UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LA SOUS-OPTIMALITÉ OBSERVÉE DANS L'APPROVISIONNEMENT DE *TAMIAS STRIATUS* RÉSULTE-T-ELLE D'ESTIMATIONS ERRONÉES DES COURBES DE CHARGEMENT?

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AVANT-PROPOS

Ce mémoire est composé d'un résumé et d'une introduction générale en français, d'un article scientifique en anglais dans lequel les données de ma maîtrise sont présentées suivi d'une conclusion générale en français. L'article présente des données originales collectées par moi, assistée en 2005 par Delphine Marchand qui était rémunérée pour ce travail. L'analyse des données a été faite par moi et les conclusions élaborées en discussion avec mon directeur de recherche Luc-Alain Giraldeau. Toutes les sections de ce mémoire ont été rédigées par moi avec des ajouts et corrections de mon directeur de recherche.

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RÉSUMÉ

Contrairement aux prédictions quantitatives, les prédictions qualitatives du modèle d'approvisionnement centralisé (AC) ont obtenu un grand nombre d'appuis expérimentaux avec le tamia rayé. Les échecs quantitatifs sont fondés sur des mesures de la courbe de chargement dont la variabilité est telle qu'il est difficile de rejeter avec certitude le modèle. Nous proposons ici une méthode capable de générer des prédictions quantitatives plus fiables. Nous avons observé le chargement de cacahuètes par des tamias rayés du Mont St-Hilaire à deux distances de leur terrier; soit 2m et 15m. Les cacahuètes étaient présentées une à la fois selon une séquence prédéterminée d'intervalles croissants permettant ainsi à l'expérimentateur de contrôler précisément la courbe de chargement pour toutes les valeurs de tailles de charges prélevées sur le terrain. Les prédictions qualitatives du modèle furent encore vérifiées puisque que la taille des charges augmente avec la distance entre le terrier et la parcelle de nourriture. Cependant, malgré notre contrôle accru des paramètres de la courbe de chargement, les charges de cacahuètes amassées demeurèrent significativement plus petites que celles prédites par le modèle. Nous en concluons que la disparité quantitative répétée entre les prédictions du modèle et les charges observées indique la nécessité de tenir compte des facteurs additionnels tel le risque de prédation plus élevé associé au temps passé dans la parcelle de nourriture.

Mots clefs: approvisionnement centralisé, Tamias striatus, test quantitatif, coûts d'approvisionnement, coût de prédation.

INTRODUCTION

L'approche d'optimisation consiste à considérer que les traits phénotypiques tendent, sous l'effet de la sélection naturelle, vers des valeurs optimales en termes de maximisation de l'aptitude phénotypique (DANCHIN, GIRALDEAU & CÉZILLY 2005). La prémisse que les animaux sont optimaux dans leurs activités d'approvisionnement a permis de tester plusieurs hypothèses au sujet de la fonction des comportements. En approvisionnement, on émet l'hypothèse que l'aptitude augmente en fonction du taux de gain d'énergie durant l'approvisionnement (ORIANS & PEARSON 1979).

Le théorème de la valeur marginale de CHARNOV (1976) applique la maximisation du taux net de gain énergétique à l'exploitation de proies regroupées au sein de parcelles de qualité variable; ces parcelles ne pouvant être exploitées qu'après un certain investissement en temps de recherche. De plus, le modèle présuppose que le taux de rencontre avec les proies d'une parcelle diminue à mesure que la parcelle est exploitée. La maximisation du taux brut de gain énergétique nécessite que l'animal cesse l'exploitation d'une parcelle pour en chercher une autre lorsque son taux instantané dans la parcelle atteint le taux espéré à la prochaine parcelle en tenant compte du temps de recherche requis.

Le même modèle s'applique avec peu de modifications à des situations où les individus ne consomment pas les proies là où elles sont prélevées, mais les rapportent plutôt à un point central fixe, c'est le cas notamment des oiseaux qui nourrissent leurs oisillons ou des abeilles ouvrières rapportant le nectar au nid. Le modèle de l'approvisionnement centralisé (AC) (ORIANS & PEARSON 1979) prédit que, pour les animaux capables de transporter plusieurs proies et ayant une vitesse de chargement décroissante (Fig. 1), la taille de la charge transportée dépendra du temps de transit entre la parcelle et le lieu central plutôt que du temps de recherche (ORIANS & PEARSON 1979). Ainsi, plus le transit est long, plus la charge optimale croît (Fig. 2).

