Time-concentrated sampling: a simple strategy for information gain at a novel,

depleted patch

By

Keith W. Gibson

Department of Biology, McGill University

Montreal, Canada

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ABSTRACT

In a variable environment, revisiting renewing patches could increase an animal's

foraging efficiency by reducing its search time and effort, but visits to non-renewing

patches or to renewing patches at inappropriate intervals could reduce its efficiency.

Little theoretical or empirical research has examined how an animal that has found and

exploited a new patch should determine whether and when it will renew. A rapid series

of visits to the patch should provide information concerning the probability of a quick

renewal. If a renewal is not encountered, however, a subsequent decrease in the rate of

visits should allow monitoring of the patch at minimal cost. After a long period

without renewal, a patch should not be visited at all. By analogy with area-

concentrated search, I propose the term 'time-concentrated sampling' (TCS) for this

pattern of visits and suggest that it should be widespread for species foraging on

patchy prey in environments where the probability of renewal and latency to renewal

of patches are variable between patches. In this study, I tested whether eastern

chipmunks (*Tamias striatus*) presented with a small number of peanuts followed by a

small patch of sunflower seeds exhibit TCS following their depletion of these and, if

so, whether their patterns of visits are influenced by potential indicators of patch value.

Thirty-six of 40 animals that hoarded the seeds returned at least once following

depletion. A mixed-effects Poisson regression analysis showed that the chipmunks

significantly decreased their visit rate over eight 30-min intervals. The number of

peanuts used to initiate a trial positively affected the rate of sampling, but not the

decline in rate over time. The volume of sunflower seeds and the distance of the patch

from the animal's burrow did not have a significant effect on sampling rate. I conclude

that chipmunks actively and repeatedly sample novel, depleted patches, that they

exhibit TCS, and that visitation patterns can be modified by experience at the patch before depletion. Although a wide range of functional and mechanistic approaches have explored animals' patterns of visits to food sources with established patterns of renewal, TCS is the first strategy to address how animals could establish such patterns of resource tracking in the first place.

RÉSUMÉ

Dans un environnement variable, des animaux qui retournent sur des sites où la ressource se renouvelle peuvent augmenter leur taux d'approvisionnement en diminuant l'effort et le temps requis pour chercher leurs proies. Cependant, l'efficacité de ce comportement est réduite lorsque la ressource ne se renouvelle pas, ou lorsqu'elle se renouvelle à un moment inapproprié relativement aux visites. Peu de recherches théoriques et empiriques sont examiné comment un animal, après avoir trouvé et exploité un nouveau site, pouvait déterminer la probabilité et la fréquence de renouvellement des proies. Une série de visites rapides au site fournirait des informations sur la probabilité d'un renouvellement rapide. Un animal ne rencontrant pas de proies devrait baiser son taux de retour et donc minimiser le coût associé à la surveillance du site. Après une période prolongée sans renouvellement, l'animal devrait cesser ses visites. Par analogie au concept 'd'échantillonnage concentré spatiallement', je suggère le terme 'd'échantillonnage concentré temporellement' (TCS) pour décrire ce patron de visites. Je propose que le TCS devrait être observé plus particulièrement chez les espèces qui s'approvisionnent dans des environnements présentant une forte variabilité inter-sites de la probabilité et de la fréquence de renouvellement des proies. Mon étude consistait à approvisionner des tamias rayés (*Tamias striatus*), avec quelques arachides et un petit volume de graines de tournesol, et à observer leurs comportements après exploitation du site. De cette manière, j'ai testé si les tamias montraient le patron prédit par le TCS, et si ce patron était influencé par des variables qui pouvaient leur indiquer la valeur du site. Trente six des 40 tamias testés sont revenus sur le site au moins une fois, après l'avoir entièrement exploité. Un modèle de régression mixte de Poisson a indiqué que les tamias ont baissé leur taux de

visites au cours de huit intervalles consécutifs de 30 minutes. Le nombre d'arachides a augmenté le taux de visites indépendamment du temps écoulé après exploitation du site. Le volume de graines de tournesol et la distance entre le site et le terrier de l'animal n'ont eu aucun effet sur le taux de visites. Mes resultats indiquent: 1) que les tamias échantillonnent les sites visités mais jamais exploités en y revenant de manière répétée, 2) qu'ils montrent le TCS, et 3) que les patrons de visites peuvent être modifiés par l'expérience acquise lors de l'exploitation du site. De nombreux travaux, utilisant une approche fonctionnelle ou mécaniste, ont examiné les patrons de visites d'animaux sur des sites dont la ressource se renouvelle de manière prédictible. Le TCS est le premier modèle permettant d'expliquer l'établissement des patrons d'échantillonnage par des animaux découvrant un site nouveau et non prédictible.

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PREFACE

This thesis carries a credit weight of 39 credits, from a total of 45 credits required for the Master's degree. Graduate credits are a measure of the time assigned to a given task in the graduate program. They are based on the consideration that a term of full-time graduate work is equivalent to 12 to 16 credits, depending on the intensity of the program.

This thesis is written in the manuscript format. A modified version will submitted for publication in a scientific journal. I will be first author of that publication, which will include Carolyn Hall, and Donald L. Kramer as second and third authors, respectively. I was responsible for the design of the current study, the organization of the data collection, data analysis, interpretation and writing. My thesis supervisor D.L. Kramer provided advice on all aspects of the project. C. Hall contributed to the development of the theoretical model and the review of related literature. A postdoctoral fellow, Denis Réale, provided important statistical advice. The data collection was assisted by several undergraduate students listed in the acknowledgements.

A senior undergraduate project that I completed in 1999 was devoted to collecting data to test one of the hypotheses of this thesis. That project will not be published. The current work is a far more robust test of the hypothesis in question. It also develops and tests a second hypothesis, and contextualizes the results of both tests in both the literature and a general ecological framework. The undergraduate project is therefore best considered as a preliminary study wherein methods and the general line of reasoning were developed.

This work is the first to formally present the concept of time-concentrated sampling, and test its predictions in the field. Although one conclusion is similar to a conclusion from a chapter in the doctoral thesis of C. Hall (in preparation), her approach was inspired by my undergraduate project, and her work was carried out in the same season as mine.

ACKNOWLEDGEMENTS

DEDICATION

This thesis is dedicated to my parents, Janet and Grant Gibson.

INTRODUCTION

Many animals forage on resources where individual prey items are aggregated in space and where such patches of prey sometimes renew following their depletion by a forager (Price, 1984). When an animal must decide where to forage in such an environment, it will likely not have current information concerning the value of all its alternatives. This is commonly referred to as the problem of incomplete information (Stephens and Krebs, 1986). Information can be gained by tracking the state of previously encountered patches over time. Tracking is accomplished by sampling, that is, by visiting previously encountered patches repeatedly over time (Stephens and Krebs, 1986). Sampling can provide information on the renewal characteristics of a patch, specifically whether it renews, the time between renewals, and the amount of prey or quality of the patch on renewal. Information about the renewal characteristics of a patch should allow an animal to exploit its environment more efficiently by selectively exploiting rich patches and minimizing time in poor patches as compared to searching randomly in space (not tracking). Animals that track the value of a patch incur several costs. An animal that is sampling a depleted patch is necessarily taking time away from exploiting other patches, and from other important activities. It is also exposing itself to any costs incurred by visiting the patch, but gaining no immediate return if a renewal is not encountered. The benefits of sampling are the value of the patch, if a renewal is encountered, and also information about the renewal characteristics of the patch, even if a renewal is not encountered. A sampling animal is therefore trading off short-term rate maximization against long-term foraging gain (McNamara, 1982).

Sampling behaviour has been shown in a variety of species in both the lab (Inman, 1990; Nonacs and Soriano, 1998; Shettleworth et al., 1988; Tamm, 1987), and

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the field (Hall and Kramer, in preparation; Kramer and Weary, 1991), and strategies for using sampling to track previously encountered patches, where animals consequently have some experience of the renewal characteristics, have been proposed in the literature (Dall et al., 1999; Inglis, 2001; Stephens, 1987; Stephens and Krebs, 1986). Such patterns of resource tracking, however, will require an animal to gain information concerning the renewal characteristics of a novel patch, i.e. a patch at a spatial location where the animal has not previously encountered a given food type. I am not aware of any research that has explicitly examined how an animal that has found and depleted such a novel patch should behave to gain information concerning its renewal characteristics.

