

## Effects of season and photoperiod on food storing by black-capped chickadees, *Parus atricapillus*

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**Abstract.** The effects of season and photoperiod on food storing by black-capped chickadees were examined in two experiments. Chickadees were captured in March (experiment 1) or November (experiment 2), and food storing was tested regularly in the birds' home cages. In both experiments, two groups were matched for initial level of food storing. The long-day group was then exposed to a summer photoperiod (16:8 h light:dark cycle) and the short-day group to a winter photoperiod (LD 8:16 h) for 2–3 months, followed by 2–3 months in identical conditions for both groups. Birds in experiment 1 stored very little at first, but those maintained on long days moulted and began to store after 6–8 weeks; the group maintained on short days eventually increased storing as well. Birds in experiment 2 began by storing about three times as much food as those in experiment 1; storing declined over time in both groups and was not affected by photoperiod. The results suggest that food storing in parids is controlled by photoperiod in a similar way to other annually varying behaviour patterns such as breeding and migration in birds.

The proximate causation of food hoarding in birds is not well understood (Vander Wall 1990). Observations of food-storing chickadees and titmice (*Paridae*) under natural conditions suggest that they store most food in the autumn or early winter (Odum 1942; Haftorn 1956). However, these observations do not permit strong conclusions about the proximate causes of food storing because many factors that might influence it vary seasonally in the wild. For example, storable foods may be most abundant in the autumn (cf. Haftorn 1956). Birds not occupied with defending a territory or feeding young, as in autumn and winter, may devote more time to storing food. Ludescher (1980) documented annual cycles of food storing by testing captive willow tits, *Parus montanus*, in a standard way throughout the year, but his birds lived in outdoor aviaries, so they experienced natural changes in temperature and daylength which could have directly influenced hoarding intensity. Short days and cool temperatures induce hoarding almost immediately in several species of small mammals (e.g. rats, Fantino & Cabanac 1984; Djungarian hamsters, *Phodopus sungorus*, Masuda & Oishi 1988; reviewed in Vander Wall 1990). Animals are more energetically stressed in short days and low temperatures, and greater energetic demands

increase hoarding in marsh tits, *P. palustris* (Hurly 1992), Carolina chickadees, *P. carolinensis* (Lucas & Walter 1991) and tufted titmice, *P. bicolor* (Lucas et al. 1993). For example, captive marsh tits store more when they have unpredictable access to food once an hour than when food is available once a minute (Hurly 1992). Like laboratory rats (Cabanac & Swiergiel 1989), Carolina chickadees and tufted titmice store more as their body weights fall (Lucas & Walter 1991; Lucas et al. 1993; Lucas 1994).

As well as being influenced by energetic factors and patterns of food availability, food storing may be linked to an annual rhythm. Annual changes in reproductive hormones, breeding behaviour and migration in birds are influenced primarily by photoperiod (Gwinner 1975, 1989). In many species that breed in temperate areas, increasing daylength in late winter stimulates the hormonal and behavioural changes associated with breeding. At the end of the breeding season, in July or August, birds become refractory to the effects of long days, the gonads regress, and moulting and migration may occur. Exposure to short photoperiods is then necessary to restore sensitivity to long days (Nicholls et al. 1988). Thus, autumn and early winter, the times when most food storing is observed in parids in the wild, are characterized by

low levels of reproductive hormones and a photo-refractory state (see Silverin et al. 1989 for an example with European parids). In some mammals, hormones such as testosterone suppress hoarding (reviewed in Vander Wall 1990). If a similar relationship exists in birds, the amount of food storing should depend on the time of year, even when energetic factors are held constant.

Laboratory studies of food storing provide some suggestive evidence that the state of a bird's annual cycle does influence food storing independently of energetic demands. For example, birds captured in autumn and kept in constant winter-like conditions in the laboratory may stop hoarding the following spring (Lucas & Walter 1991; personal observations). However, in these cases, length of exposure to laboratory conditions has been confounded with possible endogenous seasonal changes. An exception is the recent work of Lucas (1994) in which Carolina chickadees were brought into constant laboratory conditions at different times from autumn to spring. However, Lucas tested only two birds at each time.

