

## The effects of time constraints and changes in body mass and satiation on the simultaneous expression of caching and diet-choice decisions

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**Abstract.** Foraging decisions of tufted titmice, *Parus bicolor*, were monitored in a laboratory experiment in which small and large mealworm pieces were delivered on a moving conveyor belt. The effect of changes in physiological states (satiation and body mass) and environmental states (foraging time constraints and short-term variation in inter-prey intervals) on two foraging decisions (diet choice and caching) were studied. All states had a similar effect on diet choice: when the titmice were hungry, light weight, running out of time, or waiting a long time for a prey item to arrive, they were more likely to accept a small prey item. Large prey were virtually always taken. Thus when state deteriorated, diet choice decisions became more impulsive (i.e. the birds were more likely to take any prey they encountered). The correlation between body mass and diet choice is shown to be contrary to the predictions from models of risk-sensitivity. Caching decisions differed from diet choice in several respects: titmice cached less when hungry and cached less after waiting a long time for a large prey item to arrive, but they were more likely to cache when light weight and showed no response in their caching decisions to short-term time constraints. Thus, hungry titmice were more impulsive in their caching decisions (i.e. they were more likely to eat prey than to cache it), but light-weight titmice were less impulsive. The correlation between body mass and caching is consistent with predictions from recent dynamic-programming models. These results are also discussed in light of models of future discounting, or the relative discounting of future rewards under conditions when the forager chooses between an option that returns an immediate reward and an option that returns a reward some time in the future.

A decision can be thought of as a commitment of time to some particular course of action (Brockmann et al. 1979; Lucas 1985). For example, a bird that decides to eat a seed commits a certain period of time to this activity. This definition can be useful in the functional analysis of behaviour. We can evaluate decisions by comparing the reward gained from an action against the opportunity costs of that action; costs accrue as a result of the commitment of time to the action (Lucas 1985; Stephens & Krebs 1986). Unfortunately, the analysis is complicated by a wide variety of factors that can affect the balance between current rewards and lost opportunities.

The complexity of the problem is not particularly evident from classical optimal foraging theory (Pyke et al. 1977), because this theory typically assumes that opportunity costs should be based primarily on only a few variables, such as prey

size, encounter rate and patch quality. In addition, if the forager is not time constrained and chooses alternatives that maximize net energetic gain, lost opportunities are only those events that might occur while the animal is occupied with a chosen course of action (Lucas 1985). More recently, a growing body of literature has shown that maximization of net energetic intake rate, an assumption of the classical theory, is not broadly applicable when foraging decisions are dependent on an animal's physiological state (McNamara & Houston 1986; Mangel & Clark 1988). Consider the level of energy reserves. As energy reserves drop, starvation risk becomes more immediate and, as a result, current rewards should be valued more heavily than potential future rewards (Kagel et al. 1986). Thus the relative time in which a reward is expected can affect how the forager should value it. Also, any given decision can affect an animal's energy reserves long after the behaviour is finished. Sensitivity to physiological state complicates our view

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of the decision-making process by increasing the number of variables involved, and by altering the time horizon over which opportunity costs should be measured. The same is true of time constraints. A number of factors can impose constraints on the amount of available foraging time (Lucas 1985, 1990). These constraints may restrict the range of future options available to the forager, and as a result, reduce the opportunity costs.

This discussion assumes that decisions are made one at a time, but in fact, foragers may be faced with many decisions simultaneously. For example, diet choice in depleting patches presents foragers with two different types of decisions that must be made concurrently (Heller 1980; Lucas & Schmid-Hempel 1988). The problem of simultaneous decisions is particularly intriguing when the opportunity costs or relevant time horizons of the decisions differ. Here we report an empirical study in which tufted titmice, *Parus bicolor*, were offered different prey types that could be eaten immediately or cached. Thus the birds were faced with two simultaneous decisions, diet choice and caching.

Most temperate zone parids store seeds for a few days or less before retrieving them (Sherry 1989; see Petit et al. 1989 for a general description of caching by tufted titmice; note that some northern species can store for months, Haftorn 1956). This suggests that caching decisions of titmice (a southern temperate species; Bent 1964) entail time horizons of hours to days, the forager choosing between some immediate reward versus a reward from the same prey item when it is retrieved at some time within a period of days (McNamara et al. 1990; Lucas & Walter 1991). In contrast, diet choice entails time horizons measured in minutes, the forager either accepting an immediate reward from an encountered prey or rejecting the reward in order to wait for some (presumably better) prey items that may arrive while the forager is handling the encountered prey (Lucas 1985). As noted above, the effects of physiological state on foraging decisions may extend the time horizon of diet choice beyond a few minutes and may collapse the time horizon of caching behaviour. None the less, the balance between the payoffs and opportunity costs for these two patterns of behaviour are likely to be quite different.

Our research focused on three questions.

(1) Are titmouse foraging decisions consistent with predictions from classical optimal foraging

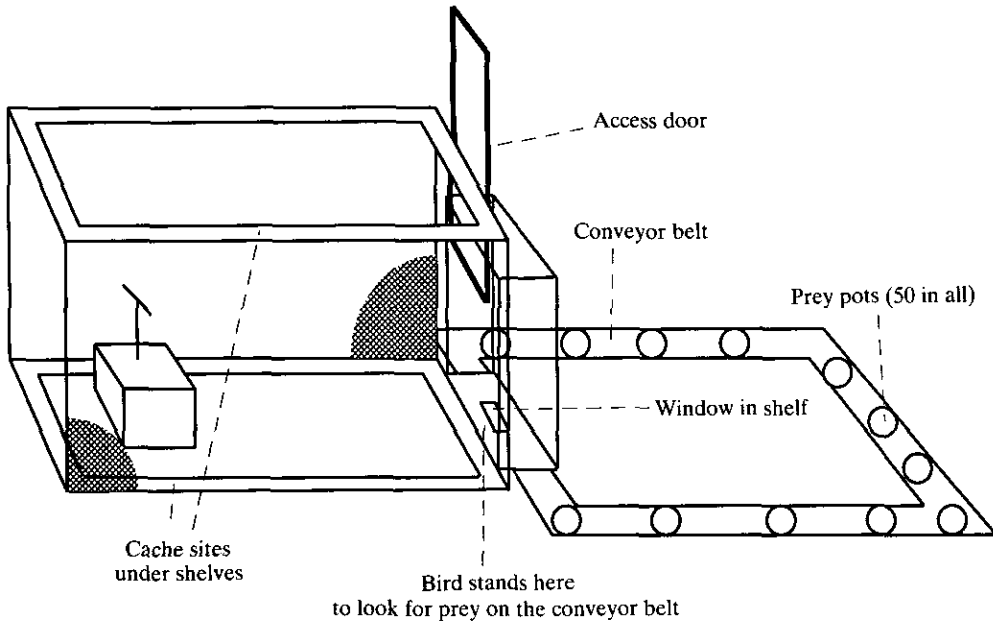
theory (e.g. Pyke et al. 1977)? Specifically, are prey ranked according to the criterion energy/handling-time, and do the birds choose a diet that maximizes net energy intake rates? Here we assume that prey biomass is correlated with energy content.

(2) Are the two foraging decisions affected by changes in physiological state (here we address satiation and body mass), and if so, are the state-dependent properties of simultaneous caching and diet choice decisions consistent with predictions from models derived for the behaviour patterns exhibited in isolation?

(a) Diet choice. (i) Body mass: predictions about the effect of body mass on diet choice do not address body mass per se, but instead consider relative changes in body mass. Stephens & Charnov (1982; see also Real & Caraco 1986) predicted that foragers should choose a diet that maximizes  $(\mu_\tau - R_{\text{net}})/\sigma_\tau$ , where  $R_{\text{net}}$  is equal to the net food requirement during some time interval  $\tau$ ,  $\mu_\tau$  is equal to the mean gain during  $\tau$ , and  $\sigma_\tau$  is equal to the standard deviation of the gain during  $\tau$ . This model, the z-score model, predicts that the forager should favour low variance options when it expects to gain weight ( $R_{\text{net}} < \mu_\tau$ ), and should favour high variance options when it expects to lose weight ( $R_{\text{net}} > \mu_\tau$ ). (ii) Satiation: a number of authors have suggested that satiation should increase selectivity, either by increasing the animal's short-term estimate of prey encounter rate (e.g. Pulliam 1974; Charnov 1976), by a greater emphasis on maximizing net energetic intake rate when hungry (Pulliam 1974; Sih 1982; Rechten et al. 1983), by a response to variability in intake rate (choosing the more certain option, i.e. prey in hand, when hungry; Stephens & Krebs 1986), or by an increase in the value of current rewards when hungry (a variant of the variability hypothesis; Kagel et al. 1986).