I propose that a rapid series of visits to the patch should provide information concerning the probability of a quick renewal. If a renewal is not encountered, however, a subsequent decrease in the rate of visits should allow monitoring of the patch at minimal cost. After a long period without renewal a patch should not be visited at all because it is unlikely to renew. A quantitative prediction of the initial rate of sampling and pattern of decline may be complicated to make, but the qualitative pattern should be robust under a wide range of circumstances.

This pattern is the temporal analog of the widely recognized area-concentrated search strategy (Benhamou, 1992), first described as area-restricted search by Tinbergen (1967) and shown to occur in a wide variety of species (e.g., Benedix, 1993; Dixon, 1959; Haskell, 1997; Smith, 1974). Animals using this strategy temporarily intensify or concentrate their search effort in space upon discovery of a prey item. The pattern I propose prescribes that animals temporarily concentrate their sampling effort in time upon discovery of a patch so I suggest calling it time-concentrated sampling (TCS). Possible alternatives to TCS include no change in an

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animal's rate of visits to an area following depletion of a novel patch as compared to before depletion and actively avoiding the location of a depleted patch, either temporarily or permanently.

I predict TCS to be used by species that exploit patches where the renewal characteristics are variable and poorly predictable between patches but have some consistency within patches. As with tracking previously experienced patches, TCS should not apply in environments where renewal characteristics are completely unpredictable because, in such cases, information has no value (Stephens, 1987). Neither should it apply to environments where all patches depend on the growth or replenishment of prey items resulting in a refractory period (e.g., Healy and Hurly, 2001), to environments where the predictability of renewal times is high so that previous experience in the environment predicts the characteristics of a novel patch, or to patchy prey that do not renew (e.g., Devenport et al., 1998).

If it is adaptive for an animal to decrease its rate of sampling visits to a depleted patch when a renewal is not encountered, it may also be adaptive for it to adjust the rate of decrease to the characteristics of the patch. If one assumes that animals can return to specific locations (that they have adequate spatial memory or some other mechanism such as scent marking), that they are sensitive to the characteristics of the patches they exploit, that they can remember those characteristics and use them to adjust their sampling pattern, and that they 'expect' the value of patch renewals to be positively correlated (so that the current experience of patch value predicts the value on subsequent renewals), then it is reasonable to expect flexibility in TCS in relation to patch characteristics. There is evidence to support these assumptions. Many vertebrates and invertebrates are able to readily return to food sources, caches, refuges and breeding sites (Goodenough et al., 2001). Foraging

studies show that the capacity to respond to patch characteristics such as patch quality, travel time between patches (Stephens and Krebs, 1986), and predation risk (Lima et al., 1985) when selecting a foraging site is widespread. Several species are known to adjust their sampling effort (sampling rate or total number of sampling visits) to the characteristics of the patch they experience. For example, laboratory studies of resource tracking have shown that several species adjust their sampling effort to the frequency of renewal (Tamm, 1987) and to the quality of an alternative (Inman, 1990; Shettleworth et al., 1988). Although three laboratory studies found little (Inman, 1990) or no (Shettleworth et al., 1988; Tamm, 1987) evidence that animals respond to the quality of the patch, a recent field study showed that eastern chipmunks adjust their sampling effort to the effect of competition on the amount of food received by each animal (Hall and Kramer, in preparation). Very little work has been devoted to exploring general patterns of renewal across resource types and ecological situations (but see Price, 1984). The assumption that, on a small temporal scale, the value of renewals will be positively correlated seems intuitively likely, at least for some patch types, but requires substantiation. Animals might adjust their pattern of sampling over time by adjusting their total sampling rate, as shown in the Hall and Kramer (in preparation) study mentioned above, by adjusting the rate of decline of their sampling rate following depletion, or both. I therefore predict that sampling animals should invest more effort (a higher sampling rate, a slower decrease in sampling rate, or both) in patches that might be more valuable upon renewal or less costly to sample and exploit.

I tested eastern chipmunks (*Tamias striatus*) foraging in the field to determine whether they show the decrease in sampling rate predicted by TCS and whether their pattern of TCS changes in response to patch characteristics. Chipmunks are central-

place foraging sciurids that hoard primarily the seeds of beech (*Fagus*), maple (*Acer*), and oak (*Quercus*) trees to a larder hoard in a burrow. Chipmunks forage in an environment where TCS should be a useful strategy. The seeds of large masting trees occur in patches under the canopy of individual trees, and can also aggregate at a smaller scale in depressions in the ground under the canopy where they roll and collect. Patches are renewed by gusts of wind that cause ripe seeds to fall and by the foraging activity of grey squirrels (*Sciurus carolinensis*) that clip seeds in the canopy before they are ready to fall spontaneously. Chipmunks have access to these seeds before the squirrels descend to collect them. Chipmunks also forage to a lesser extent on other renewing food types such as the seeds of small plants that vary in their ripening schedules, and on non-renewing food types such as the pilfered scatter hoards of conspecifics (Clarke and Kramer, 1994a) and birds' eggs and young (Elliott, 1978). In addition, at my site and many others within their range, peanuts and sunflower seeds from humans provide an important food source that may or may not renew (personal observation). Human provisioning is erratic, and the 'renewal characteristics' of one person feeding may differ greatly from those of another, even at the same spatial location. Humans, then, may be seen by chipmunks as variable and novel renewing patches. Consequently, I predicted that chipmunks should exhibit the change in sampling rate predicted by TCS.

I also expected chipmunks to be able to adjust TCS to the characteristics of the patches they exploit. Chipmunks are sensitive to various patch characteristics, as has been shown in foraging studies examining the effect of the distance of the patch from the animal's burrow (Bowers, 1995; Giraldeau et al., 1994; Kramer and Nowell, 1980), patch quality (Kramer and Nowell, 1980; Lair et al., 1994), and competition (Giraldeau et al., 1994; Lair et al., 1994) on chipmunk foraging behaviour. These

patch characteristics (distance, quality, and competition) should affect the costs and benefits of sampling and the costs and benefits of exploiting a potential renewal. Increasing the costs of sampling and/or of potential exploitation should decrease the amount of effort chipmunks invest in sampling and thereby affect the way they use TCS, if at all. Some patches may be too costly to sample. I therefore expect chipmunks to exhibit some flexibility in their TCS in response to the characteristics of the patch they exploit. I focussed on the patch characteristics of quality and the distance of the patch from the burrow.

METHODS

Study Site and Population

Eastern chipmunks were studied between June 9 and October 27, 2000, in a beech/maple forest in the public area of McGill University's Gault Nature Reserve at Mont St. Hilaire, located 35 km southeast of Montreal, Canada. The study population consisted of approximately 80 marked individuals, including male and female adults and juveniles, with a few unmarked individuals. There were rarely more than 20 animals active at any given time during the field season. This was a much smaller population than in previous studies at this location, perhaps due to loss of food supply as a result of damage to the trees during a severe ice storm in January 1998. Individuals were trapped intermittently throughout the field season in Longworth traps and marked with both an ear tag and a unique pattern clipped into the fur that allowed them to be recognized at a distance. Burrow locations were determined by providing a chipmunk with peanuts and observing where it hoarded them, and were monitored throughout the field season to record occasional changes.

Juveniles are individuals born during the current year. Those used in my trials can be considered equivalent to adults for the purposes of this study since they could

be classified as post-dispersal (see Clarke and Kramer, 1994a). They had known burrows to which they consistently larder hoarded at the time of the trials, and the weights of the six individuals near the dates of the trials (mean, 97.5 g, range, 87-106 g) fall within the range of all adult weights for that year (mean, 96.5 g, range, 69-122g).