Il existe plusieurs tests du modèle d'AC d'ORIANS & PEARSON (1979) mais pour les animaux capables de transporter plusieurs proies à la fois, bien que tous aient montré une relation positive entre la taille des charges amassées et le temps de transit, aucun n'a pu fournir un appui quantitatif au modèle (STEPHENS & KREBS 1986). Cette adéquation qualitative générale couplée à un échec quantitatif répété ne permet que deux conclusions : soit le modèle est faux, soit les mesures utilisées pour les tests quantitatifs ne sont pas fiables. Notre objectif dans la présente étude est de voir à départager ces conclusions avec à partir d'un modèle animal souvent utilisé pour tester le modèle de l'AC, le tamia rayé.

Figure 1

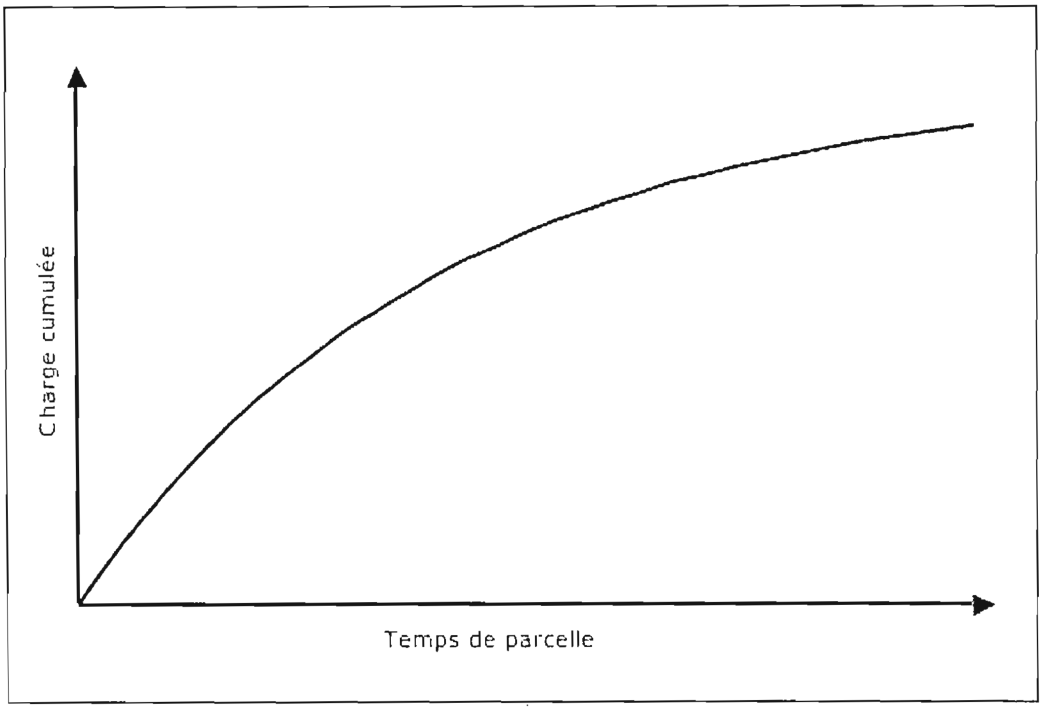

Figure 1. Courbe de chargement représentant l'accroissement décéléré de la taille cumulée de la charge de proies en fonction du temps passé dans la parcelle.