(b) Caching. (i) Body mass: Lucas & Walter (1991) predicted that birds foraging in fairly rich habitats on a single prey type should show reduced caching rates when they are relatively heavy. (ii) Satiation: the Lucas & Walter model does not consider satiation effects nor does a similar model by McNamara et al. (1990).

(3) To what extent do short-term time constraints influence both patterns of behaviour? Based on an energy rate maximization model, Lucas (1985) predicted that under time constraints,



**Figure 1.** Diagram of the conveyor belt. The back, sides and top of the cage were made of screening; thus the birds were able to perch next to the top caching shelf in order to cache seeds there. The front of the cage over the conveyor belt was Plexiglas. This let us videotape the birds with cameras placed to the right of the conveyor belt.

diet selectivity should decrease as the amount of available foraging time decreases. We test this prediction here and additionally test for a similar response in caching decisions.

## METHODS

### General

Six wild-caught birds were captured at Purdue University's Ross Biological Station using treadle traps baited with sunflower seeds and housed individually in 1-m<sup>3</sup> holding cages for about 1 month before they were tested. The sex of the birds was determined by laparotomy: two birds were females (LL and MM: maximum weights 21.0 and 21.6 g), and the rest were males (BR, OO, BB and GG: maximum weights 23.4, 24.2, 25.1 and 26.0 g). All birds were caught several times in the field before they were taken for the experiment. All were known to be at least 1 year old. Maximum ( $\pm$ SD) weight measured in the field was  $97.4 \pm 1.4\%$  of the maximum weight measured in the lab. The birds' weight at capture was  $95.9 \pm 2.3\%$  of the maximum laboratory weight. Maximum attained weight was significantly correlated with wing chord length (75.5, 78, 81, 82.5, 81, 83 mm for LL, MM, BR, OO, BB

and GG, respectively; Spearman's rank correlation  $r_s = 0.9$ ,  $P = 0.015$ ).

The birds were tested one at a time in a 1-m<sup>3</sup> cage and were offered two different types of prey, small (three-segment) and large (nine-segment) pieces of mealworm, on a moving conveyor belt (see Rechten et al. 1983; Lucas 1987; Fig. 1). The conveyor belt consisted of a series of shallow pots that ran under an open window in one corner of the cage. The window permitted a view of one pot at a time (*i.e.* prey encounter was sequential), and belt speed was set so that pots were in sight for about 1.38 s. Prey were arranged with a Poisson distribution; mean encounter rates were 1/4 pots for small prey and 1/15 pots for large prey. A large black door regulated access to the conveyor belt. A narrow shelf (0.5 cm high  $\times$  1.5 cm deep) along the entire top and bottom periphery of the cage was provided for cache sites. The birds used these sites and several additional sites (*e.g.* cracks in a door in the cage, under newspaper on the floor) for storage. A 10:14 h light:dark cycle was used throughout the experiment, with lights on at 0800 hours. Room temperature was measured every morning before the experiment started; the mean ( $\pm$ SD) temperature was  $17.9 \pm 1.5^\circ\text{C}$ .

We monitored two physiological states, changes in body mass (which correlate with changes in fat reserves; Chaplin 1974; Blem 1990) and short-term satiation (assumed to increase monotonically as time passed during a day's session and assumed to increase as food was eaten within a session). All birds were weighed just before we put them in the experimental cage. We regulated their mass, independent of their behaviour in the experiment, by varying the amount of food we provided in their holding cages. Food available in the holding cages consisted of 0.5 g grated carrots, about 1 g mealworms, 0.4–1.4 g sunflower seed pieces and 0.75–2.25 g Purina Canary Chow. All food offered in the holding cage was eaten by 1600 hours, irrespective of the amount given, therefore we assumed that all birds were hungry the following morning when the experiment began. Water with vitamins was available *ad libitum* in both the holding cages and experimental cage.

The birds usually required several days of training before they would take food from the moving belt. After this initial period, we allowed the birds a single 15-min block of continuous access per day for at least 1 week until their caching and diet choice behaviour had stabilized. The birds' body mass during the training periods was kept at about 90% of the weight they maintained under *ad libitum* access to food (*ad libitum* weight).

After training, we ran two birds a day on a series of access intervals and alternated which bird was run first each day. All experiments were run in the morning and only one bird was kept in the conveyor-belt room at any one time; the other was kept in a holding cage in a separate sound-proof room until it was tested. All birds except one (GG died after the first 15-min access interval) were tested on the same sequence of access intervals. All six birds started off with a single 15-min access interval once per day (schedule 1/15). The five remaining birds were tested on three additional daily access schedules: 15, 2-min access intervals with 90-s inter-bout intervals (schedule 15/2), followed by 15, 0.5-min access intervals with 90-s inter-bout intervals (schedule 15/0.5), then 30, 0.5-min access intervals with 60-s inter-bout intervals (schedule 30/0.5). The access schedules were chosen to provide a range of bout lengths of uninterrupted access to food (0.5–15 min) and a range of total access times to food (7.5–30 min). Instead of randomizing the bout interval for each trial, we used this decreasing series of bout lengths,

15 min then 2 min then 0.5 min, to ensure that the birds would not underestimate bout length based on previous experience (as in Lucas 1987). The birds were given 2 days of training on each new schedule before data were collected. Data collection generally lasted 2 weeks, during which time the mass of the birds was about 95% of their *ad libitum* weight for the first week and about 80% of their *ad libitum* weight for the second week. Data were collected 5 days a week. We regulated body mass by altering the birds' diet during the intervening 2 days.

One of the birds (LL) used a foraging tactic that none of the others showed; it flew to the belt, looked at a single pot, then flew away before the next pot arrived even if it found no prey. We extended the data collection for the first access schedule (1/15) to 4 weeks to see if the bird would stay longer at the belt in search of food, but it never changed tactics when tested with this schedule. However, when the access intervals were shortened, the bird began to wait at the belt until prey arrived (as did all other birds). Therefore, after running bird LL and the bird with which it was paired (OO) through the series of four access schedules, we re-tested them on a single 15-min access interval. The same sequence (1/15, 15/2, 15/0.5, 30/0.5, 1/15) was used with bird MM. The behaviour of birds OO and MM was similar for both sets of 15-min access intervals, therefore the data from both sets were combined, and data from only the second set of 15-min access intervals are reported for bird LL.

All data were taken from videotapes of the sessions. We recorded only prey that passed while the bird was looking at the belt; this was determined by the orientation of the head (tilted down and towards the conveyor belt) which was clearly visible on the videotape. Handling time and caching time consisted of two intervals: the time from when a prey was taken until handling or caching was complete, and the time required to fly back to the belt. The entire circuit (belt to perch to belt) was taken as handling time because doing so measures time invested in a decision during which no other foraging decisions could be made. We measured the first interval for every prey taken. The second interval was not measured for prey that were finished after the access door closed, and was also not measured when the bird performed other activities (e.g. flying around the cage or drinking water) after eating or caching a prey and before returning to the belt. Ignoring handling and caching times when we did

not have an estimate of the second interval could potentially bias these times downward, because the entire circuit is most likely to be observed when the circuit is short. To help correct for this bias, we estimated the mean and variance of the second interval from observations for which the entire circuit was observed, and then added a random number (taken from a normal distribution with this mean and variance) to all times for which the second interval was not measurable. A sample of 25 mealworm pieces of each size was weighed each day; prey biomass divided by handling time and prey biomass divided by caching time were used as indices of relative prey value.

Retrieval of cached food could occur only when the birds were in the experimental cage. Any stored food left at the end of the day was replaced the following morning before the birds were tested, and all prey cached by the first bird run in a day were removed before the second bird was tested. If cached prey items were left at the end of the previous day's experiments, the access door was kept closed at the beginning of the session until the bird stopped retrieving cached prey; this usually occurred after all cached prey were retrieved and eaten.

