees. There are literally five lines of text referring to food caching in Odum (1942) including a single observation on one bird and a general statement that birds cached food during the autumn and that caching activity 'was first noted on October 12 and continued into November' (Odum 1942, page 514). This information can hardly be used as the evidence of seasonal activity in food caching in black-capped chickadees or that black-capped chickadees cache most of their food during October. Only recently, Brodin (2005) reported detailed observations of natural food caching in wild black-capped chickadees in northern British Columbia. Until that study, there were no published data showing that black-capped chickadees even engage in long-term intensive food caching. Brodin (2005) started his observations at the end of September and continued until mid-November, and showed that black-capped chickadees cache food as intensely as Eurasian willow tits, *Poecile montanus*, which are well known for their food-caching prowess (Fig. 1). Brodin (2005) found that food-caching rates in black-capped chickadees were highest at the end of September (when he began his observations), then gradually declined throughout October, and had almost ceased by mid-November (Fig. 1). Thus, it is possible that food-caching rates in these black-capped chickadees were highest during September and possibly during August, as has been reported for several Eurasian species (Haftorn 1956a, b, c; Brodin 1994a; Fig. 1).

In Eurasian willow tits, there are detailed data on natural food-caching intensity during late summer and autumn from two sources (Haftorn 1956c; Brodin 1994a). Both of these sources documented the highest caching rates in September (Fig. 1), although in Norway, willow tits also cached very intensively during August (Haftorn 1956c). Brodin (1994a) reported slightly lower caching rates for willow tits in Sweden throughout the autumn, but both Haftorn (1956c) and Brodin (1994a) showed that willow tits cached more food during August than during October (Fig. 1). Caching rates actually declined from September to October, but birds continued to cache quite intensely during both October and November (Haftorn 1956c; Brodin 1994a; Fig. 1). In two other Eurasian species, coal tit, *Periparus ater*, and crested tit, *Lophophanes cristatus*, autumn natural food-caching rates in Norway were indeed highest in October, but caching rates were also very high in August, September and November in

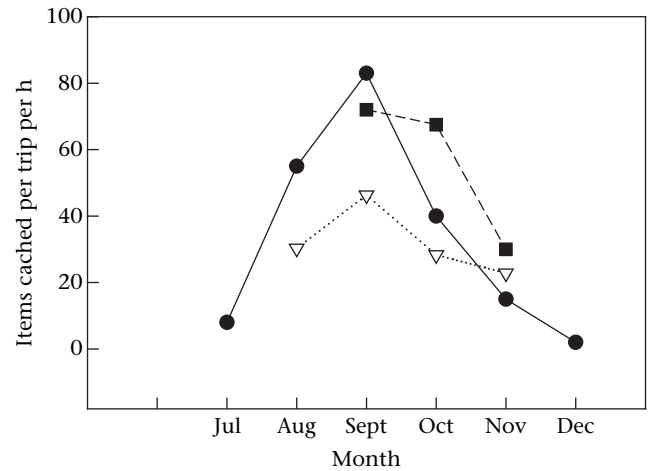


Figure 1. Food-caching intensity during autumn in Eurasian willow tits, *Poecile montanus* (●: from Norway, data from Haftorn 1956b; △: from Sweden, data from Brodin 1994a) and North American black-capped chickadees, *Poecile atricapillus* (■: from Canada, data from Brodin 2005). All observations were carried out on naturally caching, individually marked birds with no supplemental food. In black-capped chickadees, data were collected from 29 September through to the first week of November 2002 (Brodin 2005). The November data point for black-capped chickadees is an average of two data points, one at the beginning of November (ca. 52.5 items cached/h) and the other one at the end of November (ca. 7.5 items cached/h). In Swedish willow tits, data were collected from August (mostly last week of August) through to November during 1989–1993 (Brodin 1994a). In Norwegian willow tits, data were collected during 1949, 1950 and 1952, and in all 3 years, regular observations were carried out from July through to December.

crested tits (>20 items cached/h; Fig. 2), and in September and November in coal tits (Haftorn 1954, 1956a; Fig. 3). During some years, caching rates were fairly similar from July through to October in coal tits (Haftorn 1956a; Fig. 3).