Trials

To simplify subsequent discussion, I shall describe the trials as consisting of three phases: Pre-trial, exploitation and sampling. During the pre-trial phase, marked animals were located by frequenting areas where activity was known to be high, by scattering two or three peanuts in the area around an observer ($\sim$ 5 m radius) to attract animals, or by setting up a trial site and waiting for a chipmunk to arrive. Waits of several days were not unusual. Chipmunk burrows were difficult to locate. Animals traveled farther from their burrows and returned to them less frequently than during previous years. Consequently, I allowed distance to vary haphazardly rather than incorporating it as a systematic variable in the study design. When a chipmunk was observed, it was given a peanut if a trial site was not already set up. This usually induced it to return to its burrow temporarily or to begin scatter hoarding, resulting in its temporary absence from the area. During these temporary absences, the observer set up the trial site as unobtrusively as possible. Single peanuts were tossed directly to the chipmunk when it returned to the area. The number of peanuts presented to chipmunks (minimum 0, maximum 10, median 5) depended on the time required to set up the site. Peanuts were never presented to the chipmunk in the patch, but instead between 3 and 5 m from it. Consequently, chipmunks were allowed to discover the exact location of the patch on their own. The use of peanuts was added to the design in

response to the difficulty of attracting chipmunks to patches, in contrast with most previous studies at this site.

Trial sites consisted of a 1 m x 1 m patch of forest floor cleared of leaf litter, and a 2-m high observation stand placed 3 to 5 m away from it. The observer spread either 15 ml or 150 ml of large, striped sunflower seeds (*Helianthus*), sorted to remove broken or empty seeds, in a 40 cm x 40 cm area in the center of the patch. The treatment was randomly determined. A single cheek pouch load is about 10 ml of sunflower seeds (K. Gibson, unpublished data).

The exploitation phase began when the chipmunk first left the patch with a load of sunflower seeds. Exploitation phases were begun no later than 5 hours before sunset (minimum 9:10, maximum 14:34, median 11:39), and there was no significant difference between trial start times for the two treatments.

From the observation stand the observer recorded on prepared data sheets the time the focal chipmunk entered and left the patch and its behaviour (loading, feeding, searching, vigilance, vocalizing, foot stomping, and grooming) in the patch. Loading involves a chipmunk placing seeds into its cheek pouches, which can occur with the animal on its hind feet, using the front paws, or with the snout on the substrate and without the use of the front paws. When the head is down animals pause briefly and bring their head slightly backwards when they load a seed. Feeding (husking and ingesting a seed), and searching (moving the snout over the substrate with the head down, usually with a slow 'walking' gait) were the other relevant behaviour patterns. The observer also recorded whether patch visits were interrupted, including when the focal chipmunk was frightened out of the patch (e.g., by a falling branch, a gust of wind, or a movement of the observer), was chased out of the patch by a conspecific, or left the patch to chase another individual. As a result of such interruptions, not all

visits to the patch by focal chipmunks during the exploitation phase resulted in the acquisition of seeds. Although I could not record a precise measure of the amount of competition at the patch, other chipmunks sometimes exploited the patch. However, each focal individual obtained at least one load of seeds in the 15 ml treatment and more than one load in the 150 ml treatment.

I assume that the focal chipmunk had experienced an empty patch when it completed an uninterrupted search of the patch without loading or feeding. With the large seeds used, the behaviour made it possible to recognize the acquisition of even a single seed from the observation stand.

I considered the sampling phase to begin at the end of the next visit to the patch. This conservative measure was used to ensure that the animal had experienced the lack of seeds and had returned in spite of this. All subsequent visits were considered sampling visits because the chipmunk was returning to the patch after failing to find seeds in it. Rarely, a few seeds were found during such sampling visits (minimum 0, maximum 3, median 0). Even 3 seeds constitute a small fraction of the 15 ml treatment, and I assume that chipmunks did not treat such an encounter as a renewal. The patch was observed continuously for four hours after the start of the sampling phase.

Some animals exploited the patch to a low level of seeds, but did not return within an hour of their last visit. In such cases, the observer carefully scanned the patch with binoculars. If more than five seeds were still visible, the trial was abandoned because a sampling phase was not considered to have begun. If fewer seeds were visible, the observer watched the patch for a further three hours (four hours from the end of the chipmunk's last patch visit). Animals that returned during those additional hours were considered to have sampled. Animals that did not return during

those additional three hours were considered to have depleted the patch but not to have sampled. I included animals in both these categories in the analyses because excluding them would have biased the observations in favour of observing TCS. In general, observations of animals upon return and close inspection of the patch after the trial confirmed that the patch was indeed empty. Only one of the animals in this category gained seeds (one seed only) during the sampling phase. Once the trial was complete, the distance from the patch to the focal chipmunk's burrow was measured if the burrow location could be determined.

Trials were abandoned (i) if the chipmunk passed through the newly set up patch and/or examined the seeds, but did not begin to exploit the patch, (ii) if the chipmunk began to exploit the patch, but did not return for an hour although there were at least five seeds in the patch, (iii) if normal chipmunk activity was interrupted by high winds or heavy rain, or (iv) if the chipmunk was clearly subordinate at the patch. Individuals which were repeatedly chased away from the patch by one or more competitors and which never chased competitors were considered subordinate. Individuals in such situations were not used because their experience of the patch may have been too strongly affected by competition.

In the eastern deciduous forest, grey squirrels often compete with chipmunks for seeds. Squirrels remain in the patch while eating seeds, and are sometimes aggressive towards chipmunks. Therefore, they were lured away from the experimental patch using hazel nuts (*Corylus*) tossed to them by the observer. Chipmunks cannot open hazel nuts, and generally do not hoard them (personal observation).

Forty trials were completed on different individuals, of which 20 received the 15 ml treatment, and 20 received the 150 ml treatment. Burrow distances were

obtained for 27 of 40 individuals. The appendix contains summary information for each trial, including the age class and sex of the focal individuals and the number of peanuts presented to each.

Statistical Analyses

Statistical analyses were carried out using a mixed-model Poisson regression. The model was run using the program, MIXPREG (Hedeker, 2001). A mixed-model Poisson regression is appropriate because it is the only statistical model that allows for the analysis of discrete data where many values are zero or one, and that can account for the nested nature and partial dependence of the data. Time (sequential half-hour intervals) is nested within individual so measures of the number of visits per sequential half-hour interval are not independent. The dependent variable is the number of visits to the patch per half-hour interval during the sampling phase for each individual. I tested for the effect of several independent variables on the dependent variable. These variables were sequential half-hour interval (time), treatment (15 ml or 150 ml of sunflower seeds), the number of peanuts presented during the pre-trial phase, and the distance of the patch from the chipmunk's burrow. My records were insufficiently detailed to incorporate a valid measure of the amount of competition. Forty individuals and 8 half-hour intervals per individual yielded a sample size of n = 320 records of the dependent variable. Because distance data were only available for 27 individuals, a sub-sample of n = 216 records was available for analyses including distance.

The most parsimonious (minimal adequate) model was determined by using likelihood ratio tests to eliminate independent variables and two-way interaction terms (see Crawley, 1993). The maximal model includes all main effects and interaction terms. The likelihood ratio is the difference in deviance between the maximal model

and the maximal model less the variable of interest. The deviance is a measure of the discrepancy between the model and the data, and is distributed according to a χ^2 distribution (Crawley, 1993). Therefore, if the likelihood ratio is greater than the critical χ^2 value, removal of the given variable from the maximal model causes a significant increase in the deviance. That is, its removal significantly affects how well the model fits the data (Crawley, 1993). The minimal adequate model includes only those variables that significantly affect the fit (deviance) of the model.

I excluded higher order interactions from the analyses since my sample size is not large enough to include them without unbalancing the design. Although treatment is a categorical variable, it was included as a dummy variable in the regression by coding it as 0 for the 15 ml treatment and 1 for the 150 ml treatment.

In presenting the results, I have also included the maximum marginal likelihood estimates, standard errors, Z-values, and P-values of the minimal model, although their use to perform hypothesis tests under these conditions is controversial (Hedeker, 2001). The intercept is a measure of individual variation (Hedeker, 2001). Although the maximum marginal likelihood estimates give estimated values for the explanatory variables and a measure of individual variation, the model simplification procedure is a more conservative test.