**Prey Values and Biomass Intake Rates**

We estimated three indices of mean prey value: biomass, biomass/(caching time) for cached prey, and biomass/(handling time) for eaten prey. Two methods were used to estimate potential harvest rates. The first estimate is derived from the classical diet choice model (Stephens & Krebs 1986). This method is appropriate if the forager perceives no constraint on foraging time, or at least does not include finite time horizons in its estimate of energetic yield (Lucas 1985). Under this assumption, potential harvest rates ( $B/\tau$ ) for specialist and generalist diets can be estimated from handling time ( $h_i$ ), prey biomass ( $b_i$ ) and prey encounter rates ( $\lambda_i$ )

$$\frac{B}{\tau} = \frac{\sum b_i \lambda_i}{1 + \sum h_i \lambda_i}$$

Variance in  $B/\tau$  (see Stephens & Charnov 1982) is

$$\sigma_{\tau}^2 = \tau \left\{ \frac{\sigma_e^2 \lambda^*}{1 + \sum \lambda_i h_i^*} + \frac{\mu_e^2 (1 + \sigma_h^2 \lambda^{*2}) \lambda^*}{(1 + \sum \lambda_i h_i^*)^3} - \frac{2\mu_e \sigma_{hc} \lambda^{*2}}{(1 + \sum \lambda_i h_i^*)^2} \right\}$$

where  $\sigma_e^2$  is equal to the variance in prey biomass,  $\sigma_h^2$  is equal to the variance in prey handling time,  $\sigma_{hc}$  is equal to the covariance between prey handling time and biomass,  $h_i^*$  is equal to the mean handling time of prey  $i$ ,  $\lambda_i^*$  is equal to the encounter rate of prey type  $i$ ,  $\lambda^* = \sum \lambda_i$ ,  $\mu_e$  is equal to the mean prey biomass and  $\tau$  equals total foraging time. Note that we have corrected two errors in the original equation of  $\sigma_{\tau}^2$  from Stephens & Charnov (1982).

Unfortunately, the mean and variance in harvest rate can be affected by short-term time constraints (e.g. Lucas 1985). If the birds are capable of detecting this difference, this may affect the predictions concerning foraging decisions. For this reason, we used a simulation model to estimate the mean and variance in harvest rates under each of the four access schedules. In addition to the effect of time constraints on the predicted harvest rates, the simulation differed from the above equation in three aspects: (1) time was treated as a series of discrete intervals corresponding to the discrete arrival of pots on the conveyor belt, (2) harvest rates were based on the total potential biomass harvested during a day's session (e.g. during all 15 bouts in schedule 15/0.5), and (3) foraging time was taken as the amount of time the belt was accessible and therefore did not include handling time spent after the access door closed. The latter assumption is appropriate if time spent eating after the access door has closed does not detract from time that would be spent more profitably in other activities, such as singing or drinking. If this assumption is not correct, then the classical diet choice model can be used, even under time constraints (Lucas & Schmid-Hempel 1988). We simulated 250 days to generate estimates of the mean and standard deviation for each access schedule.

**Statistics**

Diet choice decisions and caching decisions were evaluated separately using step-wise logistic regression analysis (PROC LOGISTIC; SAS Institute 1988). We considered two caching alternatives, cache/eat, and two diet choice alternatives, take-small-prey/ignore-small-prey. A separate analysis was done for each of the four access schedules. Unlike discriminant analysis, logistic regression does not require multivariate normality with equal covariances (Press & Wilson 1978). Harrell & Lee

**Table I.** Value of small prey (biomass/handling time) as a fraction of large prey value for six tufted titmice

Bird ID	Access schedule (no. bouts/no. min per bout)							
	15/0.5		30/0.5		15/2		1/15	
	Take	Cache	Take	Cache	Take	Cache	Take	Cache
LL	1.24	NC	1.33	0.44	1.28	0.39	1.20	0.52
MM	1.23	NC	1.58	0.65	1.71	0.74	1.61	0.65
BR	0.95	NC	0.92	0.76	1.41	0.80	1.20	0.67
OO	1.14	NC	1.13	0.72	1.23	0.77	1.12	0.82
BB*	0.69	NC	0.76	—	0.79	—	0.63	—
GG*†	—	—	—	—	—	—	0.78	—

Take: value of prey when eating; Cache: value of prey when caching (handling times are defined in text); NC: no caching during this interval.

\*Never cached small prey.

†Tested on only one access schedule.

(1985) note that the only assumption that is likely to be violated using logistic regression analysis for binary dependent data is the assumption that the logit of the response ( $\log P/[1-P]$ ; where  $P$  = probability of a response) is linearly related to the independent variables. In fact, our data did not meet this assumption. Following the recommendations in Harrell & Lee, two methods were used to linearize the data: we added squared terms for all main effects and included interaction terms between all variables.

Six types of independent variables were used in the logistic regression analyses: time-in-bout (time passed since the access door was raised; this measures a response to time constraints), short-term variation in prey arrival times (including the time spent at the belt since the last large prey was seen, and the time spent at the belt since the last prey of any type was seen), satiation (including the sum of prey biomass eaten since the beginning of the trial plus any retrieved prey, and the number of access intervals that had passed during a trial), body mass (mass at the beginning of a trial taken as a fraction of the maximum weight measured for the bird), individual differences (including the median body mass of each bird and the mean relative prey value for each bird), and experimental condition (time of day the experiment started and room temperature). The mean relative prey value was  $RV = (b_s/h_s)/(b_l/h_l)$ , where  $b_s, b_l$  is equal to the median mass of small and large prey, respectively,

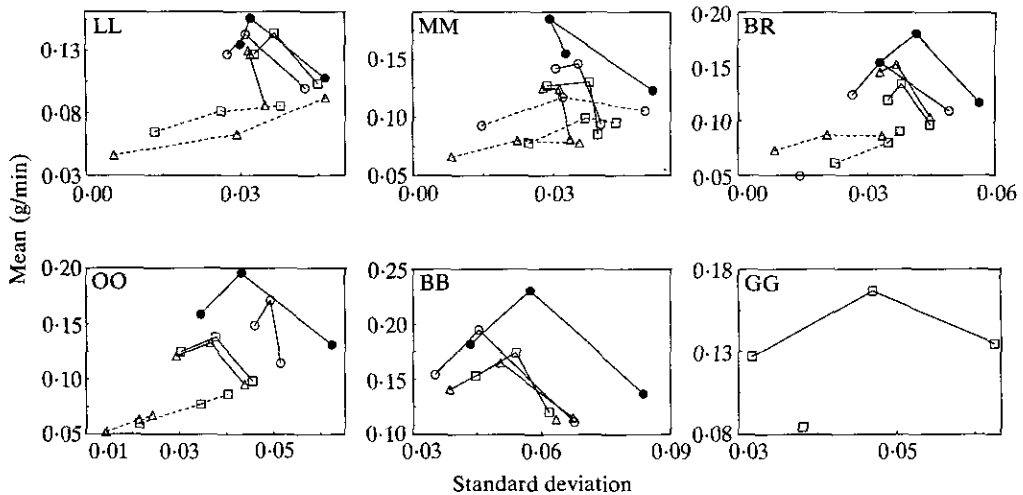
and  $h_s, h_l$  is equal to the median handling time of small and large prey, respectively. This index accounted for fairly marked differences among birds in the relative times required to eat small and large prey.

We assumed that the bird's foraging decisions had stabilized after each 2-day training period. This was tested by adding an additional variable to the models, the number of days that had passed since the beginning of the experiment. In no case was this variable significant.

## RESULTS

### Prey Values

Large mealworm pieces were about 2.5 times larger than small pieces ( $0.084 \pm 0.009$  versus  $0.033 \pm 0.005$  g,  $\bar{X} \pm \text{SD}$ ). For all birds, biomass/(caching time) was higher for large prey (Table I). However, if the birds rank prey according to biomass/(handling time), then longer handling times for large prey by some birds (the smallest four birds: BR for schedules 15/2 and 1/15, LL, MM and OO) would make small prey more valuable (Table I). This was not true of birds GG and BB, for whom large prey were more valuable than small prey when eaten; these large birds never cached small prey so no estimate of caching time is available. Thus at least some birds should rank small prey higher when eating but large prey should be ranked higher



**Figure 2.** Predicted mean and standard deviation intake rates of prey from the classical diet choice model for three alternative diets (small specialist, generalist, large specialist) available to tufted titmice (see text for equations). Each figure represents a different bird in increasing order by maximum body mass (letters above figures are identification letters), each line represents a different feeding schedule (●: 15/0.5; ○: 30/0.5; △: 15/2; □: 1/15) and the two line types represent eating (—) and caching (---). Caching rates are for the time required to cache food, not including time required to retrieve and eat the food. Each line contains three points; in all cases, the middle value represents the generalist diet and the right-most value (i.e. point with highest standard deviation) represents the large specialist diet. Points not connected by lines (in BR, BB and GG) indicate schedules for which no handling time was available for cached small prey, so only the values for caching as a large specialist are presented.

when caching, assuming these decisions are based on maximizing biomass harvest rates.