Figure 2

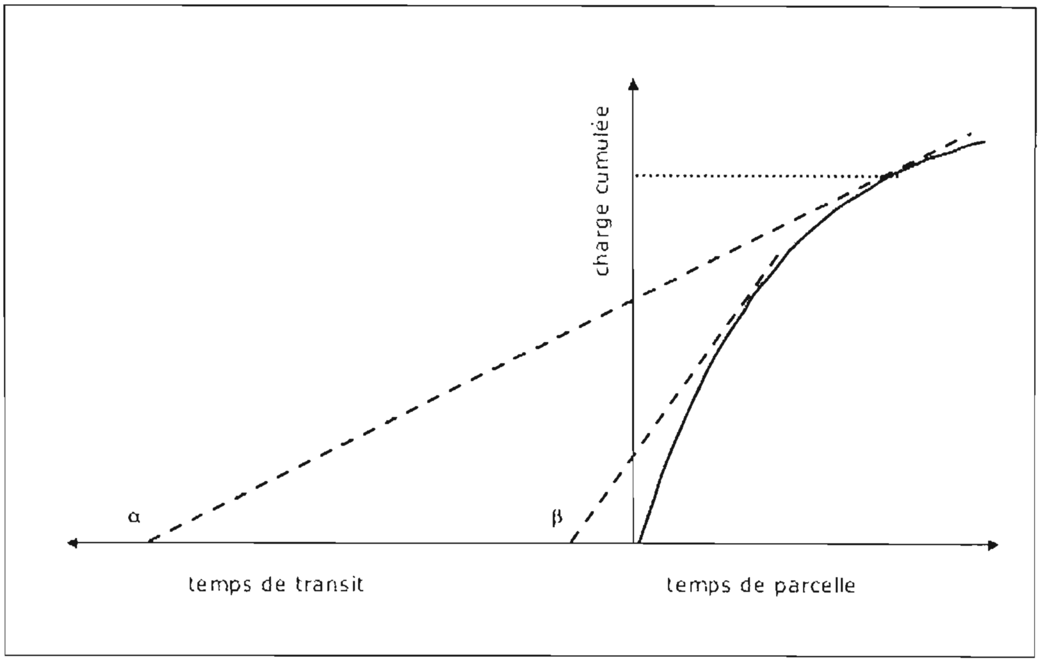

Figure 2. Méthode de la tangente utilisée pour déterminer la taille optimale des charges à rapporter au lieu central en fonction du temps de transit entre le lieu central et la parcelle (ORIANS & PEARSON 1979). Sur l'abscisse, le temps passé à charger des proies (temps de parcelle) augmente vers la droite de l'ordonné et le temps de transit augmente vers la gauche de l'ordonné. L'ordonné montre la taille cumulée de la charge. Le taux (charge cumulée/unité de temps) maximal de livraison des proies au lieu central dépend de la courbe de collecte moyenne pour une parcelle de proies et du temps de transit nécessaire entre le lieu central et la parcelle. La charge optimale, celle qui correspond au taux maximal de livraison au lieu central, est donnée par une droite partant du temps de transit sur l'abscisse (α et β) et tangente à la courbe de chargement. Le taux de livraison maximal (pente de la tangente) décroît avec un accroissement du temps de transit (comparer la pente de la droite α à β). La taille de la charge optimale croît avec un accroissement du temps de transit (comparer le point de tangence à la courbe pour les tangentes α à β.

T. striatus est un écureuil de forêt commun et diurne, occupant une bonne partie du nord-est de l'Amérique du nord. Les individus des deux sexes sont solitaires, sédentaires et logent dans des terriers. Il se nourrit principalement de samares, de glands et de faînes d'espèces d'arbres variées et transporte ceux-ci dans ses bajoues extensibles pour les engranger dans des chambres spéciales du terrier en perspective d'utilisation ultérieure. Le tamia passe le printemps, l'été et particulièrement l'automne à chercher et à engranger de la nourriture pour les mois d'hibernation (ELLIOTT 1978). Son approvisionnement correspond également aux présuppositions du modèle d'AC, notamment il présente une courbe de chargement décroissante; le ralentissement de la courbe de chargement du tamia rayé étant fort probablement dû à un accroissement du temps de manipulation au fur et à mesure que les bajoues se remplissent (GIRALDEAU *et al.* 1994; MCALEER & GIRALDEAU 2006).