RESULTS

Chipmunks exploited 15 ml seed patches in fewer visits (mean = 3.1) than 150 ml seed patches (mean = 12.2, Mann-Whitney $U = 399$, $n_1 = 20$, $n_2 = 20$, $P < 0.001$). Visits to 150 ml seed patches generally occurred at regular intervals (Figure 1, individuals 21-40). During the sampling phase, thirty-six chipmunks repeatedly visited novel patches they had depleted for up to four hours, but six of these did not return within the first hour. Four animals did not return at all (Figure 1).

Chipmunks decreased their rate of sampling with time since depletion of the patch. Time (consecutive half-hour interval) has a highly significant effect on the fit of the model (Table 1) and is a significant explanatory variable in the minimal model, with a negative estimate (Table 2). This pattern is illustrated by the trend in the proportion of animals sampling in each interval and the total number of sampling visits in each sampling interval (Figure 2). Most visits occurred during the first half-hour interval. Few individuals visited during the following three hours, and very few animals visited during the last half-hour (Figure 1, 2). The significant intercept term in the minimal model (Table 2) indicates that there is significant variation among individuals.

Chipmunks that received more peanuts in the pre-trial phase sampled at a consistently higher rate over time. The number of peanuts presented to chipmunks in the pre-trial phase significantly affects the fit of the model (Table 1), and is a significant explanatory variable in the minimal model, with a positive effect (Table 2). There is a positive trend between the number of peanuts and the number of sampling visits when treatment, time, and distance are ignored (Figure 3a). No two-way interaction terms significantly affect the deviance of the model (all P values > 0.5). This includes the interaction of time and number of peanuts. Consequently, there is no evidence that chipmunks adjusted their change in sampling rate over time to the number of peanuts with which they had been presented.

Chipmunks did not significantly adjust their pattern of sampling visits to the volume of sunflower seeds with which they were presented. Treatment did not significantly affect the fit of the model to the data (Table 1), nor did the time and treatment interaction term. A graph of the univariate trend shows that, contrary to the

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hypothesis, the average visitation rate to 15 ml patches was slightly higher than to 150 ml patches (Figure 3b).

My data fail to show that chipmunks adjust their pattern of sampling visits to the distance of patches from their burrows. When the model simplification procedure was conducted with the 27 chipmunks for which distance data were obtained (n = 216), distance did not have a significant effect on the fit of the model, nor did any of the two-way interaction terms. When other factors are ignored, there is no trend in the relationship between the total number of sampling visits in four hours per individual and the distance of the patch from each chipmunk's burrow (Figure 3c). Chipmunks with patches farthest from their burrows did visit, and some individuals with patches close to their burrows did not.

DISCUSSION

Evidence for TCS

Most chipmunks returned to patches they had depleted even after experiencing those patches as empty. If chipmunks spend most of their time within 25 m of their burrow (Elliott, 1978), their area of primary use would be about 2000 m^2, so it is very unlikely that a patch measuring only 1 m^2 would receive one or more visits during a 30-minute period simply by chance. Many of my trials took place beyond 25 m, where the probability of visits occurring by chance would be even lower. The observed pattern of visits to a new depleted patch agrees with the predictions of TCS because chipmunks visited most often in the interval immediately following depletion, then decreased their rate of sampling over time. It does not support the alternate hypotheses that chipmunks avoid returning, or do not significantly change their visit rate, following their depletion of a novel patch. This is the first study to show a decrease in rate of sampling over time following the depletion of a novel patch by animals

foraging in the field. My results suggest that visit rate may decrease in a series of steps, from a high initial rate in the first half hour to a low rate over the next three hours to a very low rate for a longer time period. Although it appears that animals may have abandoned the patch at this stage, data from a preliminary study carried out in a previous season showed that some chipmunks continued to return to novel depleted patches for at least 9 hours (K. Gibson, unpublished data). Chipmunks may continue to sample patches over a longer time period but the low rates that would be expected preclude data collection by observation of the patch.

Individual variation in the pattern of sampling visits over time is not surprising. This may be related to individual differences in the age and experience of focal animals, to differences in alternative demands on their time budgets, to variation in competition levels at the patch, predation risk, availability of alternative foraging sites, and the amount of resources in each animal's burrow. Six animals did not return to the patch for an hour following their depletion of it. This may indicate that some animals are using a different sampling strategy, but they may also have been occupied with some other activity (e.g., predator avoidance).

Previous work on resource tracking has modeled and tested how animals should track patches at which they have experienced sufficient renewals to estimate some renewal characteristics (Dall et al., 1999; Inman, 1990; Shettleworth et al., 1988; Stephens, 1987; Tamm, 1987). These studies have used a two-patch paradigm. One patch varies unpredictably from a high quality state to a low quality state (usually empty), and an alternative remains at a steady intermediate quality. Animals exploit the intermediate patch when the variable patch is in its low quality state, while regularly or randomly sampling the variable patch (Inman, 1990; Shettleworth et al., 1988; Stephens, 1987; Tamm, 1987). When animals detect a switch of the variable

patch from the low quality to the high quality state, they exploit it until it again switches. This situation differs from the paradigm for TCS which addresses the case where animals do not know whether or with what probability a renewal will occur. In such a case, it is inefficient to sample the depleted patch (equivalent to the poor state of the varying patch) indefinitely, and animals should decrease their rate of sampling over time, as prescribed by TCS.

TCS is a temporal clustering of sampling visits to a patch which is analogous to the spatial clustering of search effort seen in the many species for which an area-concentrated search strategy has been described, including *Geomys bursarius* (Benedix, 1993), *Adalia decempunctata* (Dixon, 1959), *Mustela putorius* (Haskell, 1997), and *Turdus merula* (Smith, 1974). For a more complete list see (Benhamou, 1992). ACS and TCS can be used in a complementary fashion by foraging animals, and it might be valuable to combine the concepts to predict spatial and temporal foraging patterns. However, here I simply wish to emphasize a parallel between the two, namely that where ACS predicts that animals will concentrate their search effort in space, if a prey item is encountered, then relax that search effort in space if subsequent prey are not encountered, TCS predicts that animals will concentrate their sampling effort in time, if prey are found in a patch, but relax that sampling effort if subsequent renewals are not encountered.

Although most research on the topic of ACS has dealt with invariant area concentrated strategies (e.g., Benhamou, 1992; Dixon, 1959; Nakamuta, 1985), animals may be able to improve their prey encounter rate by determining whether a novel prey type will be found in patches or not and, if the latter, adjusting their search path parameters (e.g., move length, sinuosity, speed) to the characteristics of the prey distribution they encounter. The potential for flexibility has been considered by very

few studies of ACS. Only Haskell (1997) and Smith (1974) have shown it to occur in experimental studies. No studies appear to have considered how an animal might best learn about the distribution of a new prey type. By analogy with my approach to TCS, information gain may be an unrecognized benefit in ACS. From this perspective, I suggest that upon initial encounter with a novel prey type or familiar prey in a novel area, a highly concentrated search over a large area, though often inefficient as an exploitation strategy, might provide valuable information about the patchiness of prey. I would expect the degree of area concentration to become more efficient as animals gain experience with a given patch size. An information gain perspective might be a valuable addition to studies of ACS.

Flexibility in TCS

Chipmunks adjusted their sampling rate to the number of peanuts presented near the patch while setting up the trial. In the two-patch paradigm, resource tracking theory predicts that sampling rates will vary as a function of the quality of both states of the variable patch, the quality of the intermediate constant patch, and the probability that the variable patch will switch states (Stephens, 1987). Specifically, Stephens' (1987) model predicts that animals will increase their sampling effort to the variable patch if the value of the good state of the varying patch is increased. Support for this prediction has been inconclusive in the laboratory (Inman, 1990; Shettleworth et al., 1988; Tamm, 1987). However, a field test by Hall and Kramer (in preparation) carried out at the same time as this study showed that chipmunks' total sampling rates over a two-hour period were lower when competitors reduced the number of peanuts they received during the exploitation period. My result concerning peanuts agrees with that of Hall and Kramer (in preparation) and supports the prediction of Stephens' (1987) model.