Our purpose in this study was to test whether the amount of food stored by black-capped chickadees is influenced by the bird's annual cycle and by the photoperiodic regime in the laboratory. We tested for an influence of the bird's annual cycle in the wild by comparing the amount of food stored under similar laboratory conditions by birds captured in spring (experiment 1) versus in autumn (experiment 2). If food storing is influenced only by food availability and current energetic demands, time of year should have no effect on storing in the laboratory. If, in addition, food storing is influenced by an annual rhythm, the birds trapped in autumn would be expected to store more soon after arrival in the laboratory than those trapped in spring. Within each experiment, we attempted to manipulate the birds' annual cycles by exposing one group to long days and warm temperatures and one to short days and cool temperatures for 2–3 months. Each experiment concluded with 2–3 months during which all birds were in the same room and photoperiod, permitting a test of an effect of photoperiodic history when current energetic demands were kept constant. In both experiments, we tested the birds' food storing regularly by giving them limited access to sunflower seeds in their home cages, following the method suggested by Ludescher (1980) and modified by Hampton et al. (1995).

## EXPERIMENT 1

We captured the chickadees in late March, when the early stages of breeding behaviour may be observed in the field (Smith 1991). We divided them into two groups matched for initial level of food storing and exposed one group to an 8:16 h light:dark cycle at 63°F and the other to a 16:8 h light:dark cycle at 71°F for about 2 months. They were then returned to the same room and short-day photoperiod so that both groups of birds were faced with the same energetic demands in the same environment, but one had experienced an abbreviated summer and had moulted while the other had been maintained continuously in 'winter' conditions. If food storing is a response to energetic factors alone, the group experiencing short days and cool temperatures should store relatively intensely throughout the experiment while the other group should store less during their exposure to long days and warm temperatures. In contrast, if food storing is either linked to or controlled photoperiodically in a similar manner to the annual reproductive rhythm, neither group should store much at first but the long-day group should start storing after they have experienced a period of long days.

### Methods

We captured 16 black-capped chickadees of undetermined age and sex in Potter traps in mixed woodland about 30 km west of Toronto, Ontario, on 18 March (14 birds) and 31 March 1992. In the laboratory we housed them individually in wire-mesh cages measuring 61 × 37 × 36 cm high and fed them a mixture of insectivorous bird food, grated carrot and grated whole hard boiled egg with a daily supplement of three or four peanuts and one mealworm, *Tenebrio molitor*. Cages were placed so each bird could see other birds. We provided each bird with grit, two twig or dowel perches, and a bowl of water. We hung a 46 × 9 × 4-cm thick block of wood at about the middle of the back wall of each cage for the birds to store food. Each block had 45 round holes for use as cache sites, 33 of which were 0.5 cm wide and 0.5–1.0 cm deep and 12 of which were 1.0 cm wide and 0.8 cm deep. A narrow perch stretched across the length of the block at the bottom and two perches measuring 6 cm in length protruded from the block about 14 cm from each end and 2.5–3.0 cm from the bottom.

**Table I.** Timetable of procedures used in experiment 1

Starting date	Duration	No. of tests	Long-day group		Short-day group	
			LD	Temperature (°F)	LD	Temperature (°F)
12 April	9 days	8	11:13	63 ± 1	11:13	63 ± 1
21 April	1 week	6	14:10	71 ± 1	9.5:14.5	64 ± 1
29 April	6 weeks	3–5 per week	16:8	71 ± 1	8:16	63 ± 1
17 June	1 week	5	14:10	71 ± 1	8:16	63 ± 1
24 June	1 week	5	11:13	71 ± 1	8:16	63 ± 1
1 July	1 week	5	8:16	71 ± 1	8:16	63 ± 1
8 July	13 weeks	5 per week	8:16	63 ± 1	8:16	63 ± 1