Le tamia rayé a été le sujet de nombreux tests du modèle AC (KRAMER 2001, MCALEER & GIRALDEAU 2006). Ces études ont toutes trouvé que la charge transportée et le temps de parcelle correspondant augmentent avec un accroissement du temps de transit, tel qu'attendu qualitativement par le modèle. Cependant aucune de ces études n'est en mesure de fournir un appui quantitatif, la taille des charges étant systématiquement en deçà de celle prédite par le modèle. L'appui qualitatif conséquent nous laisse supposer que les dérives quantitatives pourraient être liées plus à la difficulté de fonder des prédictions quantitatives crédibles qu'à un problème plus fondamental du modèle lui-même. En effet, les prédictions quantitatives des études antérieures se fondent généralement sur une estimation de la courbe de chargement qui est faite à partir d'observations de tailles cumulées de charges et de temps de parcelle correspondants. Cette pratique donne lieu à deux problèmes : le premier lié à la difficulté à estimer des courbes de collecte crédibles et le second lié à la crédibilité des prédictions lorsque celles-ci correspondent à des valeurs extrapolées à partir de courbes estimées par de méthodes statistiques.

Difficulté à estimer les courbes

Nous savons pour les modèles d'AC que les prédictions quantitatives sont hautement sensibles aux moindres changements de la courbe de chargement (GIRALDEAU & KRAMER 1982). Il s'ensuit que tout facteur pouvant mener à accentuer la variation de ces observations affectera aussi la fiabilité des estimations statistiques de la fonction de la courbe de chargement. De ce fait, la variation inter-individuelle importante rapportée pour les courbes de chargement de tamia, ajoutée à la variation observée selon la distance au terrier, la présence de compétiteurs et le nombre de fois qu'un individu retourne à une parcelle contribuent ensemble à miner sérieusement la crédibilité de prédictions quantitatives faites à partir de courbes estimées (GIRALDEAU *et al.* 1994).

GIRALDEAU *et al.* (1994) ont tenté de palier à ces problèmes en estimant les courbes de collecte pour chaque individu, à chaque distance du terrier en présence et en absence de compétiteurs. Malgré cette tentative de contrôler une part de la variabilité des observations utilisées pour estimer les courbes de collecte, ils ont néanmoins rapporté que les tamias auraient fait mieux en prélevant de plus grandes charges.

Prédictions extrapolées

De tous les cas où des prédictions du modèle de parcelle ont été testées, le cas du tamia semble unique. En effet il semble être le seul animal pour lequel les études montrent qu'il quitte la parcelle trop tôt avec moins de nourriture que les quantités prédites (MCALEER & GIRALDEAU, 2006). Cela veut dire que les charges prédites pour les tamias sont généralement au-delà de celles observées de sorte que les prédictions se retrouvent sur des portions de la courbe de chargement extrapolées au delà des observations. Il est toujours possible que la courbe de chargement fléchisse plus rapidement au-delà des observations que ne le suppose la courbe estimée avec les données (GIRALDEAU *et al.* 1994). Cela laisse la possibilité qu'il y ait un problème dans la manière dont le modèle est testé avec *T. striatus*.

Une nouvelle approche pour les courbes de chargement

Nous croyons que la disparité entre les tailles de charges observées et prédites chez *T. striatus* pourrait être due à l'usage de courbes de chargement peu fiables estimées à partir d'observations passablement variables et d'extrapolations au-delà des observations de routine. Un test plus crédible du modèle d'AC requiert donc un accroissement de notre confiance dans la forme précise de la courbe de chargement. En offrant lui-même des proies à ses étourneaux (*Sturnus vulgaris*) selon des intervalles croissants prédéterminés, KACELNIK (1984) a pu résoudre tous les problèmes liés à l'estimation des courbes de collecte. Cette approche, en augmentant la confiance dans les paramètres précis de la courbe de collecte, augmente la crédibilité des valeurs optimales prédites à partir de cette courbe. Nous proposons donc dans la présente étude d'adopter la méthode proposée par KACELNIK (1984) en utilisant une courbe de collecte expérimentalement contrôlée pour laquelle nous connaissons tous les détails avec certitude nous permettant ainsi de générer des prédictions quantitatives plus certaines.