The lack of a detectable effect of sunflower seed volume on the pattern of sampling visits is surprising, given the effect of the peanuts. There is not even a trend in the expected direction. The most likely explanation for this result is the effect of competition. Although I do not have adequate data on competition, there were more competitors at the larger patch, probably because it contained food for a longer period of time thereby increasing the opportunity for conspecifics to discover it. This may have reduced the difference between 15 ml and 150 ml patches. The observed average difference between the number of exploitation visits required to exploit the 15 ml and 150 ml patches was only 4-fold and although this was less then the 10-fold treatment difference, it might still be expected to yield an effect since chipmunks are sensitive to patch quality (Kramer and Nowell, 1980; Lair et al., 1994). However, in addition to reducing the volume of seed acquired by the focal individual, more competitors may have resulted in an increased number of agonistic interactions for some animals at 150 ml patches, further decreasing the value of those patches .

Chipmunks' sampling rates were not significantly affected by the distance of the patch from the burrow. There is not even a trend toward the expected effect of decreased sampling with increased distance. Increased distance should decrease TCS since it will likely increase agonistic interactions while a chipmunk is traveling, decrease the animal's dominance rank at the patch (Elliott, 1978), increase the time away from the burrow and therefore the chance of a burrow raid by a conspecific, and perhaps increase the predation risk of the animal since it may be in less familiar terrain (Clarke et al., 1993), during both sampling and potential exploitation. The energetic costs of travel are likely not an issue because they are small relatively to the benefits of a load of seeds (Humphries et al., 2002). The costs associated with increased distance, however, may have been unusually low during my field season,

because of low population density. In January 1998 a severe ice storm caused extensive damage to the forest on and around the study site (Hooper et al., 2001) and likely contributed to the near 80% mortality in the chipmunk population over the winter preceding the present study (November 1999 to March 2000, C. Hall and M. Humphries, unpublished data). During the summer of 2000, chipmunks traveled much farther from their burrows and used more scatter hoards than in previous years (personal observations). Lower population density could decrease the probability of an animal's burrow being raided by a conspecific while it is absent, decrease the number of agonistic interactions while traveling and foraging, and decrease the probability of a scatter hoard being plundered. Scatter hoarding may decrease the costs of exploiting a distant, short-lived patch (Clarke and Kramer, 1994a; Clarke and Kramer, 1994b). Consequently, the lack of an effect of distance may be due to lower costs of sampling and exploiting distant patches as compared to previous years. In summary, my data indicate that chipmunks have the capacity for flexibility in TCS. However, my data do not allow me to clearly conclude which factors are important in determining where such flexibility is expressed.

Relationships Between TCS and Other Approaches to Patch Use and Information

TCS will be useful as a concept only if the behaviour it predicts cannot be better accounted for by another theoretical paradigm. A wide range of functional and mechanistic research has examined patterns of repeated visits to renewing patches by animals with extensive experience with those patches. My study, however, proposes a strategy by which animals could establish such patterns in the first place. Here, I compare and contrast the insights provided by TCS with those provided by related fields of research.

Extinction

The decline in visitation rate that I observed appears similar to the laboratory phenomenon of extinction, a widely studied behaviour pattern in mechanistic associative learning experiments (Roberts, 1998). In such experiments, animals are rewarded for exhibiting a given behaviour (pecking a key, pressing a lever, running a maze) where the reward is contingent on the animal's response. In the free-operant paradigm, animals are able to respond continuously without pauses imposed by the experimenter (Roberts, 1998). Extinction in this situation is the decline in the rate of response of an animal over time without a reward. There are parallels between my field study and extinction in a free-operant paradigm. In my field study the foraging chipmunk is rewarded for performing a behaviour, returning to the food patch, until the patch is depleted at which point the behaviour is no longer rewarded and consequently extinguishes. Free-operant extinction studies have shown that animals' total number of responses and their rate of response are sensitive to the conditions of reward, including the frequency of reward and the quantity of reward (Gollub and Urban, 1958; Mellgren and Elsmore, 1991; Nevin, 1974; Tombaugh, 1974). In such cases, the magnitude of extinction, namely, the persistence of the response when reinforcement is no longer provided, is used to measure the strength of an association learned on a given reinforcement schedule (Mellgren and Elsmore, 1991; Nevin, 1974). Such sensitivity is similar to my expectation that chipmunks would sample at a higher rate following depletion of a richer patch. However, I suggest that persistent visiting of a depleted patch may not be simply an outcome of a learning constraint that makes it difficult for an animal to learn that a patch is empty but may be an adaptive way of determining the potential for renewal. Although this suggestion is intriguing, it is not easy to draw predictions concerning adaptive behaviour from the existing

literature on extinction since mechanistic studies are not designed with a view to explaining the behaviour of animals foraging in the field (Shettleworth, 1989). For example, it is not clear that animals will respond to the experimental apparatus as they would to a field foraging situation where many alternative activities are available. Also, all animals in free-operant trials must have experience with the experimental apparatus and, consequently, cannot be presented with a novel patch. My study, then, is not simply a field replication of extinction studies.

Win-shift and Win-stay

The win-shift/win-stay paradigm has addressed whether animals avoid or return to recently exploited sites. Laughlin and Mendl (2000, p. 403) describe this paradigm as follows: 'After a successful foraging bout, an animal can either return to the location where food was found previously, or avoid such locations and search elsewhere. These two strategies are termed 'win-stay' and 'win-shift', respectively.' The win-shift/win-stay dichotomy is treated as a spatial learning problem and is generally tested in some form of radial maze. An animal is given an opportunity to forage in a maze, where certain arms contain food and others do not. The animal is then removed for an interval, subsequently returned to the maze, and the arm it visits first is recorded. A propensity to win-shift contradicts the traditional notion of reinforcement in which an animal is expected to return to a place where it has received a reward. None the less, such a spontaneous propensity has been shown in a wide variety of species, as has the inverse, win-stay (see Laughlin and Mendl, 2000; Olton et al., 1981).

My perspective suggests that the proposed win-shift/win-stay dichotomy is over simplified. The appropriate response may not always be a characteristic of species but rather a characteristic of the time since an animal depleted a patch and its

previous experiences of renewals at that patch. For an animal foraging in the field, its response to encountering no food at a previously exploited patch should depend on its previous experience, its foraging alternatives, and the costs and benefits of gaining information concerning the renewal characteristics of that patch. Consequently, an animal foraging in the field and faced with multiple foraging and tracking options might exhibit win-shift under certain conditions and win-stay under others. For example, as a foraging chipmunk exploits a patch it exhibits win-stay since it returns repeatedly and immediately to the patch. As the patch depletes, however, the chipmunk begins to explore alternatives before returning to the patch (Kramer and Weary, 1991). It has switched to a win-shift strategy although it exhibits win-stay at times, on a larger time scale, since it still returns to the original patch. Even for animals with prior expectations, genetic or learned, of a particular patch or food type that does not renew, or renews only after a refractory period, win-shift may not be the only viable strategy. For example, (Devenport et al., 1998) showed that least chipmunks foraging in a simulated environment could learn to return to patches they had exploited and would otherwise avoid, if they were taught that those patches could renew.

Traplining

Animals foraging on resources that renew following a refractory period (e.g., floral nectar) may be best served by revisiting patches in a systematic fashion, and some literature has treated this 'traplining' strategy (Garrison and Gass, 1999; Thomson, 1996; Thomson et al., 1987; Thomson et al., 1997; Williams and Thomson, 1998). Traplining is often studied by examining the visits of an animal to a single patch (Gill, 1988; Williams and Thomson, 1998) to estimate an animal's behaviour towards a series of renewing patches. This observation of an animal's pattern of visitation is

similar to my study of TCS. In contrast to TCS, however, the emphasis is on the animal's established exploitation pattern rather than its acquisition of information about patch renewal. TCS may provide a strategy by which a trapline could be established, and patches added and removed.