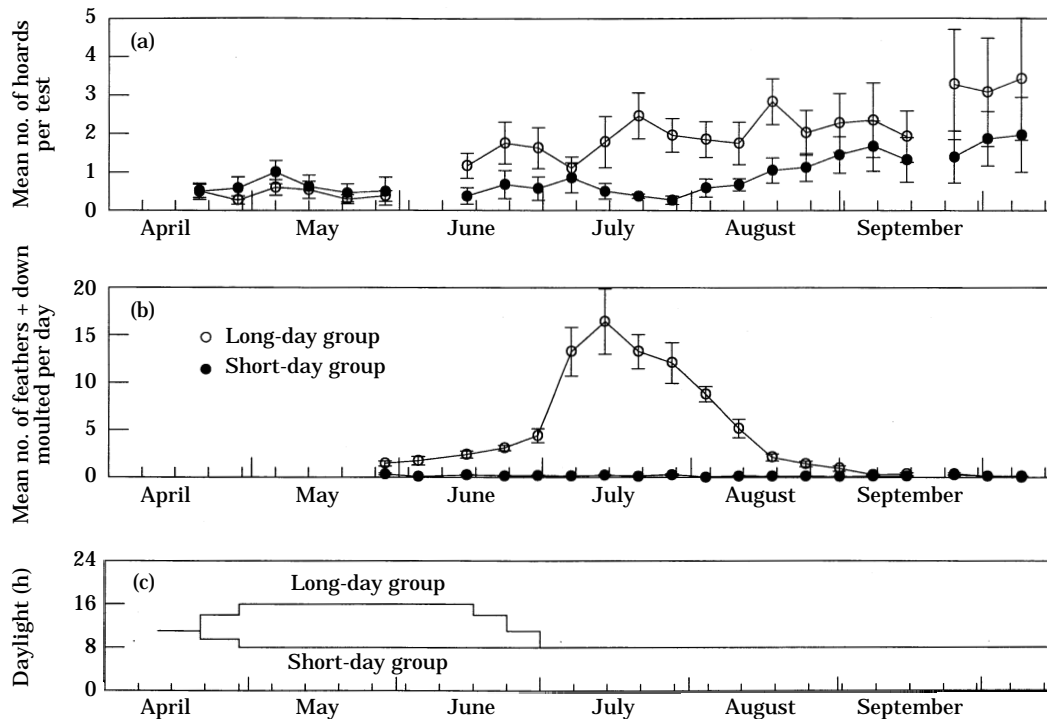
Initially, all birds were housed in the same room at  $63 \pm 1^\circ\text{F}$  on an 11:13 h light:dark cycle with lights on at 0700 hours local time, a schedule approximating natural daylength at the time of capture. To allow the birds time to adjust to the laboratory food, we gave them extra peanuts and mealworms and a daily handful of sunflower seeds for the first 2–3 weeks. The experiment began on 11 April, when we restricted the birds' access to sunflower seeds to 90 min beginning at 1030 hours, 3–5 days per week, in order to induce them to hoard when seeds were given. We tested hoarding by placing a bowl containing over 100 sunflower seeds, some with and some without shells, in each cage and removing the bowl with the maintenance diet. We left the birds undisturbed for the next 90 min, after which we counted the number of holes in each block containing one or more food items, removed the bowls of sunflower seeds, cleaned out the trays in the bottoms of the cages to remove feathers and unhoarded sunflower seeds, and replaced the maintenance diet. Before giving seeds, we checked the wood blocks for items previously hoarded. However, to avoid disturbing the birds too much, we only removed and cleaned out the blocks about once a week. Beginning on 21 May, we scored moulting after each test of hoarding by counting the number of feathers and bits of down present in the bottom of each cage. Feathers and down were given equal weight in the moulting score.

On 21 April we ranked all 16 birds on total number of seeds stored in the eight tests that had taken place so far and divided them into two groups matched as closely as possible for both mean seeds stored and mean ranks. We moved the

birds in the long-day group into another room similar in size and arrangement to the original housing room, where the short-day group stayed. Beginning on 8 July, we again housed the long-day group in the same room as the short-day group, distributing the cages of both groups around the room and labelling them in such a way that no one recording data knew to which group any bird belonged. Both times we moved the long-day birds to a new room, we moved the short-day birds around within their room. The photoperiods and temperatures that the two groups experienced throughout the experiment are listed in Table I. Whenever photoperiods were altered, the light period changed an equal amount at each end.