DOES *TAMIAS STRIATUS*' SUB-OPTIMAL FORAGING RESULT FROM EXPERIMENTERS' ERRONEOUS ESTIMATIONS OF LOADING FUNCTIONS?

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1.1 ABSTRACT

The rate-maximizing central place foraging model (CPF) predicts that load sizes should increase with increasing distance between patch and central place. Tests of this model with eastern chipmunks (*Tamias striatus*) carrying loads of seeds to its burrow have provided consistently ambiguous results: qualitative support coupled with quantitative rejection. Quantitative rejection of the model has been hampered by the lack of confidence in quantitative predictions often extrapolated beyond the data used to obtain statistical estimates of loading curves. In this study we increase our confidence in quantitative predictions by providing subjects in the field with single kernels of shelled peanuts presented successively according to a pre-determined schedule of increasing intervals resulting in a single loading function for all subjects in all conditions. We tested the CPF model by presenting chipmunks with these artificial patches at 2m and 15m from their burrow. Results confirm qualitative support for the model as the load sizes increased with distance to the burrow. However, the observed load sizes remained consistently below those predicted on the basis of the experimental loading curve. Our results, therefore, provide a convincing rejection of the model in its current form. We propose that the omission of predation hazard while collecting seeds from a patch is the most likely explanation for the model's shortfall.

Key words: central place foraging, Tamias striatus, quantitative test, foraging costs, predation costs.

1.2 INTRODUCTION

Patch exploitation models of foraging theory have been the subject of a large number of experimental tests (reviewed in STEPHENS & KREBS 1986; NONACS 2001). One version of the patch exploitation model in particular, the central place foraging (CPF) model (ORIANS & PEARSON 1979) that applies to situations where prey are carried back to a central place rather than eaten upon discovery, has been repeatedly tested with eastern chipmunks (*Tamias striatus*; reviewed by KRAMER 2001; MCALEER & GIRALDEAU 2006). The model predicts that load sizes carried back to the central place should increase with travel time and hence distance between patch and the central place. The precise nature of this increase depends on the details of the loading function, the function that depicts the cumulative increase in load size with time spent in the patch collecting items. Most tests of the CPF model with chipmunks produce ambiguous results: qualitative support coupled with quantitative failure (see STEPHENS & KREBS 1986; KRAMER 2001). Most find a positive relation between load sizes and travel times but many report a quantitative discrepancy between observed and predicted load sizes and patch times; observations are generally smaller than predictions (NONACS 2001). This ambiguous result can be due either to the model being wrong or to something problematical in the way it is tested. Given the consistent qualitative support for the model it is likely that the problem is due to the difficulty of testing the model quantitatively.

The Eastern chipmunk is a small diurnal ground dwelling sciurid that collects loads of seeds in its extensible cheek pouches and carries them back to its underground burrow to be used later, often during winter hibernation (ELLIOTT 1978). It meets the main assumption of the CPF model; the chipmunk shows a decelerating loading function that could be due to increased handling times required to load successive items as the cheek pouches fill (GIRALDEAU *et al.* 1994). The predicted optimal load sizes are calculated from statistically estimated loading functions fitted through observations of loading behavior in the field. The confidence in these estimated functions can be questioned for a number of reasons. The chipmunk is notoriously variable in its observed loading behavior which has been reported not only to vary among individuals but to be affected by the distance to the burrow, the presence of competitors and the number of return trips to the patch (GIRALDEAU *et al.* 1994). This variability in observed loading behavior likely affects the shape of curvilinear functions fitted through the data. Moreover, we know that small changes in the shape of this function yield large changes in predicted optimal load size (GIRALDEAU & KRAMER 1982). This variability reduces the confidence that can be placed on the quantitative predictions calculated from those statistically estimated functions.

A second problem arises in the case of chipmunks because observed load sizes and patch times are consistently smaller than the predicted optimal load sizes (KRAMER 2001). This means that the load sizes predicted lie on a portion of the statistically estimated loading function that is extrapolated beyond the usually observed load sizes. The model predicts that chipmunks would have done better by collecting larger loads, on the assumption that larger loads would have corresponded to loading behavior extrapolated beyond the observed behavior. Rejection of a model based on such predictions depends on the confidence we place on the extrapolated values. It is always possible, some may say plausible, that simple monotonic functions may not account for the loading behavior beyond the usual range of observed behavior.