Bayesian Updating

Some animals forage in environments in which the temporal and spatial distribution of food is relatively stable or predictable. Animals then face a small number of types of resource distributions and information about a novel patch may be collected to classify its type. Put another way, animals with prior experience in a relatively stable environment should expect novel patches to behave similarly to other patches they have experienced. Bayesian models have been used to help understand the behaviour of foraging animals in such systems (see Giraldeau, 1997; Stephens and Krebs, 1986). TCS applies to a situation which is not addressed by Bayesian models, where animals must sample to gain information about a highly variable temporal distribution of food where novel patches cannot be assumed to have the same renewal characteristics as other previously experienced patches. If an unexpected change in stable distributions is encountered, however, TCS should allow animals to learn about the novel patch (see Nonacs and Soriano, 1998).

Learning Rules

Learning rules are quantitative descriptive models of how animals estimate the value of multiple patches. They calculate a weighted average of all experiences at each patch to predict patch use when a change in the value of a patch is detected (Kacelnik and Krebs, 1985; Kacelnik et al., 1987). In practice, they are tested using animals' acquisition of preference for one of two alternate operant feeders with different values (Kacelnik and Krebs, 1985). In one experiment (Kacelnik et al., 1987), animals

exploited a patch of high value relative to the alternative, which made an unsignaled drop to zero value. Like TCS, then, studies of learning rules address the allocation of an animal's visits to a depleted feeder (patch). However, TCS focuses on the timing of information gain, whereas learning rules focus on the weighting of the information gathered. Consequently, by ignoring information gain about renewal, learning rules that model a delay in abandoning an operant feeder in response to a cessation of rewards have been considered inefficient (Kacelnik and Krebs, 1985). From the perspective of TCS such a delay may be an adaptive strategy to hedge against the possibility of a quick renewal. In turn, where TCS predicts the best strategy to evaluate only a single patch, learning rules model the behaviour of animals in a more realistic situation of multiple patches and provide rules, albeit descriptive ones, to describe how animals update information following patch visits. The two approaches are therefore complementary.

One failing of learning rules has been the difficulty in objectively selecting parameters (see Kacelnik and Krebs, 1985). Devenport and colleagues (Devenport and Devenport, 1993; Devenport et al., 1997; Devenport, 1998; Devenport and Devenport, 1994; Mazur, 1996) have addressed this issue with the 'temporal weighting rule', which provides a formula to devalue information with time since it was acquired. This model successfully predicts the patch choices of several species in both the lab (*Rattus norvegicus*, Devenport et al., 1997; Devenport, 1998; *Columbia livia*, Mazur, 1996) and the field (*Spermophilus lateralis* and *Tamias minimus*, Devenport and Devenport, 1994), but it has not been tested as a predictive model of animals' rates of sampling over time.

I have argued that, theoretically, TCS provides a useful perspective on information gain. Although a great deal of work has addressed the topic of animal

learning, TCS uniquely provides an adaptive framework for examining how animals in particular ecological circumstance might learn about the renewal characteristics of a novel patch in a variable environment.

Future Directions

TCS is a qualitative model that predicts the behaviour of animals towards a single patch in particular ecological conditions, and I have shown that eastern chipmunks foraging under such conditions exhibit the predicted change in rate of visits. To show definitively that chipmunks are indeed gaining information, however, it will be necessary to show that they use the information I assume they are collecting to adjust their subsequent foraging and sampling activities. Future work should attempt a quantitative formulation of TCS, expand it to predict the behaviour of animals towards multiple patches and, most importantly, predict and test how animals respond to a renewal to determine whether they use the information gained by sampling. It may be possible to use the temporal weighting rule to generate a quantitative formulation of TCS to predict when animals should visit multiple patch options. One could examine the pattern of visits prescribed by the model to a high value patch following its depletion when a single low value patch alternative is available to represent the approximately constant value of the rest of the environment.

Since each animal made only a few sampling visits in my experiment, it was not possible to analyze the frequency of sampling visits by animals to the patch. One would expect that at some scale, animals should avoid the patch since presumably even the most quickly renewing patches have some refractory period and future work might examine whether such avoidance occurs in a system where more visits per individual could be documented.

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TABLES

Table 1. The minimal adequate model selection procedure using a mixed-effects Poisson regression analysis of factors affecting the sampling pattern of 40 chipmunks over eight consecutive half-hour intervals (n = 320). The null model represents the total deviance of the data. The maximal model includes all the factors; no two-way interaction terms were significant and so are not included. The models that follow show the deviance of the maximal model without the specified factor. The P values are derived from a χ^2 test of the likelihood ratio. The critical χ^2 value in all cases is 3.841. 'Time' is the half-hour interval (1-8), 'peanuts' is the number of peanuts presented (0-10), and 'treatment' is the volume of seed presented (15 ml or 150 ml). The minimal model is includes only those factors which, when removed, significantly affect the model deviance.

Model	Model Deviance	df[1]	Likelihood Ratio	Likelihood Ratio df[1]	P-value
null model	836.744	319			
maximal model: (time + peanuts + treatment)	577.044	316			
maximal model minus (time)	727.856	317	150.812	1	< 0.001
maximal model minus (peanuts)	529.731	317	15.687	1	< 0.001
maximal model minus (treatment)	577.353	317	0.309	1	0.578
minimal model: (time + peanuts)	577.353	317			

[1] indicates degrees of freedom.

Table 2. A maximum marginal likelihood analysis of the minimal model derived from model simplification using mixed-effects Poisson regression analyses for factors affecting the sampling patterns of 40 chipmunks over eight consecutive half-hour intervals (n = 320).

Factor	Estimate	Standard Error	Z-value	P-value
time	-0.455	0.037	-12.144	< 0.001
peanuts	0.134	0.017	7.754	< 0.001
intercept	0.614	0.062	9.919	< 0.001

All P-values are two-tailed except for the intercept, which is one-tailed.

FIGURES

Figure 1. The pattern of visits to a food patch by 40 chipmunks. Each horizontal bar

represents the duration of the trial of a different individual. Filled circles indicate

visits during which at least one seed was collected and open diamonds indicate visits

during which no seeds were collected. Records are aligned for the time at which

observation of the sampling phase began (see text for definition). Values to the left of

0 represent the exploitation phase. The vertical bar at the right indicates the food patch