Twice during the experiment we conducted a series of deprivation tests in which the birds were left without food for the hours of darkness plus 2 h after the lights came on. After deprivation we gave each bird a bowl containing 40 sunflower seeds without shells for 90 min and calculated the number of seeds eaten as well as counting the number hoarded. We ran one 4-day series of tests under food-restriction when the birds were in the short-day and long-day environments and one 3-day series when they were back together near the end of the experiment (see Fig. 1).

We analysed the data in 1-week blocks, except that we treated each condition that lasted slightly more or less than a week (see Table I) as a single block. We converted the total number of holes used per week by each bird to a mean per test. We converted the total moulting score per bird per week to a mean moulting score per day.



**Figure 1.** (a) Mean ( $\pm$  SE) number of storage sites used in each 90-min test, averaged over all the tests in each week for each group of chickadees in experiment 1. The gaps signify the weeks with deprivation tests described in the text. (b) Mean ( $\pm$  SE) number of feathers plus down moulted per day. Moult was not measured before the end of May. (c) Hours of light/day that the two groups experienced throughout the experiment. The two groups were housed in the same room and light regime prior to differential photostimulation in April and again starting 1 week after differential photostimulation in July. On the X-axis, long ticks indicate the months; short ticks indicate the weeks.

## Results

The chickadees stored very little at first (Fig. 1). After a few weeks in long days and relatively warm temperatures, birds in the long-day group moulted and began to show some storing. Their storing reached a relatively high and stable plateau before moult was complete and stayed high for the remainder of the experiment. Meanwhile, the short-day birds never moulted; nevertheless, around the beginning of August their hoarding gradually began to increase until by the end of the experiment they were storing about as much as the long-day birds. Because the two groups were in the same room from early July onwards, the differences between them at this time could not have reflected differences in immediate energetic demands but rather some factor linked to their different histories.

We tested the effect of photoperiodic history on storing using the data from the final phase of the experiment, when the birds were in identical conditions. We performed a repeated-measures analysis of variance (ANOVA) on the log-transformed storing data in 2-week blocks for the last 12 weeks of the experiment, that is, beginning 1 week after the two groups of birds were put into the same environmental conditions and including the weeks before and after the second deprivation test. The ANOVA revealed a significant difference between long-day and short-day groups ( $F_{1,14}=6.70$ ,  $P<0.05$ ), significant variation between 2-week blocks ( $F_{5,70}=3.80$ ,  $P<0.01$ ) and a significant interaction between the group effect and the block effect ( $F_{5,70}=2.67$ ,  $P<0.05$ ). Student–Newman–Keuls post-hoc tests confirmed that the two groups tended to converge over the 12-week period: they differed significantly in the first five

**Table II.** Mean ( $\pm$  SE) seeds stored per day before, during and after deprivation in experiment 1

	Before	During	After
<b>Test 1*</b>			
Long-day group	0.38 $\pm$ 0.13	0.66 $\pm$ 0.29	1.16 $\pm$ 0.32
Short-day group	0.50 $\pm$ 0.36	0.81 $\pm$ 0.35	0.38 $\pm$ 0.21
<b>Test 2†</b>			
Long-day group	1.88 $\pm$ 0.63	0.83 $\pm$ 0.35	3.58 $\pm$ 1.31
Short-day group	1.67 $\pm$ 0.74	0.54 $\pm$ 0.27	1.46 $\pm$ 0.70

\*June, 4-day blocks.

†September, 3-day blocks.

2-week blocks, but they did not differ in the last 2-week block ( $P < 0.05$ ). Because we matched the two groups' hoarding to start with, the fact that they were hoarding different amounts after approximately 2 months in different photoperiods and temperatures confirms these treatments did produce a difference in storing.

The birds in the short-day group lost an occasional feather, but they never moulted (Fig. 1). In contrast, birds in the long-day group began to moult while they were in the relatively warm long days. Moulting increased dramatically soon after we began to shorten their daylength and reached a peak soon after they returned to 'winter' conditions. By the end of the experiment these birds had finished moulting.