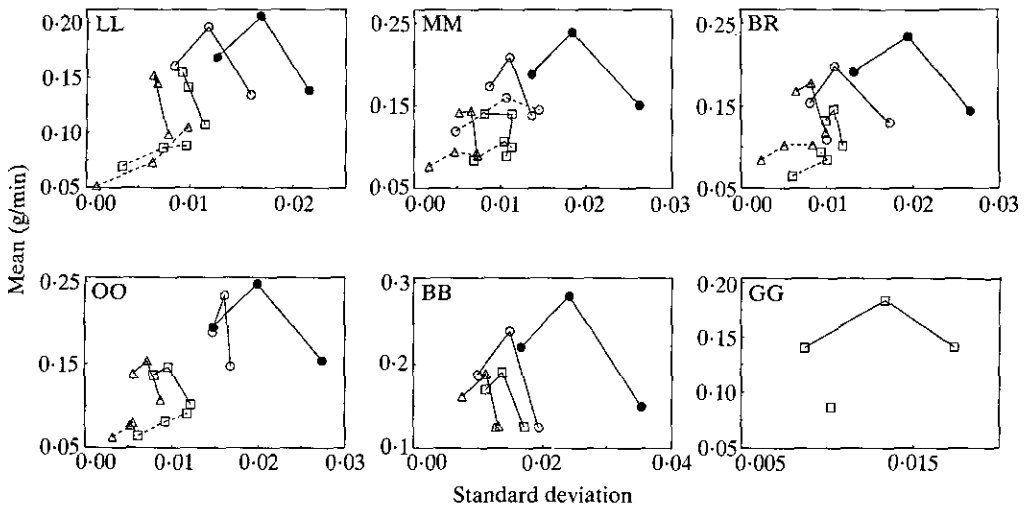
#### Diets that Maximize Biomass Intake Rates or Minimize the z-score

Handling times differed for eaten and cached prey, therefore we calculated separate intake rates for prey choice followed immediately by eating, and prey choice following by caching. The birds would generally maximize intake rates while eating if they took both prey types during all four access schedules (classical diet choice model: Fig. 2; simulation: Fig. 3). Expected gain rates differed between bouts as a result of lower handling times during shorter bouts (Tukey's studentized range test,  $\alpha=0.05$ ; for birds MM and BR: schedules  $15/2 > 1/15 > 30/0.5 = 15/0.5$ ; for birds LL, OO and BB:  $15/2 = 1/15 > 15/0.5 = 30/0.5$ ).

Taking only large prey would maximize caching harvest rates for three birds (LL, BR and OO), while taking both would maximize caching harvest rates for MM. (No comparison is possible for GG or BB because they never cached small prey.) However, comparing the choice of eating or caching, the birds should never cache if they maximized intake rates because the birds' potential caching harvest

rate was only about 70% of eating harvest rate (classical model:  $67 \pm 8$  (SE), Fig. 2; simulation:  $70 \pm 5$ , Fig. 3).

In general, Stephen & Charnov's (1982) z-score model predicts a generalist diet when the birds were eating and a specialist diet (on large prey) when they cached. Deviations from this pattern should be as follows: when birds were light weight they should have preferred large prey and when heavy they should have preferred small prey. The z-score model predicts that the optimal diet is that which maximizes the slope of a line in Fig. 2 (or Fig. 3) through the value for a given diet with a Y-intercept at the daily net requirement ( $R_{net}$ ; Stephens & Krebs, 1986). The equation of this line is  $\mu = R_{net} - Z(\sigma)$ ; the optimal diet minimizes  $Z = (R_{net} - \mu)/\sigma$ . Thus in order to evaluate the predictions of the z-score model, we need an estimate of the bird's perception of its daily requirement. There are two possible estimates. First, the net requirement could approximate the yield from the birds' diet because the birds' weights were relatively stable while the data were collected. When the birds ate food immediately, the generalist diet generally yielded the highest mean harvest rate and an intermediate standard deviation; the small specialist had a lower gain and lower



**Figure 3.** Predicted mean and standard deviation intake rates of prey from simulations of titmice foraging using three alternative diets (small specialist, generalist, large specialist). Details as in Fig. 2. See text for discussion of the simulation.

standard deviation, and the large specialist had a lower gain and a higher standard deviation. The three points together form an inverted 'v', with the generalist diet at the apex (see solid lines in Figs 2, 3). If  $R_{net}$  is roughly the level of the mean energetic gain, then a line from  $R_{net}$  through the return from the generalist diet would have the highest slope of the three alternative diets. The patterns for caching behaviour (dashed lines in Figs 2, 3) indicate that bird MM should cache both prey types, and birds LL, BR and OO should cache only large prey (no caching times for small prey were available for BB or GG).

Alternatively, the birds could estimate that  $R_{net}$  was higher relative to their intake rates when they were light weight than when they were heavy. Strictly speaking, this is true because the birds were given less food in their holding cages when they were light weight, so they had to eat more during the experiment if they were to compensate for this loss. Thus deviations from the generalist diet should be systematic: the birds should tend to prefer large prey when they are light weight (because this diet increases variance) and small prey when they are heavy (because this diet decreases variance). This is true for both diet choice and caching decisions.

#### Diet Choice

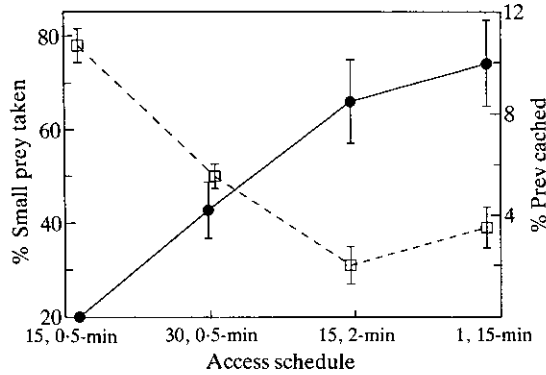
Under the strictest constraints (schedule 15/0.5), the birds chose the diet that maximized net energetic

intake rates; they took most of the small prey they encountered (Fig. 4). The proportion of small prey taken decreased two-fold under relaxed constraints (schedules 15/2 and 1/15; difference between schedules:  $\chi^2 = 482.7$ ,  $df = 3$ ,  $P < 0.001$ ; difference between birds:  $\chi^2 = 1042.7$ ,  $df = 5$ ,  $P < 0.001$ ).

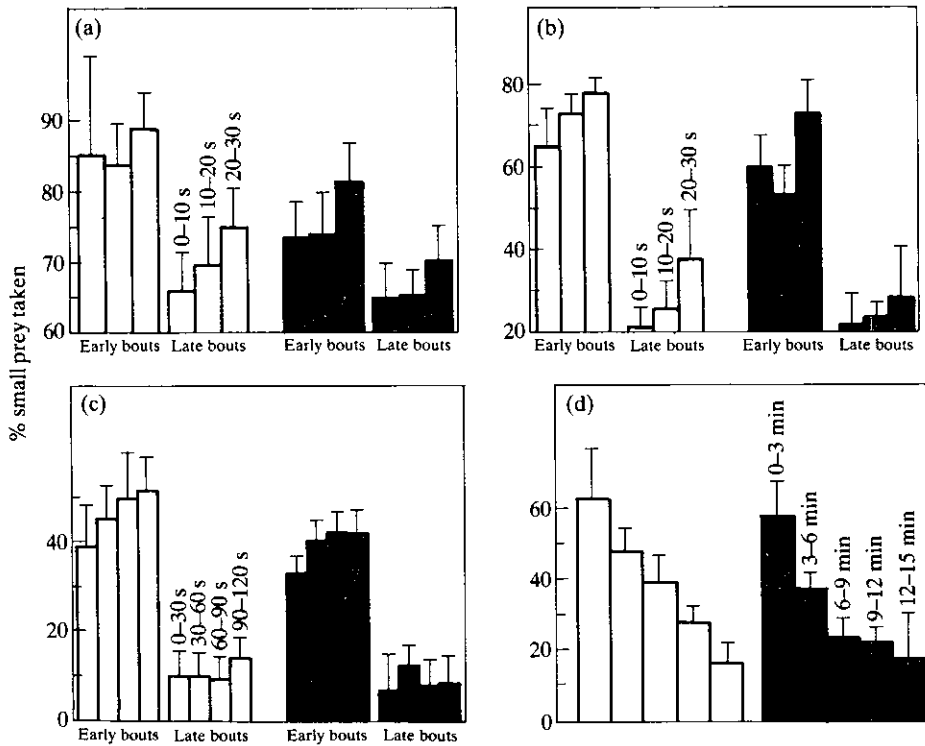
The predictions from the classical diet choice and z-score models were not generally supported. Despite the fact that at least three of the birds should have preferred small prey to large, large prey were taken virtually every time they were encountered by all birds. The probability that small prey were accepted was correlated with all of the variables we measured. Logistic regression analyses showed that the birds were more likely to reject small prey when they were heavy for schedules 15/0.5, 30/0.5 and 1/15 (Fig. 5; see %body mass in Table II); this result is opposite to the prediction of the z-score model. No significant relationship was found for schedule 15/2. In the short-bout schedules, the quantitative relationship between body mass and selectivity was exaggerated by correlates of satiation (the number of bouts the bird had experienced for schedule 15/0.5; the sum of prey ingested for schedule 30/0.5; Table II).