quality treatment for each individual.
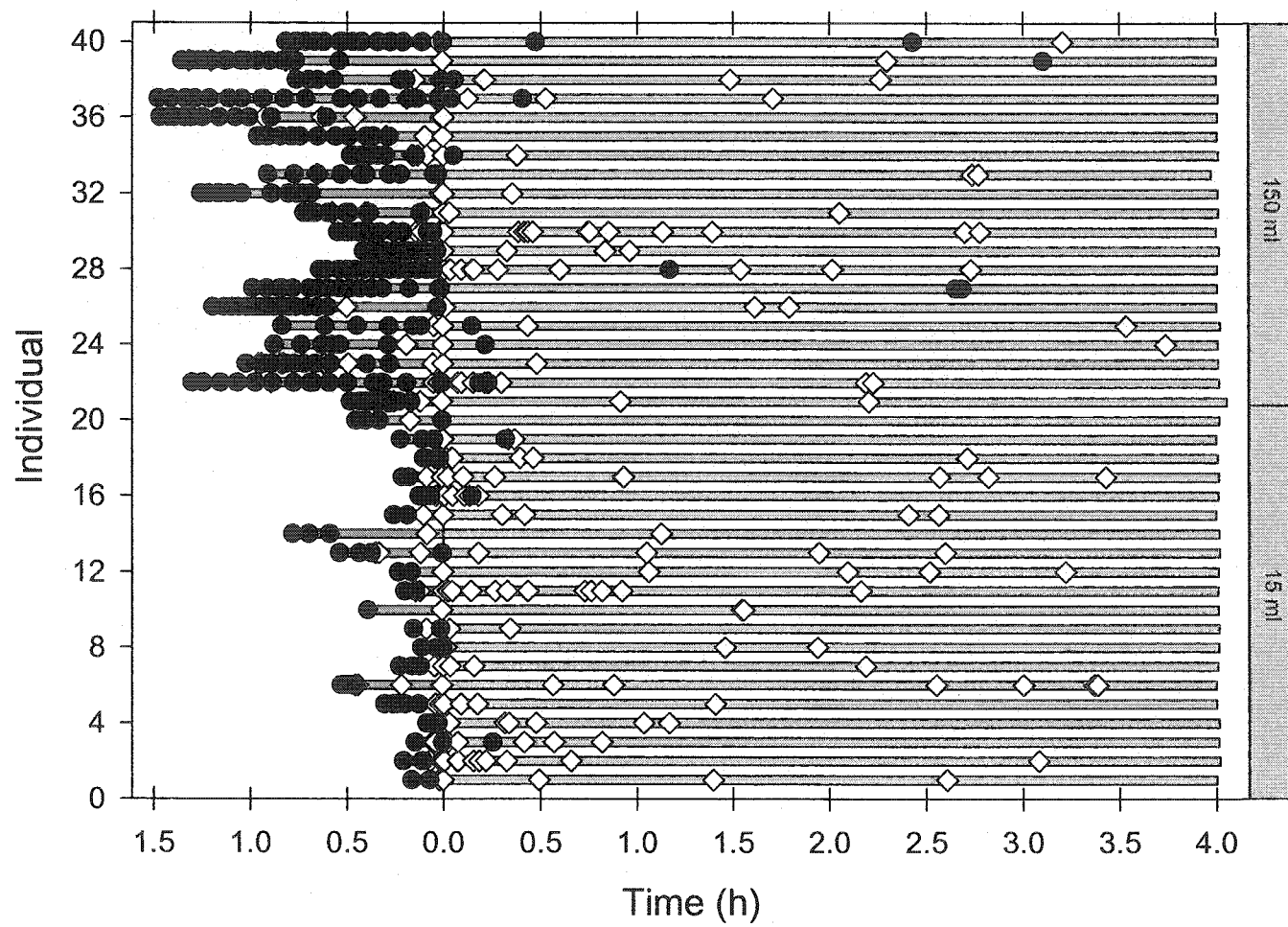
Figure 2. The percent of chipmunks that visited a small patch at least once (bars) and the total number of visits made by all chipmunks (filled circles) in each of eight half hour intervals following depletion (n_1 = 40 chipmunks, n_2 = 169 visits).
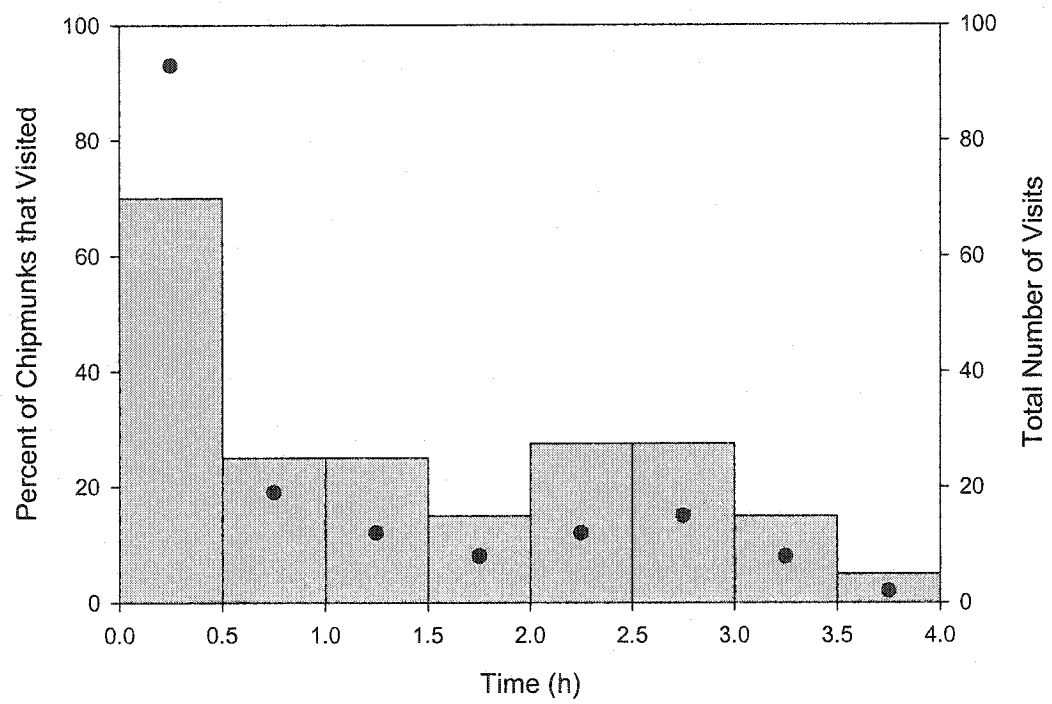
Figure 3. Univariate plots of the number of sampling visits by each of 40 chipmunks to small, depleted patches during a four hour observation period in relation to (a) the number of peanuts provided while initiating the trial, (b) the volume of sunflower seeds provided in the patch, and (c) the distance of the patch from the animal's burrow (n = 27, because some distances could not be determined). In (a), large dots represent three individuals, medium sized dots represent two individuals, and small dots represent one individual. In (b), the thick line of each box is the median, the extremities of the box are the 25th and 75th percentiles, the vertical lines delineate the 10th and 90th percentiles, and dots indicate outliers. The 10th percentile for the 150 ml treatment is 0. In (c), each dot represents an individual.
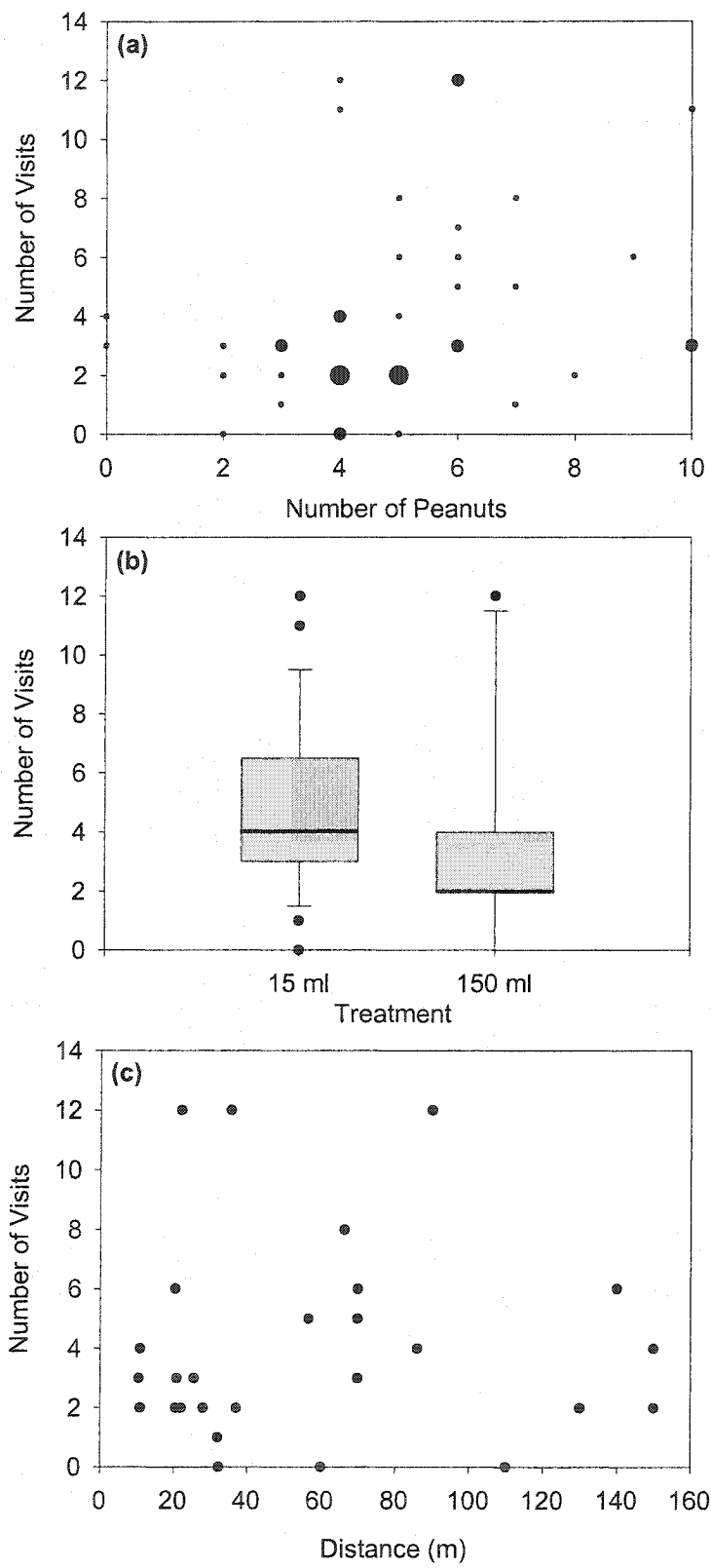
APPENDIX