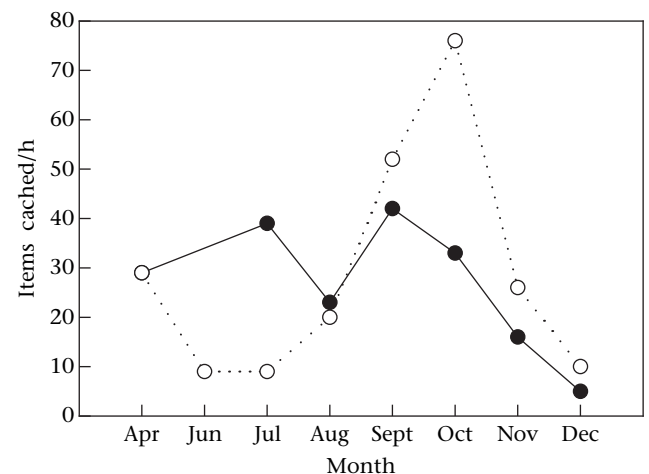


Figure 2. Food-caching rates (per hour) in crested tits during 2 years near Drummen, Norway (data from Haftorn 1954). ●— 1949; ○····· 1950. All observations were carried out on naturally caching birds with no supplemental food. Data were collected regularly during July–December in each year. Regular observations were also carried out in April in 1949, and in January, March, April and June in 1950.

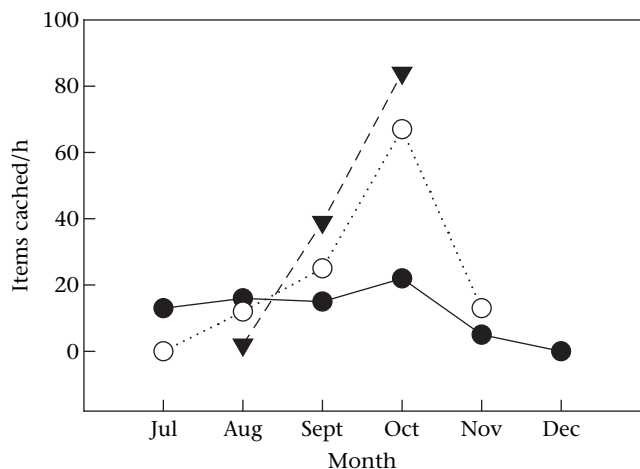


Figure 3. Food-caching rates (per hour) in coal tits during 3 years near Drummen, Norway (data from Haftorn 1956a). All observations were carried out on naturally caching birds with no supplemental food. Data were collected regularly during July–December in 1949 (—●—), July–November in 1950 (··○··) and August–October in 1952 (—▼—).

Nakamura & Wako (1988) reported that willow tits in Japan had the highest food-caching rates in October, but these birds still cached approximately 35% of all food found in September, and 60% in November. No statistical analyses have been performed on these data, and caching rates in October and November seem to be very similar (Fig. 4).

All these data suggest that intense food-caching activity might persist from August through to December, and not just during the month of October. Caching intensity during autumn shows a lot of variation between months, seasons and latitudes (Haftorn 1954, 1956a, b, c; Brodin et al. 1996; Figs 2, 3). Parids also appear to start caching food earlier at northern latitudes (Brodin et al. 1996).

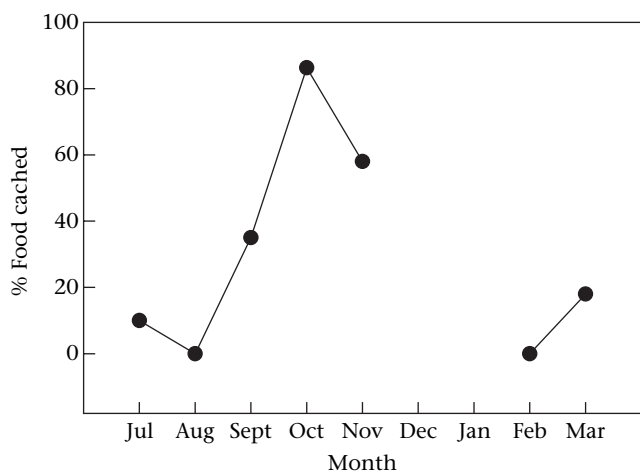


Figure 4. Percentage of food cached during the year in willow tits in Japan (data from Nakamura & Wako 1988). All observations were carried out on naturally caching birds with no supplemental food. Data were collected during August–November and February–July in 1974–1986.

