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The effect of handling time on the decision to cache by grey squirrels

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Animals that store food must decide which items to eat immediately and which to store for future consumption. Clearly, a starving animal should eat and a satiated animal should store, but other factors must influence this decision in partially satiated foragers. Characteristics of the food could affect the decision; eastern woodrats, *Neotoma floridana*, eat highly perishable food and store food that is less perishable (Reichman 1988). If caching a food item takes less time than eating it, however, then foragers under time constraints might be affected by an item's handling time.

Such time constraints should affect the caching decision in the grey squirrel, *Sciurus carolinensis*. Grey squirrels eat and store the large seeds of hickory, *Carya* spp., and oak, *Quercus* spp., trees during a short autumn harvest (Thompson & Thompson 1980), competing with conspecifics at communal food trees (Jacobs 1987). I hypothesized that a squirrel could increase its foraging efficiency by always choosing the behavioural option, eating or caching, that was least time consuming. If one food item took longer to eat than another, and if a squirrel could cache an item in less time than it took to eat it, then a squirrel should preferentially cache those items that took longer to eat.

I tested this hypothesis with five hand-raised adult male grey squirrels. The squirrels were kept in individual outdoor cages, measuring $1 \times 1 \times 1{\cdot}5$ m, and maintained on a diet of laboratory rodent chow, unshelled peanuts, hazelnuts and black walnuts, and water ad libitum. All squirrels had experience eating, caching and retrieving the foods (hazelnuts, laboratory rodent chow) used in this experiment. Squirrels were deprived of food for 24 h before testing. They were then given a series of 20 food items, in their cage, one at a time, as illustrated in Fig. 1a. Ten items each of two food types, which differed in consumption time, were given alternately to the squirrel, beginning with the item of greater consumption time. I noted the squirrel's decision, to eat the item or cache it, and the time (in seconds) spent eating or caching. Squirrels generally either ate or cached each item; in the few cases where the squirrel started eating the item and then cached it or started caching an item and then ate it, the second behaviour was considered the final decision. As soon as the squirrel finished one item, it was given the next item.

To test the hypothesis that squirrels would be more likely to cache items of greater consumption time, squirrels were offered two items of equal energetic and nutritional content, but the items required different consumption times: 10 hazelnuts with shells and 10 hazelnuts without shells. I predicted that squirrels should cache more nuts with shells because the shell increased consumption time.

However, nuts with shells are also less perishable and the perishability hypothesis would also predict this result. Therefore, a second series of choices was required to distinguish between the two hypotheses. I predicted that a highly perishable food that must be consumed slowly would be preferentially cached over a less perishable food that could be eaten quickly. Thus, squirrels were offered two other foods from their maintenance diet, blocks of laboratory rodent chow and shelled hazelnuts. Chow blocks have a high consumption time yet are highly perishable, disintegrating quickly when cached in damp ground. Moreover, all subjects had previous experience caching and retrieving partially disintegrated chow blocks. In contrast, shelled hazelnuts are less perishable when cached but can be eaten quickly. The perishability hypothesis predicted that squirrels should preferentially cache hazelnuts, whereas the consumption time hypothesis predicted they should preferentially cache chow blocks.

The squirrels were given two series of 20 items, separated by a period of 24 h. Each of the five squirrels received one trial (a series of 20 items) on

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each day. Because a chow block is a less preferred food and squirrels might be less motivated to eat it if they had recently eaten and cached the more preferred hazelnuts, the chow block and hazelnut series was given on the first day, to conservatively bias their behaviour. The mean ($\pm$SE) total time per trial per squirrel was $32{\cdot}0 \pm 2{\cdot}8$ min for the first series, and $36{\cdot}6 \pm 6{\cdot}2$ min for the second series ($N = 5$ squirrels, for all results). Squirrels generally began by eating every item and then became satiated and started caching (Fig. 1a). The number of each type of food cached yielded a measure of the squirrel's preference to cache one type or the other.