Summary information for each trial. The time of day at which the trial started and ended is listed, as well as the length of the exploitation phase and the total length of the trial. Treatment is either 15 ml or 150 ml of seed. The distance from the experimental patch to the chipmunk's burrow is listed for individuals whose burrow location was known. The number of peanuts provided during the pre-trial phase and the number of competitors during the exploitation phase are also listed. Throughout the table (u) indicates unknown. Sex is female (f) or male (m). Age class is adult (a) or juvenile (j). Trial category is coded as (4) for a four hour sampling phase, (3) for the alternate category of sampling phase, or (no) for no sampling visits (see text for a complete explanation).

Trial	Sex	Age Class	Date (dd/mm)	Trial Category	Start Trial (hh:mm:ss)	Stop Trial (hh:mm:ss)	Exploitation Length (hh:mm:ss)	Trial Length (hh:mm:ss)	Treatment	Distance (m)	Peanuts
1	m	a	12/6	4	11:57:09	16:07:00	0:09:45	4:09:51	15 ml	u	10
2	f	a	23/6	4	10:08:34	14:22:00	0:12:22	4:13:26	15 ml	u	10
3	u	u	12/7	4	12:07:28	16:17:00	0:08:43	4:09:32	15 ml	u	6
4	f	a	13/7	4	12:05:04	16:11:00	0:05:02	4:05:56	15 ml	u	5
5	m	a	20/7	4	11:09:41	15:28:00	0:18:11	4:18:19	15 ml	u	4

Appendix continued.

Trial	Sex	Age Class	Date (dd/mm)	Trial Category	Start Trial (hh:mm:ss)	Stop Trial (hh:mm:ss)	Exploitation Length (hh:mm:ss)	Trial Length (hh:mm:ss)	Treatment	Distance (m)	Peanuts
6	f	a	28/6	4	14:34:06	19:06:00	0:31:49	4:31:54	15 ml	20.4	9
7	m	j	25/8	4	10:59:50	15:14:00	0:13:38	4:14:10	15 ml	u	10
8	f	a	7/9	4	13:10:32	17:18:00	0:06:40	4:07:28	15 ml	10.6	6
9	m	j	24/9	4	11:55:54	16:06:00	0:09:11	4:10:06	15 ml	11	4
10	m	a	28/9	3	13:06:43	17:31:00	0:23:31	4:24:17	15 ml	22	4
11	f	a	2/10	4	11:38:20	15:51:00	0:12:00	4:12:40	15 ml	22	4
12	m	j	25/10	3	12:15:22	16:30:00	0:13:54	4:14:38	15 ml	11	5
13	f	a	9/6	4	10:38:39	15:12:00	0:32:17	4:33:21	15 ml	86.1	0
14	f	a	13/6	3	11:41:10	16:29:00	0:46:57	4:47:50	15 ml	32	7
15	f	a	22/6	4	9:49:33	14:05:00	0:15:24	4:15:27	15 ml	150	4
16	m	a	24/6	4	10:12:44	14:21:00	0:07:30	4:08:16	15 ml	140	5

Appendix continued.

Trial	Sex	Age Class	Date (dd/mm)	Trial Category	Start Trial (hh:mm:ss)	Stop Trial	Exploitation Length	Trial Length (hh:mm:ss)	Treatment	Distance (m)	Peanuts

Trial	Sex	Class	(dd/mm)	Category	(hh:mm:ss)	(hh:mm:ss)	Length (hh:mm:ss)	(hh:mm:ss)		(m)	
17	f	a	28/6	4	13:00:16	17:14:00	0:12:46	4:13:44	15 ml	66.4	7
18	f	a	6/7	4	12:42:23	16:49:00	0:06:06	4:06:37	15 ml	70	6
19	f	a	11/7	4	11:12:33	15:26:00	0:13:20	4:13:27	15 ml	70	3
20	m	j	10/27	no	10:10:50	14:39:00	0:27:11	4:28:10	15 ml	32.2	2
21	m	a	22/6	4	10:12:44	14:45:00	0:28:58	4:32:16	150 ml	u	8
22	f	a	6/7	4	11:22:53	16:42:00	1:18:08	5:19:07	150 ml	u	4
23	m	a	13/7	4	12:12:52	17:15:00	1:01:26	5:02:08	150 ml	u	3
24	m	a	3/9	4	9:10:42	14:04:00	0:52:43	4:53:18	150 ml	u	4
25	m	a	8/9	4	11:56:18	16:48:00	0:50:18	4:51:42	150 ml	u	6
26	f	a	9/10	4	9:14:06	14:26:00	1:11:41	5:11:54	150 ml	20.8	2
27	f	j	10/13	no	13:12:18	18:12:00	0:59:19	4:59:42	150 ml	20.5	5

Appendix continued.

Trial	Sex	Age Class	Date (dd/mm)	Trial Category	Start Trial (hh:mm:ss)	Stop Trial (hh:mm:ss)	Exploitation Length	Trial Length (hh:mm:ss)	Treatment	Distance (m)	Peanuts

Trial	Sex	Age Class	Date (dd/mm)	Trial Category	Start Trial (hh:mm:ss)	Stop Trial (hh:mm:ss)	Exploitation Length (hh:mm:ss)	Trial Length (hh:mm:ss)	Treatment	Distance (m)	Peanuts
28	f	a	20/6	4	10:22:02	15:01:00	0:38:32	4:38:58	150 ml	35.5	6
29	f	a	20/6	4	12:05:03	16:31:00	0:24:50	4:25:57	150 ml	u	0
30	f	a	23/6	4	11:35:12	16:32:00	0:32:49	4:56:48	150 ml	90	6
31	f	a	24/6	4	11:58:46	16:43:00	0:43:24	4:44:14	150 ml	150	5
32	m	a	26/6	no	11:34:52	16:51:00	1:15:22	5:16:08	150 ml	110	4
33	m	a	29/6	3	10:44:36	15:38:00	0:54:46	4:53:24	150 ml	130	5
34	f	a	4/7	4	12:01:21	16:31:00	0:28:51	4:29:39	150 ml	37	3
35	m	a	10/7	no	10:11:51	15:10:00	0:57:45	4:58:09	150 ml	60	4
36	m	a	12/7	no	11:06:30	16:35:00	1:28:00	5:28:30	150 ml	u	5
37	f	a	24/7	4	10:07:44	15:37:00	1:28:34	5:29:16	150 ml	70	7
38	f	a	29/8	4	12:10:57	16:57:00	0:45:55	4:46:03	150 ml	56.7	6

Appendix continued.

Trial	Sex	Age Class	Date (dd/mm)	Trial Category	Start Trial (hh:mm:ss)	Stop Trial (hh:mm:ss)	Exploitation Length (hh:mm:ss)	Trial Length (hh:mm:ss)	Treatment	Distance (m)	Peanuts

| 39 | f | j | 29/9 | 3 | 12:39:30 | 18:01:00 | 1:21:23 | 5:21:30 | 150 ml | 28 | 2 |
| 40 | m | a | 30/9 | 4 | 12:59:07 | 17:49:00 | 0:49:07 | 4:49:53 | 150 ml | 25.5 | 3 |

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