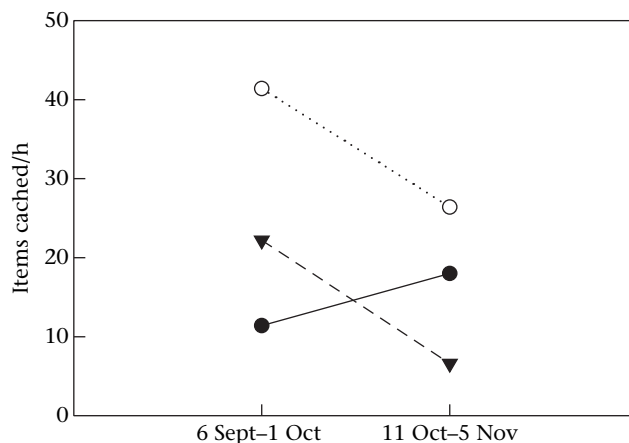


Figure 5. Food-caching rates by willow tits in southern and northern locations in September and October (data from Brodin et al. 1996). —●—: Antwerp, Belgium (most southern location); ···○··: Stockholm, Sweden (intermediate northern location); —▼—: Oulu, Finland (most northern location). All observations were carried out on naturally caching, individually marked birds with no supplemental food. All observations were done using the same sampling methods at the same time of day during 6 September–1 October and 11 October–5 November of 1993 using 93 individual willow tits (Belgium, $N = 20$ birds; Sweden, $N = 36$ birds; Finland, $N = 37$ birds).

Willow tits around Antwerp (Belgium) cached more food in October than in September (Fig. 5). In contrast, northern willow tits near Stockholm (Sweden) and near Oulu (Finland) cached more food during September than during October (Brodin et al. 1996; Fig. 5). Unfortunately, Brodin et al. (1996) did not collect any data for caching rates in August, November and December. However, all combined data on autumnal food caching in parids suggest that these species spread their intense long-term food caching over more than a 3-month period starting in August and ending in December (Haftorn 1954, 1956a, b, c; Pravosudov 1985; Nakamura & Wako 1988; Brodin 1994a; Brodin et al. 1996). During these months, parids cache significant amounts of food compared to June or January, when very little food caching has been reported. If changes in hippocampal structure result from the high memory demands of intensive food caching, why would birds have larger hippocampus only in October (Smulders et al. 1995) even though food caching might be quite intense during August, September and November?

Another critical detail missed in all recent studies concerns the fact that food-caching parids appear to have a second significant peak in natural food caching during spring. Both Haftorn (1954, 1956a, b, c) and Pravosudov (1985) reported significant food-caching activity during a few spring months (April, May) in all four Eurasian species (willow tits, coal tits, crested tits and Siberian tits, *Parus cinctus*) when these birds stored mainly spruce and pine seeds (Figs 2, 6). Nakamura & Wako (1988) also reported a second peak in willow tit food caching in March even though caching activity at that time was significantly lower compared to that during autumn (Fig. 4). Haftorn (1954) obtained detailed data on food-caching rates during spring in only one species, crested