For each series of deprivation tests, we compared the mean number of cache sites used per 90-min test during the days of deprivation with the mean number of sites used per test in an equal number of days both before deprivation and after deprivation. Table II displays these data as means for the two groups in each of the three periods (before, during and after deprivation) for each series of tests. We log-transformed these data and analysed the effect of each series of deprivation tests using a repeated-measures ANOVA. The only significant effect of the first series was an interaction between long-day versus short-day group and time periods ( $F_{2,28} = 3.76$ ,  $P < 0.05$ ). Post-hoc Student–Newman–Keuls tests showed that the long-day group stored more than the short-day group in the block of days following deprivation but not otherwise. The birds in the short-day group ate a mean of 14.8 seeds per deprivation test; those in the long-day group ate 9.8 seeds per test. Amounts eaten did not differ

significantly ( $t$ -test). The increase in storing that the long-day group showed just after the deprivation test was sustained for the rest of the experiment (Fig. 1). However, it seems unlikely that the 4-day deprivation test by itself caused this increase. We repeated experiment 1 in 1993 with new birds but without the deprivation tests, and group differences like those shown in Fig. 1 still appeared at about the same time (J. R. Krebs, N. S. Clayton, R. R. Hampton & S. J. Shettleworth, unpublished data).

During the second series of deprivation tests the birds ate means of 19.1 seeds (short-day group) and 17.7 seeds per test (long-day group). A  $t$ -test showed that these means did not differ significantly. Storing differed significantly across the three blocks of days before, during and after deprivation ( $F_{2,28} = 12.99$ ,  $P < 0.01$ ). Birds in both groups stored less during the deprivation test than immediately before or after (Table II). Thus, in these conditions, deprivation caused food storing to decrease rather than to increase. Although it seems that the birds could have both stored more and eaten to satiation during the 90-min presentations of sunflower seeds, the decrease in storing during the second series of tests may have occurred because the birds were spending so much time eating. It may also be that deprivation did not increase storing because it was not continued long enough to produce a loss in weight. Weight loss is an important causal factor for storing in other parids (e.g. Lucas et al. 1993; Lucas 1994), and because our birds had at least 6 h per day of unrestricted access to food it is unlikely that they lost much, if any, weight when deprived each morning.

## Discussion

In experiment 1, changes in photoperiod and temperature similar to those that occur seasonally in nature influenced the intensity of food storing by black-capped chickadees. Several features of the results support the conclusion that photoperiod and temperature influenced food storing by changing the birds' state over a period of weeks or months rather than by directly altering energy demands. First, when we placed the two matched groups of birds into markedly different photoperiods and temperatures at the beginning of the experiment, they continued to store similar amounts of food for over a month afterwards (i.e. food storing remained the same while energy demands presumably differed). Conversely, at the end of the experiment when current energy demands were the same because the birds were housed together, the two groups differed in food-storing behaviour. However, although it is clear that the birds' different experimental histories resulted in different levels of food storing, this experiment by itself does not clearly establish which aspect of the long-day group's history induced them to increase storing earlier than the short-day group. The long-day birds experienced a period of both long days and warmer temperatures, followed by a gradual reduction in both daylength and temperature. Increases in energetic demands accompanying the change towards winter conditions may have played a role in their increased food storing. Although they had begun to moult before the daylength had been reduced, the long-day birds stored significantly more than the short-day group only during the last week before daylength was reduced (see Fig. 1, Table II), and the fact that a deprivation test preceded this week complicates interpretation of these data. Further experiments will be necessary to disentangle the effects of temperature, long days, reduction in daylength, reduction in temperature and the increase in energetic demands from shortened days and lower temperature. For example, it is important to test whether food storing still increases in chickadees exposed continuously to long days from April onwards.

Although we did not assess the chickadees' reproductive condition directly, the pattern of results suggests that food storing is linked to the birds' annual reproductive rhythm, occurring when the birds are not in reproductive condition.