As predicted, the birds were generally more likely to accept small prey early in a day's sessions than late ('Early' versus 'Late' bouts in Fig. 5), suggesting that the birds were less selective in their diet choice when hungry. This is reflected in a significant bout-number effect for schedules 15/0.5,





**Figure 4.** Mean (+SE) percentage of small prey taken (□) and percentage of any prey type cached (●) by tufted titmice during each of the four access schedules. Data were generated by taking the percentage of prey taken and cached for each bird separately, and then taking the mean of these values across birds. Data from five birds were used; bird GG was tested for only one schedule (1, 15-min bout), but these data were not incorporated into the value for this schedule. Error bars are corrected for the overall differences in prey selectivity and caching rates between birds ( $N = 5$ ).



**Figure 5.** Mean (+SE) percentage of small prey taken by tufted titmice as a function of time-in-bout, time-in-session and initial body mass, for access schedules 15/0.5 (a), 30/0.5 (b), 15/2 (c) and 1/15 (d). Time-in-bout effects are shown by differences in height within each cluster of bars. For schedules in which multiple bouts were given in a day's session, the mean selectivity is given for the first half of the bouts (early bouts: 1–7 for schedule 15/0.5, 1–15 for schedule 30/0.5, 1–7 for schedule 15/2) and for the second half (late bouts). Selectivity shown by animals that started the experiment below (low weight, □) and above (high weight, ■) their median weight. Percentages were calculated for each bird separately ( $N = 5$ ).

**Table II.** Significant ( $P < 0.05$ ) logistic regression coefficients for the probability of titmice accepting a small mealworm piece,  $P(\text{take small})^*$ 

Independent variable	Access schedule			
	15, 0.5-min bouts	30, 0.5-min bouts	15, 2-min bouts	1, 15-min bout
Intercept	$-807.6 \pm 193.1$	$-1.674 \pm 0.299$	$+4.21 \pm 0.70$	$-1675 \pm 172$
Time in bout (s)	Increase $+0.0180 \pm 0.0071$	Increase $+0.0269 \pm 0.0082$	Increase $+(0.00054 \pm 0.00026$ bout number)	Decrease $-0.0228 \pm 0.0024$ $+(0.0080 \pm 0.0009$ prey value)
Time since last large prey (s)	Increase $+0.0226 \pm 0.0047$		Increase $+0.0120 \pm 0.0025$	Increase $+0.0293 \pm 0.0035$
Time since any prey (s)	Increase $-(0.0180 \pm 0.0063$ bout number) $+ (0.370 \pm 0.081$ $\Sigma$ prey ingested)	Increase $+(0.0978 \pm 0.0166$ $\Sigma$ prey ingested)	Increase $+0.0490 \pm 0.0139$	Increase $+0.0852 \pm 0.0169$
Bout number	Decrease $-(0.307 \pm 0.028$ % body mass)	Decrease $-0.625 \pm 0.120$ $+(0.0033 \pm 0.0010$ bout number) $+(0.0203 \pm 0.0045$ body mass)	Decrease $-0.469 \pm 0.057$ $+(0.0314 \pm 0.0038$ bout number) $-(0.125 \pm 0.023$ $\Sigma$ prey ingested) $+(0.00054 \pm 0.00026$ bout time)	Not applicable
$\Sigma$ Prey ingested (g)	Increase $+(0.370 \pm 0.081$ time since last prey)	? $-(1.226 \pm 0.267$ % mass) $+(0.0978 \pm 0.0166$ time since last prey)	Decrease $-(0.125 \pm 0.023$ bout number)	Large birds: increase; small birds: decrease $-45.15 \pm 5.75$ $+(2.22 \pm 0.29$ body mass)
% Body mass	Decrease $-(0.307 \pm 0.028$ bout number)	Decrease $-(1.226 \pm 0.267$ $\Sigma$ prey ingested)		Decrease $+222.6 \pm 57.5$ $-(11.87 \pm 2.90$ body mass)

30/0.5 and 15/2 (Table II). Surprisingly, when time-in-bout and bout number were controlled for, there was no consistent relationship between selectivity and the sum of prey ingested.

The response to time constraints also met the predictions for the shorter bouts; the birds took more small prey later in the 0.5- and 2-min bouts, but the opposite was found for schedule 1/15 (Fig. 5; 'time in bout' in Table II). The lack of the predicted pattern for schedule 1/15 appears to have been caused by the overriding effect of satiation, causing the birds to be more selective at the end of the 15-min bouts, even though time was running out. In fact, several prey were typically eaten in both the 2-min and 15-min bouts (means  $\pm$  SD for each bird: schedule 15/2:  $1.36 \pm 0.30$  for large prey, and  $1.3 \pm 0.8$  for small prey; schedule 1/15:

$10.2 \pm 2.9$  for large prey, and  $12.9 \pm 8.8$  for small prey), although satiation does not appear to have eliminated the response to time constraints in the 2-min bouts.

The implication for a satiation effect in the 15-min bouts is supported by similar satiation curves for all four schedules. We calculated the mean selectivity during each bout for schedules 15/0.5, 30/0.5 and 15/2 and plotted this as a function of the sum of access time to the conveyor belt (i.e. belt access summed across bouts). These relationships showed a significant decrease in small prey taken as access time increased; the decline in per cent small prey taken within the single 15-min access bout (schedule 1/15) was similar to the decline across bouts for the other schedules (Fig. 6a).

Table II. Continued

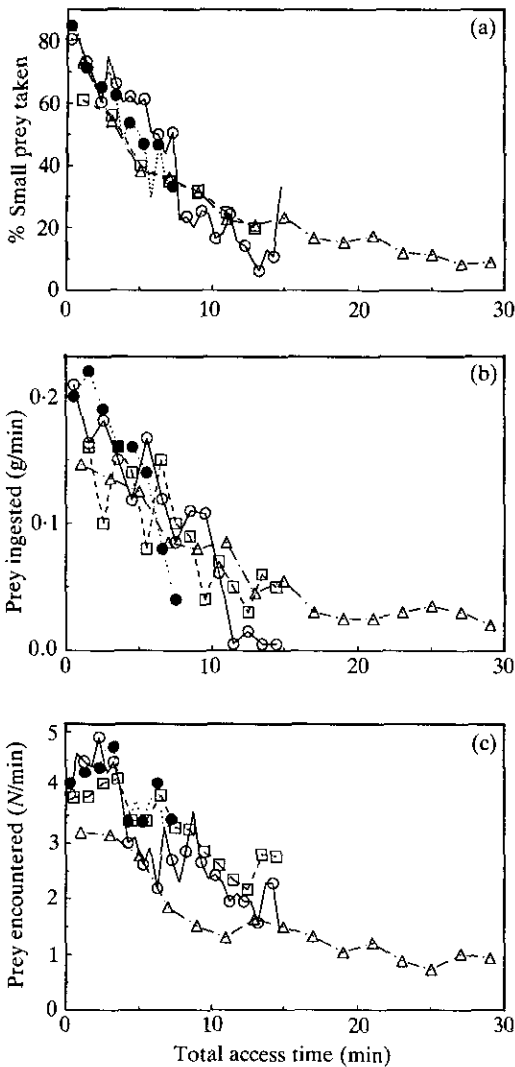
Independent variable	Access schedule			
	15, 0.5-min bouts	30, 0.5-min bouts	15, 2-min bouts	1, 15-min bout
Median body mass (g)	Increase +90.2 ± 16.5 +(5.59 ± 2.08 prey value) -(2.46 ± 0.36 body mass)	Increase +(0.1027 ± 0.0075 prey value) +(0.0203 ± 0.0045 bout number)	Increase +(0.0928 ± 0.0067 prey value)	Increase +154.0 ± 14.8 -(3.445 ± 0.315 mass <sup>2</sup> ) -(11.87 ± 2.90 % body mass) +(1.932 ± 0.335 prey value) +(2.22 ± 0.29 Σ prey ingested)
Prey value (s/l)	Large birds: increase; small birds: decrease -115.0 ± 44.3 +(5.59 ± 2.08 body mass)	Increase +(0.1027 ± 0.0075 body mass)	Increase +(0.0928 ± 0.0067 body mass)	? +35.43 ± 6.42 +(0.0080 ± 0.0009 bout time) +(1.932 ± 0.335 body mass)
Starting time (h since 00:00)				Decrease -0.266 ± 0.097
Temperature (°C)			Decrease -0.423 ± 0.047	
	N = 1332 83% correct	N = 1705 77% correct	N = 2258 77% correct	N = 3106 87% correct

\*All significant main effects and interactions (covariance) are listed for each independent variable. Where a variable name is listed under that variable (e.g. bout number under bout number), the quadratic term is significant (e.g. bout number<sup>2</sup>). Note that interactions between independent variables are multiple-listed under each of the component variables. Unequivocal correlations between  $P(\text{take small})$  and the independent variables are indicated: increase: increase in  $P(\text{take small})$  with an increase in the independent variable; decrease: decrease in  $P(\text{take small})$  with an increase in the independent variable. ? represents circumstances for which there were several covariates and no simple correlation between  $P(\text{take small})$  and the independent variable. % correct: per cent of observations correctly predicted by the model. % Body mass: body mass measured before the experiment as a fraction of the maximum mass measured for each bird. The numbers listed are the best fit coefficients (using maximum likelihood) to the following equation:  $P = 1 - \{\exp(\beta_i V_i / [1 + \exp(\beta_i V_i)]\}$ , where  $P$  is equal to the probability of accepting an encountered small prey, or caching an item taken from the belt,  $\beta_i$  = best-fit coefficient,  $V_i$  =  $i$ th independent variable (or covariance term).