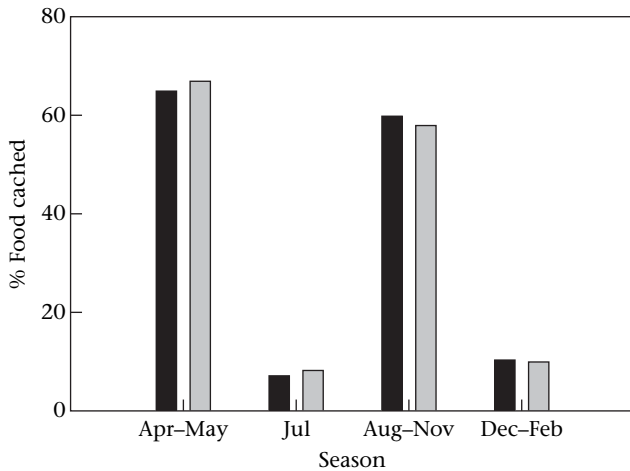


Figure 6. Percentage of food cached during the year in willow (■) and Siberian (□) tits in northwestern Russia (plotted using data in Pravosudov 1985). All observations were carried out on naturally caching birds with no supplemental food during all four seasons during 1980–1982.

tits (Fig. 2), but he noted that, in all four species, spring food caching was significant (Haftorn 1956a, b, c). Crested tits were reported to cache 29 items/h during April (Fig. 2), which is similar to the food-caching rates of willow tits during August and October reported by Brodin (1994a). Haftorn (1956b) also noted that even though he did not carry out systematic observations on willow tits during spring, he observed these birds intensively caching spruce seeds in March and April. Pravosudov (1985) reported that both willow tits and Siberian tits had a distinct peak in food caching during spring, when these birds cached as much food as during autumn (Fig. 6). Interestingly, males in these species have been observed to cache food intensely even when females were incubating, so intensive food caching might continue into the beginning of breeding season depending on availability of pine and spruce seeds (Haftorn 1956a; Pravosudov 1985). Haftorn (1956b) noted that willow tits cached pine seeds intensely during May and June 1953, and he concluded that these birds were males because males are not involved in incubation. Food caching appears to cease almost completely during the young-rearing period and to begin again after young become independent in July (Haftorn 1956a, b, c; Pravosudov 1985). Intensive spring caching thus appears to be limited to years with good pine and/or spruce seed production, because parids seem to cache these seeds only during spring, but when seed production in spring is high, food-caching intensity can match or exceed autumn caching activity.

It is not clear when spring caches are utilized but it appears likely that these caches might be used in late spring and summer to feed nestlings (varied tits, *Parus varius*: Higuchi 1977; Eurasian nuthatches, *Sitta europaea*: Pravosudov et al. 1996; mountain chickadees, *Poecile gambeli*: V. V. Pravosudov, personal observation).

Potential presence of two caching peaks in food-caching parids has several important implications. First, it shows that decreasing photoperiod is unlikely to be a trigger for

long-term food-caching behaviour in parids. Decrease in daylength indeed causes these birds to cache more food in captivity (Krebs et al. 1995; Clayton & Cristol 1996; MacDougall-Shackleton et al. 2003; but see Karpouzou et al. 2005), but this result could also be an indirect effect of reduced food availability. Reduction in food availability and increased variability in foraging success also result in more intense food caching in the laboratory (Hurly 1992; Pravosudov & Grubb 1997a), but these factors are unlikely to account for long-term food caching during early autumn or spring, when naturally available food is overly abundant. So it appears that food caching in parids consists of long-term caching (late summer–autumn, spring) and short-term caching (winter), and that these two behaviours might be regulated by different mechanisms (Brodin & Clark 1997; Pravosudov & Grubb 1997b). Available field data clearly show that intensive food caching may occur when daylength is decreasing (autumn) as well as when daylength is increasing (spring), which suggests that food caching is not under strict photoperiodic control. Numerous studies have shown that, in laboratory conditions, food caching might be affected by both food availability and predictability as well as by energy balance (McNamara et al. 1990; Lucas & Walter 1991; Hurly 1992; Lucas et al. 1993; Pravosudov & Grubb 1997a, b). Energy balance might be affected by the history of food availability and predictability and by various other parameters of the environment, both social and physical. Therefore, natural food-caching rates may be influenced by environmental parameters that affect energy management in birds. Thus, high variability in environmental conditions between locations and between years might result in high variability in seasonal food-caching patterns.