Our birds stored very little at a time of year when they would be expected to be at the beginning of their breeding cycle (Smith 1991). Exposing birds prematurely to long days can accelerate the breeding cycle, bringing on reproductive behaviour, followed by moulting and migration (Gwinner 1975; Silverin et al. 1989). The observation that the long-day birds moulted after a few weeks in long days supports the conclusion that they had passed through the peak of reproductive condition and were becoming photorefractory (Nicholls et al. 1988). Birds in the short-day group, however, began to store food in late August even though they had not been exposed to long days and had not moulted. These results suggest that some endogenous factor independent of the reproductive changes indicated by moulting causes food storing to increase in the autumn. On this interpretation, development of the internal state responsible for food storing may have been accelerated in the group exposed to long days by the same photoperiodic influence that brought on moulting.

## EXPERIMENT 2

In this experiment chickadees were captured in November and then treated similarly to the birds in experiment 1. The long-day group experienced long days and relatively warm temperatures starting in December while the short-day group experienced a sequence of daylengths more appropriate to the season. Their days shortened in early December and then lengthened in mid-February. We compared the initial levels of food storing in this experiment to those observed in experiment 1 to test whether the season in which birds are captured influences food storing soon after arrival in laboratory conditions. If food storing is at least partially determined by a photoperiodically controlled annual rhythm, not only would birds captured in November be expected to store more than those captured in March, but the effects of long versus short days in this experiment would be expected to be opposite to those in experiment 1. Increasing daylength should reduce hoarding, possibly by accelerating the development of breeding condition, while continued short days should allow hoarding to persist.

## Methods

We captured 12 black-capped chickadees on 30 October ( $N=5$ ) and 6 November 1992 in the same

**Table III.** Timetable of procedures used in experiment 2

Starting date	Duration	No. of tests	Long-day group		Short-day group	
			LD	Temperature (°F)	LD	Temperature (°F)
22 November	9 days	8	10:14	63 ± 1	10:14	63 ± 1
1 December	1 week	5	13:11	71 ± 1	9:15	64 ± 1
8 December	11 weeks	4-5 per week*	16:8	71 ± 1	8:16	64 ± 1
23 February	1 week	4	16:8	71 ± 1	12:12	64 ± 1
2 March	9 weeks	3-4 per week*	16:8	71 ± 1	16:8	71 ± 1

\*Four tests per week in most cases.

place and manner as the birds in experiment 1. We housed the birds under the same conditions as in experiment 1 and scored food storing in the same way. When they arrived in the laboratory the birds were maintained in one room on a 10:14 h light:dark cycle, with lights on at 0700 hours local time. This schedule approximated the local lighting conditions in the field at the time the birds were captured. Tests of hoarding began on 22 November. We divided the birds into two groups, matched as in experiment 1, on 1 December. Table III shows the duration and nature of the treatments each group experienced throughout the experiment. For the last 9 weeks, all birds were in the same room, and hoarding was scored blind. We recorded moulting throughout the experiment by thoroughly cleaning the cages on Fridays and counting the number of feathers and bits of down on Mondays, thus giving the total number of feathers moulted over a 3-day period. There were no deprivation tests in this experiment.