Two other pieces of evidence suggest that satiation was occurring. As McCleery (1977) notes, satiation typically causes a reduction in food intake rates. We calculated the ingestion rate during bouts when the birds were visiting the conveyor belt; ingestion rates decreased with total access time in a manner similar to that shown with diet choice (Fig. 6b).

The birds should also spend less time searching for food at the belt at the end of a day's sessions if they are becoming satiated. We can indirectly measure the overall attendance at the conveyor belt by estimating the rate at which the birds see prey at all times while the experiment is running. Obviously, if

the birds are not at the conveyor belt, they will see no prey, and if they spend all their time at the belt (without eating), they will see about 13.8 prey/min (this value is based on the spacing of prey). If the birds take prey, handling time will decrease the time spent searching, and therefore decrease the number of prey seen during the experiment. For this reason, the birds should see more prey if they take only large prey than if they take any prey that arrives, because they will spend a larger fraction of their time handling prey (and not searching for them) if they take every prey item they encounter, assuming all time in the aviary is spent either at the conveyor belt (searching) or handling prey. Thus if the birds



**Figure 6.** (a) Mean percentage of small prey taken, (b) sum of all prey ingested during bouts when the bird searched at least once on the conveyor belt, and (c) the rate at which prey were encountered in all bouts, each as a function of the sum of access to the conveyor belt. Values for schedules 15/0.5 (●), 30/0.5 (○) and 15/2 (△) are the means for each bout; values for schedule 1/15 (□) are the means for each 2-min access interval in the 15-min bout. Percentages were calculated for each bird separately; the data presented here are the means across birds.

were not satiated during a day's experiment and therefore foraged during the entire experiment, the increase in selectivity shown by the birds should increase the number of prey they see towards the

end of the day. These estimates can be quantified as follows: if all encountered prey were taken, the birds should see about 3.9 prey/min (based on handling times of 9 and 21 s for small and large prey, respectively), or if they took only large prey, they should see about 7.2 prey/min. In fact, just the opposite occurred. The birds saw fewer prey towards the end of the day (Fig. 6c), showing that the birds spent less time at the belt, presumably because they were less hungry.

The satiation curves also indicate why diet selectivity was so low for schedule 15/0.5; satiation decreased monotonically through the first 15 min of the longer bouts, thus when the birds were given only 7.5 min of access to food (as in schedule 15/0.5), they would have been hungrier on average during this session than during one in which they were offered more access to food. Time constraints also contributed to the difference between schedules, because, by definition, proportionally more time is spent under the threat of terminated belt access when foraging bout length is shorter.

Three additional factors had a significant effect on diet choice: short-term variation in prey arrival rates, individual differences among birds, and environmental conditions. The birds were more likely to accept small prey if they had waited a long time since they last saw a large prey or a prey of any type (Table II). The effect was diminished in schedule 15/0.5 during later bouts, but surprisingly the effect was exaggerated in schedules 15/0.5 and 30/0.5 when the birds had eaten a large number of prey (Table II).

Individual differences between birds were accounted for by two variables, the median body mass of each bird and the relative prey value for each bird. These measures were estimated separately for each access schedule. As noted above, the biggest birds showed the lowest relative prey values. Adjusting for differences in prey value (and other variables), bigger birds tended to accept more small prey than smaller birds ('mean body mass' in Table II); although the quantitative effect of body size covaried with a number of other variables. The most striking effect was the relative value of small prey. Adjusting for differences in median body mass, birds for which small prey were valued relatively high compared with large prey were more likely to accept small prey, and the relative value of small prey exaggerated the effect of body size for all schedules (Table II).

**Table III.** Significant ( $P > 0.05$ ) logistic regression coefficients for caching decisions of tufted titmice (see Table II for details)

Independent variable	Access schedule			
	15, 0.5-min bouts	30, 0.5-min bouts	15, 2-min bouts	1, 15-min bout
Intercept	$-7.16 \pm 1.00$	$+24.3 \pm 4.8$	$+393.0 \pm 171.0$	$-12.50 \pm 3.75$
Time in bout (s)				Increase $+ (0.00226 \pm 0.00088$ % body mass)
Time since last large prey (s)		Decrease $-0.0333 \pm 0.0117$		Decrease $-0.0164 \pm 0.0056$
Bout number		Increase $+ (0.0405 \pm 0.0147$ prey value)		
$\Sigma$ Prey ingested (g)		Increase $+ (1.33 \pm 0.45$ prey $\times$ % body mass)	Increase $+ 60.80 \pm 11.72$ $- (2.38 \pm 0.68$ $\Sigma$ prey ingested) $- (26.1 \pm 5.4$ % body mass) $- (1.348 \pm 0.469$ body mass)	Increase $+ 14.11 \pm 3.36$ $- (3.99 \pm 1.17$ $\Sigma$ prey ingested)
% Body mass		Decrease $+ (1.33 \pm 0.45$ prey $\times \Sigma$ prey ingested) $- (16.0 \pm 3.3$ prey) $+ (1.45 \pm 0.26$ body mass)	Decrease $- (26.1 \pm 5.4$ $\Sigma$ prey ingested)	Decrease $- (1.102 \pm 0.122$ body mass) $+ (0.00226 \pm 0.00088$ bout time)
Median body mass (g)		Small prey: increase; large prey: decrease $+ (0.545 \pm 0.141$ prey) $- (1.45 \pm 0.26$ % body mass)	? $- 19.3 \pm 8.2$ $+ (8.91 \pm 3.18$ prey value) $- (1.348 \pm 0.469$ $\Sigma$ prey ingested)	Decrease $- (1.102 \pm 0.122$ % body mass)
Prey value (S/L)		Increase $+ (0.0405 \pm 0.0147$ bout number)	Decrease $- 183.7 \pm 65.8$	Decrease $- (0.219 \pm 0.030$ prey)
Prey (0 = small, 1 = large)		Fewer small $+ (1.33 \pm 0.45$ % body mass $\times$ $\Sigma$ prey ingested) $- (16.0 \pm 3.3$ % body mass) $- (0.545 \pm 0.141$ body mass)	Fewer small $- 0.483 \pm 0.120$	Fewer small $- (0.219 \pm 0.030$ prey value)
Temperature ( $^{\circ}\text{C}$ )				Decrease $- 0.309 \pm 0.079$
	$N = 1292,$ 99.9% correct	$N = 1314,$ 96% correct	$N = 1184,$ 91% correct	$N = 1754,$ 91% correct

Two environmental factors influenced diet choice. In schedule 15/2, birds were more selective when the room was relatively warm (Table II). In

schedule 1/15, birds that were tested later in the morning were more selective than those tested early (Table II).