A credible quantitative test of the CPF model requires increased confidence in the precise shape of the loading function used to generate the predictions. By offering prey to starlings (*Sturnus vulgaris*) according to a predetermined schedule in all situations and with all individuals, KACELNIK (1984) and VASQUEZ & KACELNIK (2000) resolved the confidence problem with this species known to take larger loads than predicted by gross maximization of energy. The approach of providing animals with experimentally pre-set curvilinear loading functions gives increased confidence in the predicted optimal values because the experimenter controls the shape of the function over the entire spectrum of load sizes observed to be collected. Therefore, in this study we use an experimentally generated loading function to generate quantitative predictions of load sizes; a method that should provide better fit to observations if the systematically smaller load sizes observed in preceding studies are in fact due to erroneous estimations of loading functions.

1.3 METHODS

1.3.1 Species and study site

The Eastern chipmunk is a common, solitary, diurnal forest-dwelling sciurid that nests in underground burrows and whose range covers most of eastern North America. We observed chipmunks from May to October 2004 and 2005 at a time during which they hoarded seeds to their burrow using their extensible cheeks pouches (ELLIOTT 1978). This study was conducted in a 5.2 ha section of a beech, sugar maple and red oak community at McGill University's Gault Natural Reserve on Mont St-Hilaire, Québec, 35 km southeast of Montréal. Chipmunks were live-trapped in May of both years weighted, sexed and ear-tagged. We shaved small unique patterns in the guard hairs of their back for recognition at a distance. Actual data for the main experiment were collected in August 2004 and June 2005. The burrows were localized by observing a hoarding chipmunk's movements from burrow to food patch.

1.3.2 Generating an experimental loading function (pre-test)

The schedule of increasing intervals used to produce the experimental loading function for the main experiment was based on an exponentially declining function fitted through observations of loading behavior in a pre-test. The same type of peanut kernels were used in the pre-test and the main experiment. We presented chipmunks with food patches (plastic containers of 30 cm x 45 cm x 5 cm) loaded with a sufficient density of peanut kernels without shells (19±1 mm x 10±1 mm) to eliminate nearly all search time within the patch. Once a chipmunk started making round-trips from the patch to its burrow, the observer (S.B.) noted when the animal was in the patch and the loading time (Lt) of each kernel calling out the event into a tape recorder. A total of 122 loading episodes were observed for nine unidentified chipmunks. The average observed load size was 7.8 ± 1,7 kernels (ranging from 4 to 12) and the mean time spent in the patch between arrival and departure was 11,2 ± 3,6s (ranging from 1,9 to 20,7).

The exponential decay function fitted through loading times of consecutively loaded peanut kernels was estimated from least squares regression using GraphPad Prism 3.0 (GraphPad software, Inc. San Diego, USA), and provided a good fit to the data (r^2=0.91; Fig. 3) considering the spread of the data cloud. If the experimenter is to maintain control over the animal's loading speed, the experimental loading function must be slower than the chipmunk's normal loading rate. We therefore modified the parameters of the estimated exponential decay function to produce a function that was slower than the observed loading episodes (Fig. 3).