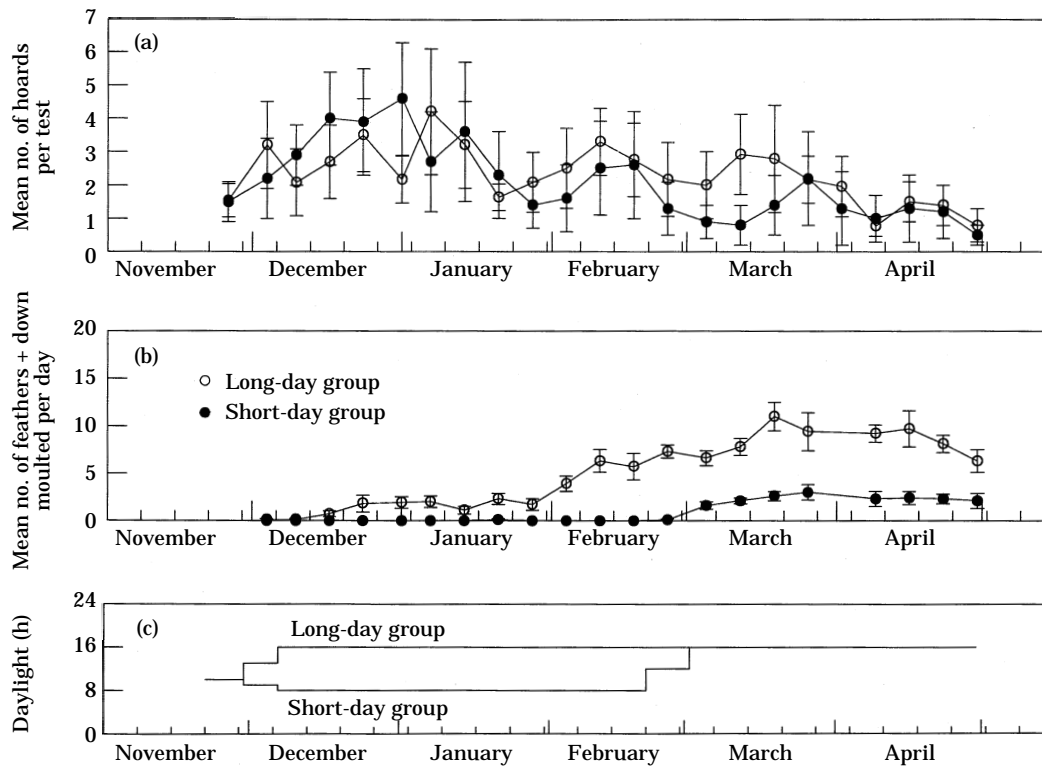
## Results

In contrast to the case in experiment 1, hoarding in this experiment was highest soon after the experiment began and declined thereafter (Fig. 2). There was no tendency for hoarding to decline faster in the group prematurely exposed to long days. If anything, the reverse was true. As in experiment 1, the effect of photoperiodic history was tested statistically using the data from the final weeks of the experiment, when all birds were in the same conditions. A repeated-measures ANOVA on the log-transformed number of hoards made per test for the last 8 weeks, in 2-week blocks, revealed that storing changed significantly over time ( $F_{3,10}=3.22$ ,  $P<0.05$ ) while

there was no significant difference between long-day and short-day groups and no significant interaction of groups and time. That hoarding declined over time in this experiment while it increased over time in the first experiment shows that neither an increase nor a decrease in hoarding necessarily results from prolonged exposure to the laboratory.

The difference in initial level of food storing between this experiment and experiment 1 was confirmed statistically using a *t*-test on the log-transformed total numbers of hoards made by each bird in the 8-day baseline phase ( $t=2.71$ ,  $df=26$ ,  $P<0.05$ ). Time of capture was not the only factor that differed between the two experiments, however. The photoperiod during the baseline phase was LD 11:13 h in experiment 1 and LD 10:14 h in this experiment. We conducted baseline testing slightly sooner after the birds were captured in experiment 2 than in experiment 1. However, it seems unlikely that these procedural differences were responsible for the three-fold difference in storing at the beginning of the experiments because in neither experiment did the level of storing change differentially for the first few weeks after the birds were put into different photoperiods, that is, it did not show any short-term immediate effect of photoperiod or temperature.

An unexpected effect of exposure to long days and warmer temperatures was a slight loss of feathers (Fig. 2). A low level of feather loss also appeared in the birds maintained on short days about 2 weeks after they joined the long-day group later in the experiment. However, the temporal pattern of feather loss differed from that observed in experiment 1 when the long-day group's days began to be shortened (see Fig. 1).



**Figure 2.** (a) Mean ( $\pm$  SE) no. of storage sites used in each 90-min test, averaged over all the tests in each week for each group of chickadees in experiment 2. (b) Mean ( $\pm$  SE) no. of feathers plus down moulted per day. (c) Hours of light/day that the two groups experienced throughout the experiment. The two groups were housed in the same room and light regime prior to differential photostimulation in November and again starting 1 week after differential photostimulation in March. On the X-axis, long ticks indicate the months; short ticks indicate the weeks.

The temporal pattern of feather loss in experiment 1 had a relatively sharp onset and a clear high peak followed by a sharp decline, features indicating that it was a true post-nuptial moult (cf. Payne 1972). In contrast, feather loss in this experiment was desultory and prolonged.

