Benefits of food hoarding

SIR — Field experiments of hoarding birds of the genus *Parus* (titmice and chickadees) suggest that stored food is retrieved within a few days after storing[1–3]. The reason that stored food is retrieved shortly after storing could be to withdraw a temporary food surplus from competitors, or to reduce the time that night energy reserves have to be carried around as body fat.

Another reason for food hoarding could be to increase access to energy during a seasonal decrease in food availability, like in winter. The seasonal pattern in food hoarding among parid birds, with a peak in autumn[4,5], is consistent with this. Still, reports that hoarded food makes up part of the winter diet[4] is no direct evidence for long-term hoarding since it has not been directly observed when that food was actually stored. Here we use a new technique to demonstrate a long-term selfish benefit of hoarding in the willow tit *Parus montanus*. Our results imply that food storing in parids may well have evolved in response to seasonal changes in the food supply.

The risk of pilfering is obvious when foraging areas are shared with conspecifics as in non-kin flocks of many parids[6]. To balance the cost in time and energy spent on hoarding, caches must be retrieved more efficiently than at random search, while the evolutionary stability of such behaviour calls for a recovery advantage for hoarders compared with conspecific scroungers[7]. Demonstration of a high recovery success for hoarders compared with others simultaneously meets both requirements as conspecifics without prior knowledge of the caching sites should retrieve caches at a random search rate.

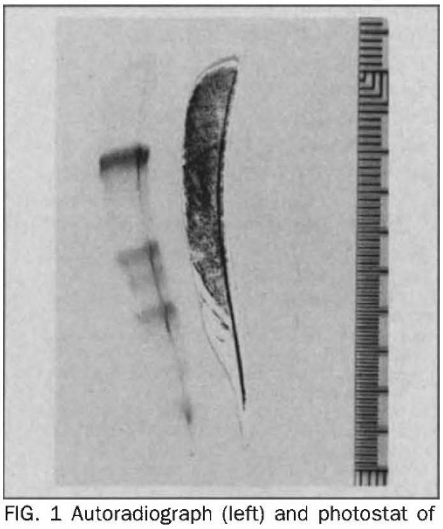

FIG. 1 Autoradiograph (left) and photostat of the outermost left rectrix of an adult male willow tit. The upper limit of the dark band is formed the day the labelled food item is consumed. With a delay of 11 days before the replacement feather protrudes, the actual date of consumption can then be calculated by counting the growth bars (on the photostat) from the tip of the feather.

We used the radio-ptilochronology technique[8] to follow the consumption of hoarded food in the field over extended time periods. Bird feathers display growth bars as bands perpendicular to the axis (rachis), with each bar representing one day's growth. Ptilochronology (literally feather time-reading) is the reading of such daily growth bars in tail feathers (rectrices)[9]. Elements ingested while the bird is growing a feather will be incorporated in the current growth bar on the day of consumption. Growth bars containing a radioactive marker can then be identified on an autoradiograph of the feather[8].

During the winter of 1992/93 and 93/94 we administered food items injected with ^{35}S-containing cysteine to willow tit flocks outside Stockholm, south-central Sweden (59°10′N, 18°20′E) and Arvidsjaur (65°40′N, 19°0′E) in northern Sweden. Earlier all birds had been individually colour-ringed while we removed a rectrix. We provided a particular bird (called the hoarder) with 20 labelled items and the other flock members (called non-hoarders) only with unlabelled items. The provided food items had been labelled with an approximate activity of 5 kBq. The specific activity ranged from 2.9×10^3 to 5.1×10^3 MBq mmol^{-1}.

A minimum of 2 months after provisioning, we recaptured the birds and collected the induced rectrices. With an initial delay of 11 days before the replacement feather protrudes[8], the induced feathers emerged on average 5.9 days (s.e. = 1.3; n = 25) after the labelled food was provided. Subsequent growth then occurs such that growth bars represent an approximate period of 35 days from this on.

The autoradiographs of replacement feathers confirm that hoarders consumed labelled items on 5.1 (s.e. = 0.9; n = 9) different occasions per individual as compared with only 1.0 (s.e. = 0.4; n = 16) for their conspecific flock mates during the approximately 6 to 40 days after storing when growth bars were laid down, a significant difference (P = 0.007, Z = 2.7, n = 9; Wilcoxon matched pairs). The advantage probably lasted longer as there was no decline in the relative selfish benefit with time (Fig. 2). Also, for one of the hoarders, the regrowth was delayed to approximately 52–86 days after provisioning, during which time this bird retrieved two food items.

Because the bird's memory may not last long enough[10] to account for the selfish benefit in our study, the delay before retrieval raises the question of how caches are retrieved. One possibility is that caches are retrieved over longer time periods by updating the memory through

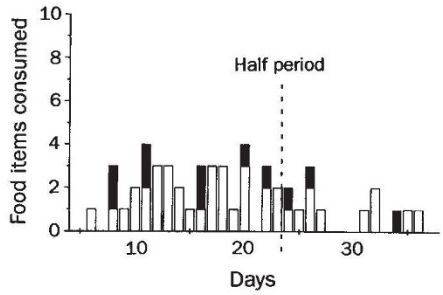

FIG. 2 Ingestion of labelled food during the main period covered by the growing feathers. Replacement feathers emerge after a delay of around 11–14 days[8], and depending on when we pulled the original feather the induced feathers grew from 6–40 days after storing. Open bars correspond to food consumed by the hoarder, black bars to pilfered items; vertical dashed bar, day 23 (the mid-point of the time window). The recovery advantage for the hoarder compared with pilferers, measured on the total number of ingestions, was very similar before (4.1) and after (4.0) day 23, suggesting that the advantage was not transient. The items retrieved before 6 or after 40 days are not shown.

rehoarding (retrieving and storing in new positions), but the empirical evidence for this is meagre[5]. Individual preferences and exclusive hoarding sites could be other mechanisms securing a recovery advantage. In willow tit flocks there is a spatial separation of feeding and hoarding sites, and this separation is even more pronounced when the flock members choose caching sites[11]. Hence, with a spatial separation of caching areas the hoarders do not necessarily have to remember the sites to enjoy a recovery advantage.

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

* Present address: Division of Population Biology, Department of Zoology, University of Uppsala, Villavägen 9, S-752 36 Uppsala, Sweden.

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