Figure 3

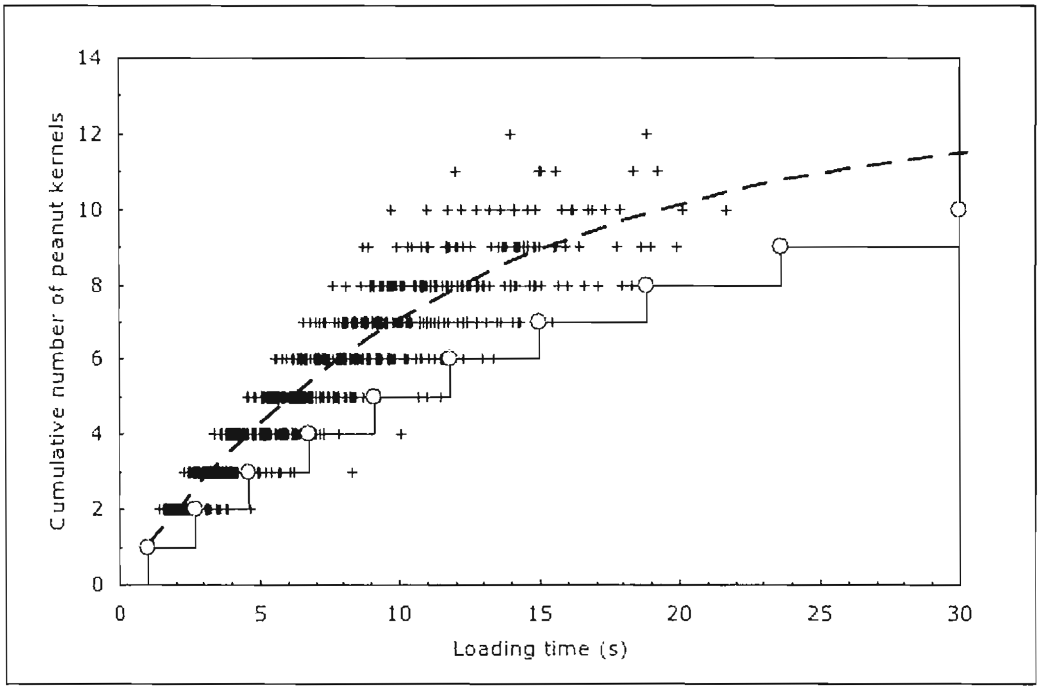

Figure 3. Observed loading times (crosses) of each unshelled peanut kernel and the exponentially decaying function (dashed line) that provided the best fit through the data (**kernel** = **-12.49**$*$**e**$^{(-0.082*Lt)}$**+12.51**). The discrete step function gives the schedule of increasing intervals (open circles) used to generate the experimental loading function for the main experiment. This function is same as the one described above but using **-0.052Pt** as the exponent. Doing this flattens the function so that it lies mostly under the observed handling times without changing the intercept nor the asymptote (which is 12,51).

We used this slow version of the estimated curve to generate exponentially increasing kernel delivery intervals during the main experimental trials.

1.3.3 Experimental procedure

The unshelled kernels were delivered to the chipmunks through a black 2 cm diameter, 150 cm long PVC pipe placed at a 30° angle from the forest floor following the exponentially increasing interval schedule described above. Four wooden sticks supported the pipe (two at each extremity) and the seeds fell into a plastic container. To ensure the chipmunk's familiarity with the interval schedule, the delivery of the next food item was postponed if the animal left the experimental patch to search elsewhere. Animals quickly learned about the rules and restricted their searching to the experimental patch. Actual data collection began on the 11th consecutive round-trip to the patch.

The location of patches was chosen randomly at a radius of 2 m and 15 m from the burrow with the restriction of being at least 2 m away from trails to prevent disturbances from walkers. All patches were located in a homogenous forest habitat with nearly 100% cover from canopy trees. Experimental distances of 2 m and 15 m were chosen because they lie in the spectrum of distances used in preceding studies and for practical reasons given that burrows and patches had to be surveyed by the same experimenter in 2004.

As the chipmunk loaded kernels at the patch the observer either called out observations into a tape-recorder (2004), or recorded them directly into a Psion Workabout (Noldus Information Technology b.v. Wageningen, The Netherlands) running The Observer Mobile 4.1 (Noldus Information Technology b.v. Wageningen, The Netherlands) with a precision of 0.1s (2005). In 2004 the following was noted: arrival at the patch, departure from the patch and the number of kernels loaded at each visit. In 2005, time of burrow entry and departure as well as the time at which each kernel was actually loaded was also noted. Data were transcribed from the vocal record to a computer running The Observer 5.0 (Noldus Information Technology b.v. Wageningen, The Netherlands) or downloaded directly from the Psion.