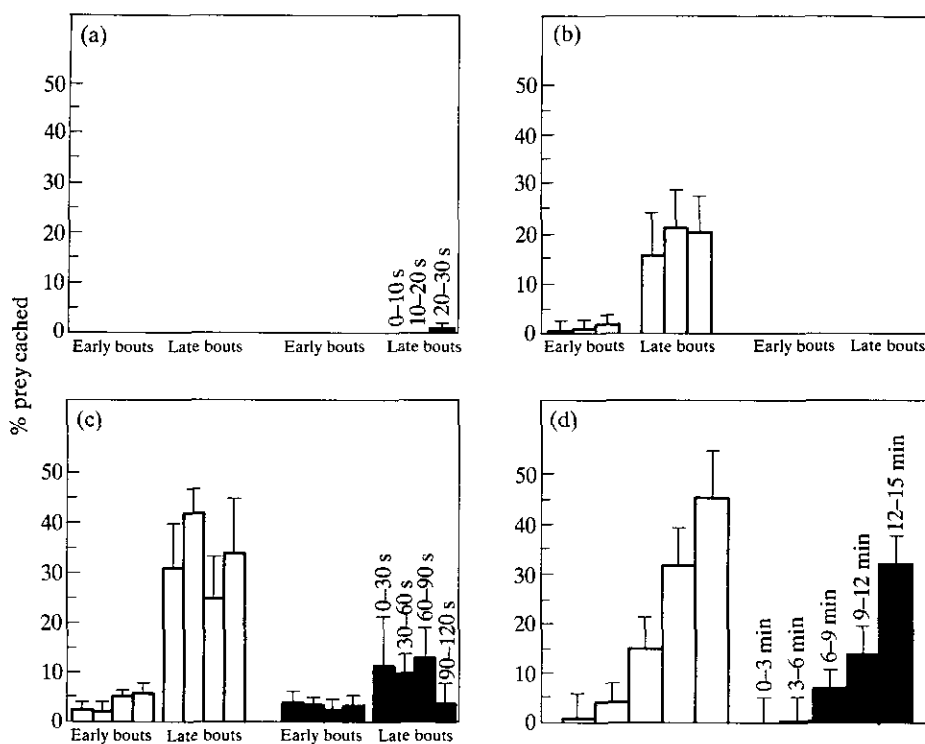


Figure 7. Mean (+SE) percentage of prey cached by tufted titmice as a function of time-in-bout, time-in-session and initial body mass, for access schedules 15/0.5 (a), 30/0.5 (b), 15/2 (c), and 1/15 (d). See Fig. 5 for details.

### Caching

The general caching patterns shown by the birds under the four schedules was the mirror image of the patterns shown in diet choice (Fig. 4); under severe constraints (schedule 15/0.5) the birds took more small prey but cached virtually nothing (one prey cached out of 1291 taken). Under relaxed constraints, the birds took fewer small prey and were more likely to cache the prey they took (difference between schedules:  $\chi^2 = 59.9$ ,  $df = 3$ ,  $P < 0.001$ ; difference between birds:  $\chi^2 = 29.6$ ,  $df = 5$ ,  $P < 0.001$ ). Thus under constraints, the birds chose the alternative with the highest expected gain, eating with a generalist diet.

As predicted, the birds were much more impulsive in their caching tendencies when they were fat, in that they were less likely to store food under these conditions ('% body mass' in Table III; Fig. 7). Indeed, for schedule 30/0.5 no bird ever cached prey when it was heavier than its median weight (Fig. 7, schedule '30/0.5'). The birds uniformly preferred to cache larger prey ('Prey' in Table III), although the tendency to cache any prey was

affected by a large number of variables, and the effect of the variables was not always similar to that shown in diet choice. For example, short-term time constraints had no effect on caching decisions ('Time in bout' in Table III, schedules 15/0.5, 30/0.5 and 15/2), but was a significant factor in diet choice for all three of the schedules with shorter bouts.

Satiation had the same effect on caching behaviour as it did on diet choice; sated animals were less impulsive for both behaviour patterns. Caching increased with both the sum of prey eaten (for all schedules) and the amount of access to the belt (bout number for schedule 30/0.5 and time-in-bout for schedule 1/15; Table III).

The effect of short-term variation in prey arrival on caching decisions was similar to the effect on diet choice, at least for schedules 30/0.5 and 1/15; the birds were more likely to eat a prey if they had waited a long time since a large prey had arrived. Individual differences were significant for all three schedules in which the birds cached, but no consistent trends were found. Temperature was a

significant factor for only one schedule, 1/15, when the birds cached less at warmer temperatures.

### Retrieval

Most prey were retrieved a day after they were cached and before the access door was raised for the first time on that next day (58/67 prey for schedule 30/0.5; 80/112 prey for schedule 15/2; 216/224 prey for schedule 1/15). The percentage of prey retrieved the same day they were cached differed significantly among schedules ( $\chi^2 = 325$ ,  $df = 2$ ,  $P < 0.001$ ), with the highest percentage eaten for schedule 15/2 (22.2%) and the lowest percentage eaten for schedule 1/15 (3.4%). These differences correlated with the total amount of time the experiments lasted (access time plus inter-bout intervals), and could result from the birds in schedule 15/2 having more time to empty their crop before the session ended on any given day.

## DISCUSSION

The regulation of titmouse foraging decisions is multifaceted and hierarchical. Short-term factors, such as satiation, inter-prey intervals and time constraints, work within longer-term factors such as changes in body mass. In addition, the structure of this hierarchy is quite different between diet choice and caching decisions, even though these decisions are made concurrently.

State-dependent attributes of diet choice are similar for all states and all levels of the hierarchy: as state degrades, titmice are more likely to accept small prey. This pattern holds whether state is the time since the last prey item was seen, impending cessation of access to food, short-term hunger or low body mass. Similar results have been obtained in studies designed to measure each state in isolation. For example, reduced selectivity under time constraints was shown in blue jays, *Cyanocitta cristata* (Yoerg & Kamil 1988), great tits, *Parus major* (Lucas 1987) and pigeons (Plowright & Shettleworth 1991). Great tits also reduce selectivity in response to an increase in time since they last saw prey (Lucas 1987). The reduction in selectivity for hungry animals is well established (Schoener 1971; Pulliam 1974; Rechten et al. 1983; Snyderman 1983; but see Richards 1983

and Christensen-Szalanski et al. 1980 for counter-examples).

Unfortunately, the effects of short-term changes in hunger (in our experiment, changes within sessions) and body mass (which vary over a longer time scale) are often not differentiated in the literature. In our experiment, both factors had similar effects on diet choice, but this does not mean that they should be treated in a similar way; the caching results, discussed below, underscore this point. One of the most important reasons why they should not be treated as similar phenomena is that the fitness consequences of the two states are different. Short-term hunger levels may correlate with local variation in prey densities (Pulliam 1974), but can be a poor predictor of long-term starvation threat, especially for animals that can store enough fat to survive more than a day's fast. In contrast, changes in body mass may be a better predictor of starvation risk, but changes in mass may be a poor predictor of local resource variation.

The difference between the effect of hunger and body mass is important in our interpretation of these results in light of the theoretical predictions. Several authors have suggested that foragers should maximize net energy intake rate when they are hungry (Pulliam 1974; Sih 1982; Rechten et al. 1983); others have suggested that foragers should maximize net energy intake rates when sated, because hungry animals cannot afford to pass up suboptimal prey (e.g. Croy & Hughes 1991). In fact, hungry titmice chose the diet that maximized net energy intake rate, but this does not rule out the alternative that hungry animals are more impulsive in their diet choice irrespective of energetic gain. This problem was addressed by Snyderman (1983) who showed that hungry pigeons are less choosy in their diet even under conditions where impulsiveness reduces long-term yield from the diet.

Similarly, because the titmice could harvest more by eating than by caching, the reduction in caching rate when the birds were light weight increased harvest rates. However, it may be premature to assume that the titmice were choosing to maximize harvest rates instead of simply being more impulsive. Carolina chickadees, *Parus carolinensis*, have been shown to cache less when light weight (Lucas & Walter 1991), but harvest rates in the chickadee experiment were five times higher for caching than for eating (because it took much longer to eat a seed than to cache one). Thus, chickadees showed a

similar response to state (cache when light), but they clearly did not maximize harvest rates by doing so.

Our results on the effect of prey value (i.e. biomass/handling time) on diet choice were equivocal. None of our titmice preferred small prey, even though the biomass/handling time of small prey was higher than that for large prey for some birds. However, individual differences in selectivity were correlated with prey value; birds for whom small prey were relatively higher valued showed a stronger preference for this prey type, but still preferred large prey to small.

Models of risk-sensitivity (e.g. Caraco 1980; Stephens 1981; Real & Caraco 1986) have been offered as a more realistic representation of the functional significance of foraging decisions. These models predict that foragers will devalue variable rewards when starvation is unlikely (note that variable delays to reward may generate different results; McNamara & Houston 1987). While this has been demonstrated numerous times in problems of patch choice (e.g. Barnard & Brown 1985; Hamm & Shettleworth 1987; Caraco et al. 1990; Cartar & Dill 1990; but see Wunderle et al. 1987; Ha et al. 1990) and foraging mode (e.g. Uetz 1988), our results show the opposite trend. Titmice chose the highest variance, lowest mean-reward option when energetic stress was relaxed, whether energetic stress was measured over the short term (i.e. hunger) or over the long term (i.e. body mass). However, these risk-sensitivity models fail to consider sequential decisions or the absolute state of the forager at any specific time of day. Houston & McNamara (1985) and McNamara & Houston (1986) have shown that when these factors are included, predictions similar to the non-sequential models arise, except when the forager is near starvation weight; near starvation, low variance options should be chosen to ensure that the forager survives starvation threat in the near term. Houston & McNamara (1985) suggested that the reduction in selectivity observed in deprived foragers (Rechten et al. 1983 and Snyderman 1983 were cited) is consistent with this prediction. Our data indicate that foragers near ad libitum weight (thus unlikely to be at risk of starvation) show the same qualitative response to hunger as those near starvation. In fact, the logistic regression analyses (Table II) suggest that the hunger response is, if anything, greater for animals when they are fat. We are left with the conclusion that foragers cannot

distinguish short-term hunger from the effects of low weight (although the caching data suggest otherwise), or that these models are not well suited to deal with hunger effects. Instead, it may be useful to model the functional aspects of hunger as it relates to short-term changes in physiological state (e.g. McCleery 1977), and use models of risk and starvation threat to consider longer-term changes in state, such as body mass. Any correlation between short-term hunger and foraging decisions should probably not be taken as evidence for or against predictions from risk-sensitivity models.