Measurements of eating and caching times confirmed that the two items differed in consumption time. Squirrels spent 66·0% more time eating chow blocks than hazelnuts without shells (Mann–Whitney U-test, $P < 0{\cdot}005$), and 29·9% more time eating hazelnuts with shells than hazelnuts without shells (Mann–Whitney U-test, $P < 0{\cdot}043$). Moreover, regardless of food type, squirrels spent less time caching a particular food type than they spent eating it (Mann–Whitney U-test, $P < 0{\cdot}022$), confirming an important assumption of the consumption time hypothesis.

The major prediction of the hypothesis, that squirrels should preferentially cache those items of greater consumption time, was supported by the results. Squirrels preferentially cached chow blocks in the first series and hazelnuts with shells in the second series. Squirrels cached an average ($\pm$SE) of $8{\cdot}0 \pm 0{\cdot}3$ chow blocks and only $1{\cdot}6 \pm 0{\cdot}5$ hazelnuts without shells, a significant difference (Mann–Whitney U-test, $N = 5$, $P < 0{\cdot}001$; Fig. 1b). In the second series, squirrels cached an average ($\pm$SE) of $6{\cdot}6 \pm 1{\cdot}0$ hazelnuts with shells and only $1{\cdot}8 \pm 0{\cdot}4$ hazelnuts without shells, again a significant difference (Mann–Whitney U-test, $N = 5$, $P < 0{\cdot}006$; Fig. 1c).

Thus, in deciding which items to eat and which to cache, the squirrels appeared to estimate the relative time costs of eating and caching, and then chose the option that took less time. The relative perishability of the item had less effect on this decision than did consumption time, as squirrels preferentially cached chow blocks despite their higher perishability relative to nuts without shells. The sensitivity of their response to this variable is surprising, given the necessarily artificial conditions. Because squirrels had to cache in a small area, the time cost of this behaviour was greatly reduced, particularly in comparison with the cost of

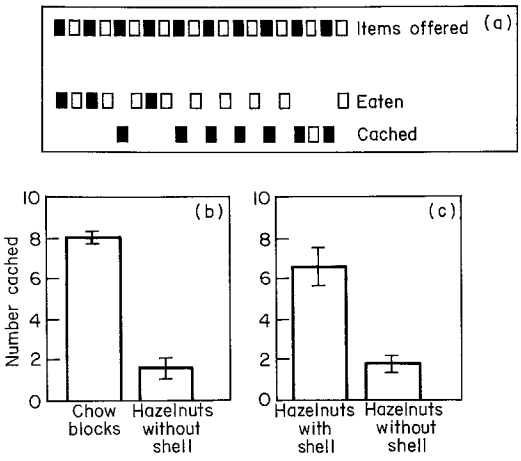

Figure 1. The effect of consumption time on the caching decision. The schematic shows a representative trial from the second series. Histograms represent the mean ($\pm$SE) number of items cached of each type ($N = 5$). (a) ■, hazelnuts with shells; □, hazelnuts without shells. The top row of symbols represents the order in which items were presented; the second and third rows show the decisions made in response to the series of items. Items that were eaten are shown in the second row and cached items are shown in the third row. (b) Number of each type of food cached in response to a series of chow blocks and hazelnuts without shells. (c) Number of each type of food cached in response to a series of hazelnuts with and without shells.

caching under natural conditions (Thompson & Thompson 1980). Thus, one might have expected the squirrels to eat or cache different foods with equal frequency, in contrast with their observed sensitivity to small differences in the costs of this behaviour.

The consumption time hypothesis may also shed light on other studies of the caching decision. Woodrats preferentially cache chow blocks and eat grapes (Reichman 1988). Although the food-storing behaviour of woodrats and grey squirrels differ in important ways, it is intriguing that the woodrat results are consistent with the consumption time hypothesis because of the greater consumption time of chow blocks relative to grapes.

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