### Discussion

It is puzzling that there was no differential effect of photoperiod on the two groups in this experiment. Why did premature exposure to long days not suppress hoarding behaviour? One possible answer to this question is that while the onset of hoarding may be influenced by photoperiod, as demonstrated in experiment 1, it is no longer susceptible to photoperiodic influence once it has been initiated. A more likely answer is based on the assumption that food storing is linked to or

controlled in a manner similar to that of other annually varying behaviour patterns and physiological changes in birds. On this account, food storing was not suppressed by increased daylength in this experiment because the birds in the long-day group were exposed to long days while they were still photorefractory (see Nicholls et al. 1988). Photorefractoriness is a physiological insensitivity to long days associated with the end of breeding. In most species studied, a period of exposure to short days is necessary after breeding before the bird can again be stimulated by long days. How short the days have to be and how many of them are required varies across species (Nicholls et al. 1988). Conditions necessary to terminate photorefractoriness in black-capped chickadees do not seem to have been studied. However, it is likely that the birds in the long-day group in this experiment were not ready to be

photostimulated because exposure to long days began before the shortest day of the year and at a time when they had never experienced less than a 10-h day. On this reasoning, long days beginning in February should have caused a sharper decline in food storing in the short-day group. There was a suggestion of such an effect during the first half of March (see Fig. 2), but it was not statistically significant. In the light of these results, a better test of whether exposure to long days can reduce or terminate storing by birds in winter conditions might be to keep two groups of birds on short days until January or February and then expose one to long days while keeping the other on short days.

### GENERAL DISCUSSION

Recent studies of the proximal causation of food storing in parids have emphasized the role of the bird's state of energy balance and the predictability of the current food supply (e.g. McNamara et al. 1990; Lucas & Walter 1991; Hurly 1992; Lucas et al. 1993; Lucas 1994). The comparison of initial levels of food storing between experiments 1 and 2 shows, however, that with energy balance and food supply constant, the amount stored by black-capped chickadees soon after they arrive in the laboratory depends on the season in which they are captured. This conclusion is supported by the observation that in each experiment considerable differences in photoperiod and temperature between long-day and short-day groups did not immediately affect food storing. Any changes in amount of food stored took place after weeks, if not months. These results confirm reports on other parid species using smaller numbers of animals (e.g. Lucas & Walter 1991; Lucas 1994). They indicate that the seasonality of food storing in parids exposed to natural seasonal changes (e.g. Ludescher 1980) is not merely a response to changes in energy demands or food supply. The experiments were designed to maximize any possible effect of immediate environmental conditions by varying temperature along with daylength. Therefore, we cannot be sure whether the effects we observed were due to changes in daylength, in temperature, or in both. However, the pattern of results was so similar to that typical of photoperiodic effects on other behavioural systems in birds that it seems unlikely that temperature played much of a role.

In each experiment, the group kept from the beginning in constant conditions showed a gradual change in food storing in the direction that would be expected for that time of year. In experiment 1, the short-day group increased storing at the end of August. In experiment 2, the long-day group decreased storing in late March. These observations suggest that long-term endogenous changes occur, but confirmation of their existence would require experiments involving much longer exposure to constant conditions (cf. Gwinner 1986).

Our results suggest that the effects of body weight and predictability of food found in other experiments may be modulated by an annual rhythm (see Lucas et al. 1993). The kind of food available for storing is doubtless also important. For instance, the fact that the chickadees in experiment 1 stored almost no sunflower seeds in March does not mean that they would not have stored other more highly preferred items such as waxworms, *Galleria melonella* (see Hampton et al. 1995). We suggest that the type of item and substrate available would simply raise or lower the level around which storing would vary, but it is possible that storing preference rather than general storing motivation varies seasonally. Nevertheless, the results of experiment 1 do demonstrate that, at least under some conditions, food storing is influenced by photoperiod in a way similar to breeding and migration in numerous avian species. This demonstration opens the door to further study of food storing in parids and other birds as a behaviour pattern with an annual rhythm that may be photoperiodically controlled. It also suggests a comparison of the factors controlling food-storing behaviour with those controlling migration, the alternative strategy for surviving the winter used by many non-storing species.

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