It appears that birds might always cache food when it is available and when energy balance favours food caching rather than eating. Food-caching parids seem to cache least during the summer and winter. In summer, food is plentiful but birds are engaged in other energetically expensive activities such as reproduction and moult. In winter, naturally available food is limited and maintaining energy balance is more challenging (short days, low air temperature, snow cover). Birds seem to engage in food caching at all other times, even in spring, when naturally available food (pine and spruce seeds) becomes abundant.

Another issue that is still not entirely clear concerns the timing of cache recovery. Initially, it has been assumed that food-caching parids cache food when it is abundant and then retrieve it months later when food is limited, usually during winter (Haftorn 1956c). For example, stomachs of tits collected during winter contained food items that were unavailable during winter, so these foods must have been cached during autumn (Haftorn 1956c). Varied tits were reported to retrieve their caches months after making them (Higuchi 1977). On the other hand, a few experimental studies reported that seeds cached by marsh tits, *Poecile palustris*, from feeders disappeared within hours, suggesting a short-term cache use (Cowie et al. 1981; Stevens & Krebs 1986). It is likely, however, that caches that disappeared so quickly in these studies might have been recached and not consumed (Pravosudov & Grubb 1997b). When parids cache food from a single

source such as a feeder, they seem to cache it near the feeder, which would maximize their rate of food removal from an ephemeral food source (Brodin 1992). These birds might later recache these items to reduce cache density, which would minimize the potential risk of cache pilferage (Brodin 1992, 1994a; Pravosudov & Grubb 1997b). Recaching of naturally stored food items appears to be a common phenomenon in parids (Pravosudov 1985; Nakamura & Wako 1988). Brodin (1992) found that when willow tits cached seeds from several feeders, the caches were more widely distributed and they disappeared more slowly than those created from a single feeder. Data on disappearance rates of naturally made caches also suggest that parids might recover their caches after many days rather than just a few hours and the half-life of naturally cached food items was reported to be 20 days in willow tits (Brodin 1994b). Finally, Brodin & Ekman (1994) used radiotilochronology to show that willow tits consumed their radioactively labelled caches up to 40 days after creating them. Radiotilochronology is limited to the time of tail feather regrowth, which is usually no longer than 2 months (Brodin 1993), so it is possible that parids consume some of their caches after even longer time intervals. In conclusion, it seems that food-caching parids do use their caches over fairly long periods, ranging from days to months, even though two studies suggested that parids could use memory to find their caches only up to 28 days in laboratory conditions (Hitchcock & Sherry 1990; Brodin & Kunz 1997). Laboratory conditions provide an unnatural environment that might negatively affect parids' memory performance, and thus, more studies are necessary to investigate the longevity of memory in these species.

A complex seasonal dynamic of food caching in parids has important implications for neuroecological research that attempts to correlate changes in the brain with variation in food-caching behaviour. Conclusions of Barnea & Nottebohm (1994) and of Smulders et al. (1995, 2000) are valid as long as the birds in these studies indeed had a single narrow peak in food caching during October. Barnea & Nottebohm (1994) and Smulders et al. (1995, 2000) obtained no data on seasonal changes in food-caching rates in their populations of black-capped chickadees and thus the data on seasonal changes in the hippocampus in these studies are difficult to interpret knowing that food-caching behaviour might show significant month-to-month and year-to-year variation. Available data suggest that caching rates in black-capped chickadees in October might have been similar to caching rates in late August, September or November, yet there were differences in hippocampal structure between birds sampled in August, October and December (Smulders et al. 1995, 2000). Presence of the second food-caching peak in spring would also introduce additional uncertainty about the results of these studies.

In conclusion, all available evidence suggests that food-caching parids have a flexible seasonal food-caching behaviour that depends on seasonality of food types available for storing and that a simple assumption about a single peak of food caching occurring in a single month may be misleading. More field data are needed

on seasonality of food caching in American parids before any conclusions can be reached about correlations between naturally occurring food-caching behaviour, memory and the brain. Except a single study on black-capped chickadees that focused on a fairly narrow time period (end of September–mid-November; Brodin 2005), no data are available on natural food-caching intensity in any North American species of Paridae. Because food-caching activity appears to vary within and between seasons, any investigation relying on seasonal variance in natural food-caching behaviour should first document this behaviour in specific populations under investigation.

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