A more proximal set of models that seems to hold promise in addressing our data are future discounting models (Kagel et al. 1986). As discussed in the Introduction, one way that behaviour patterns can be evaluated is to compare the reward from that current alternative against expected future rewards. The high ranking of large prey by the titmice, even when biomass/handling-time was lower than for small prey, may represent future discounting (P. Smallwood, personal communication). A large, certain prey item may be preferable to a number of smaller, more profitable items expected to arrive at unknown times in the future. Also, under deteriorating conditions (hunger, short-term decrease in encounter rates, light weight), foragers may be expected to discount future rewards, and thus be more prone to accept current rewards. The discounting of future rewards is most obvious for animals foraging under time constraints (Lucas 1985, 1987), but also holds for other environmental or physiological states (Kagel et al. 1986). Future discounting should be stronger under deteriorating conditions, as shown in our results from titmouse diet choice. But the same cannot be said for caching behaviour.

The state-dependent properties of caching decisions differed from those of diet choice; with caching decisions, the response to different hierarchical states was not consistent across hierarchical levels. Degradation of short-term states (hunger and short-term reductions in the arrival rate of preferred prey) promoted eating, while degradation of long-term states (body mass) promoted caching. And unlike diet choice, the birds did not alter their caching decisions when subjected to time constraints under 2 min.

The reduction in caching rates with an increase in body mass was predicted assuming that the birds were balancing the need for food to reduce starvation risk against the need for non-foraging related



activities (e.g. territorial defence or predation risk, Lucas & Walter 1991; also see McNamara et al. 1990). When the forager is relatively light weight, the risk of starvation should dominate foraging decisions. Under these conditions, the forager should cache to ensure that stored food is available in the future in case no food is encountered. Thus, caching is predicted, unless the forager is so light weight that immediate starvation is possible, in which case no caching is expected. When the forager is heavy, non-foraging requirements become relatively more important and should indirectly affect foraging decisions. Specifically, the decision to eat instead of cache commits less time to foraging (because caching requires additional time invested in the storage and retrieval of food) and therefore frees time for other behaviour; assuming that the bird should decide to expend any time on foraging, eating should be favoured when the forager is fat. The negative correlation we found in titmice between body mass and caching is consistent with this prediction, and has been reported for Carolina chickadees (Lucas & Walter 1991) and in several studies on laboratory rats (Fantino & Cabanac 1980, 1984; see Vander Wall 1990 for a review of this literature). Logger-head shrikes, *Lanius ludovicianus*, tend to eat several prey before caching (Wemmer 1969), a response to short-term hunger similar to that shown by titmice. Other studies have reported that deprivation increases hoarding rates (e.g. in hamsters, Lea & Tarpay 1986; in red-tailed chipmunks, *Eutamias ruficaudus*, Lockner 1972), but these studies did not distinguish between short-term hunger effects and the effect of variation in body mass. Because titmice cache more when sated but less when fat, clearly these two states must be differentiated.

Predictions from the caching models (McNamara et al. 1990; Lucas & Walter 1991) are similar to those of the diet choice models (e.g. Houston & McNamara 1985): conservative strategies (eating or generalist foraging) are expected of animals near starvation and of animals that are far from starvation risk, whereas intermediate conditions should promote more risky strategies (caching or specialist foraging). The models are also similar in that they are not particularly good at accommodating short-term hunger effects. We could predict that hungry, thin animals should eat anything they encounter in our experiment (and this is what we found), but it is unclear from this theory what hungry fat animals should do. The models differ in their ability to

predict our results; predictions from the caching model were generally supported, whereas the predictions from the diet choice model were not.

We suggested that future discounting (Kagel et al. 1986) could account for the diet choice results; future discounting may also account for some of the caching results. Short-term hunger and local increases in inter-prey intervals should increase the relative value of food eaten immediately and thus reduce the tendency to cache food. In addition, when the animal is fat, the relative value of cached food (i.e. the future reward) is diminished because stored food is less important, at least for animals that store for short periods. The enhanced value of alternative non-foraging behaviour patterns that are available to the forager when foraging stops would also decrease the value of future foraging rewards (Lucas & Walter 1991). Both of these factors should cause greater future discounting and therefore should select for reduced caching intensity at high weights.

The lack of response in caching decisions to short-term time constraints is intriguing, in part because the birds clearly responded to time constraints in their diet choice. We suggest that the difference between the two decisions lies in the nature and timing of future rewards. For diet choice decisions, lost opportunities associated with the acceptance of prey are realized immediately. As foraging time runs out, the forager loses fewer opportunities to find alternative prey while handling accepted prey, thus the relative value of low-quality prey types will increase (Lucas 1985). With caching decisions, lost opportunities are somewhat more complicated because time will be invested immediately irrespective of whether the forager eats a prey or caches it, thus no immediate opportunities are lost with either alternative. In addition, the opportunities lost while the forager retrieves food are realized long after cessation of the short bouts we imposed on the birds in our experiment. Thus short-term time constraints should not be particularly important in the future discounting of caching decisions because the time horizon over which the future is measured is relatively long.

We used an open-economy experimental design (Hursh 1980); the amount of food available to the birds was determined by the experimenter, and the birds' weights were determined by conditions extrinsic to the experiment. Some behaviour patterns, such as how hard animals work for food, can

differ between open and closed economies (Collier 1983; Hursh 1980), but some studies have found no difference (e.g. Timberlake 1984), raising the question as to which condition is more preferable. As Houston & McNamara (1989) point out, the problem with open economies is that nature is a closed-economy system, and the problem with closed economies is that it is difficult to recreate natural ones. They suggest that open economies are particularly appropriate for studies of the functional significance of foraging decisions, whereas closed economies are appropriate for studies of time sharing. In our experiment, we used an open-economy design to regulate body mass experimentally in order to evaluate state-dependent properties of foraging decisions. While we have no reason to expect that the trends will change in a closed economy, it might be useful to repeat these experiments under closed-economy conditions to test whether the same relationships are shown when the animals regulate their own state. Along these lines, we have some evidence that the same mass-dependent relationships in caching behaviour shown by titmice in an open economy are exhibited under a closed economy by Carolina chickadees (J. Lucas, unpublished data).

Our results indicate two important properties of animal decision making. First, they indicate how rich in structure animal foraging decisions are. Everything matters: body mass, short-term satiation, time constraints, and seemingly insignificant differences in the arrival intervals of prey items. The time scale of these effects runs from seconds, in the case of sensitivity to inter-prey intervals, to days, in the case of sensitivity to body mass. Second, this rich structure also indicates a rich response to the temporal properties of an animal's environment. By definition, titmice plan ahead, otherwise they would accept every prey item they saw and never cache. But how far ahead they look changes incredibly rapidly and is affected by every state we thought of measuring.

The recent emphasis in optimality theory on dynamic models (see Mangel & Clark 1988) has caused a shift in emphasis in how we look at behavioural systems. There are lots of ways that we can think about behaviour. Fifteen years ago, most people, if pushed, would have described behaviour graphically as a fixed multidimensional surface, with each dimension being the value of prey types, arrival rates of prey, or other fixed factors. Linear programming (Belovsky 1978), for example,

explicitly treats behavioural decisions in this way. The advantage of these multidimensional surfaces is that they are relatively easy to characterize; one need only describe the surface to understand what the animal should be doing.

State dependence and sequential dependence change this picture dramatically. Now the multidimensional structure has no fixed shape; it changes over time. It is harder to describe. But is it worth the effort? We think the answer is yes. The view takes into account factors that are clearly important in the expression of behaviour. And it is the only way that we can fully understand the functional role of certain classes of behaviour; we think that diet choice and food storage are examples. So under certain circumstances, the study of this writhing surface is an important component of the study of animal behaviour.

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