1.3.4 Experimental design

Data for each individual was collected at 2m and 15m from their burrow. A total of 18 round-trips between patch and burrow while collecting seeds were obtained with six individuals at both distance in 2004. 10 round-trips were obtained in 2005 with nine chipmunks (different from those observed in 2004) at both distances.

For each individual, trials at the two distances were conducted the same day. The order in which the two distances were tested for each individual was determined randomly by the flip of a coin. Visits where a seed was not loaded immediately as it rolled onto the patch were excluded from the analysis. This happened in ~10% of the loading episodes, usually in response to some disturbance. More rarely (~2%), once again because of a disturbance, visits where the chipmunk left the patch between the loading of successive seeds were also excluded. To minimize interference from neighboring chipmunks, seeds were placed next to the burrow entrances of neighbors and some neighbors had to be trapped for the duration of the experiment.

1.3.5 Statistical analysis and predicted load sizes

All data analyses were conducted using JMPin 4.0.2 (SAS institute Inc. Cary, USA). The effect of distance and year of study on load size were analyzed with a restricted maximum likelihood (REML) linear mixed model (LMM) with individual identity fitted a random effect. The residuals were normally distributed.

The means of the number of kernels loaded, calculated from each individual's replicates at each distance, were compared using a *t*-test to the predictions of the CPF model based on the experimental loading curve. The travel time that was used to predict load size for a given distance using the tangent method was the mean of each individual's minimum travel times for each distance.

1.4 RESULTS

1.4.1 Effects on load size

There was no significant year*distance interaction ($F_{1,12}$=2.04; p=0.1786), and so data from both years were pooled and analyzed with a REML without the interaction term. The year significantly affected load size ($F_{1,13}$=18.97; p=0.0008); the loads were smaller in 2005. Distance had a significant effect on load size; the load sizes at 15m were larger than those at 2m ($F_{1,13}$=10.26: p=0.0069) (Fig. 4).

1.4.2 Comparing observations with predictions

Predicted load sizes were considerably larger than observed load sizes for both distances (t test: df=14; p<0.0001; Fig. 5).

Figure 4

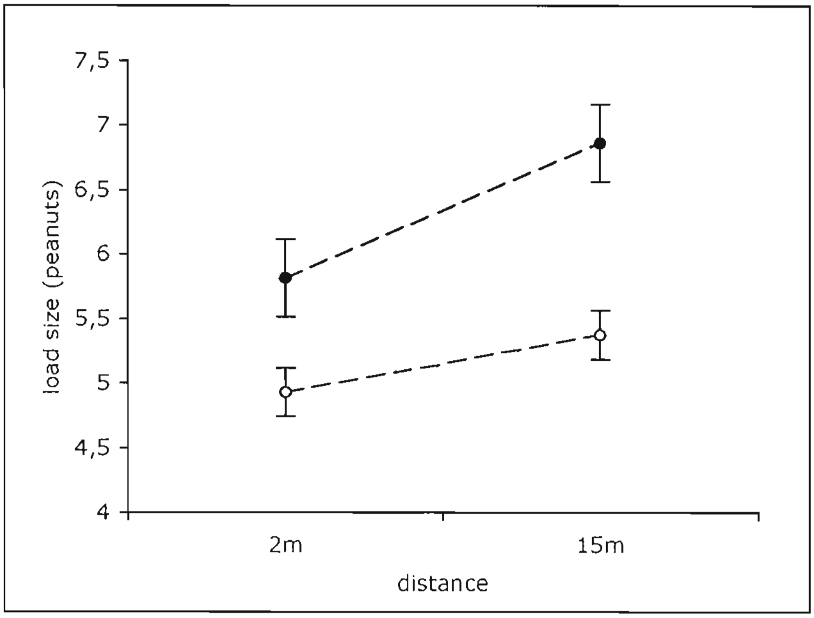

Figure 4. Number of peanut kernels loaded by chipmunks as a function of distance to burrow and year of study. Load sizes were lower in 2005 (open circles) than in 2004 (filled circles). Pooled load sizes of both years were also higher in the 15 m treatment than in the 2 m treatment (N=15).

Figure 5

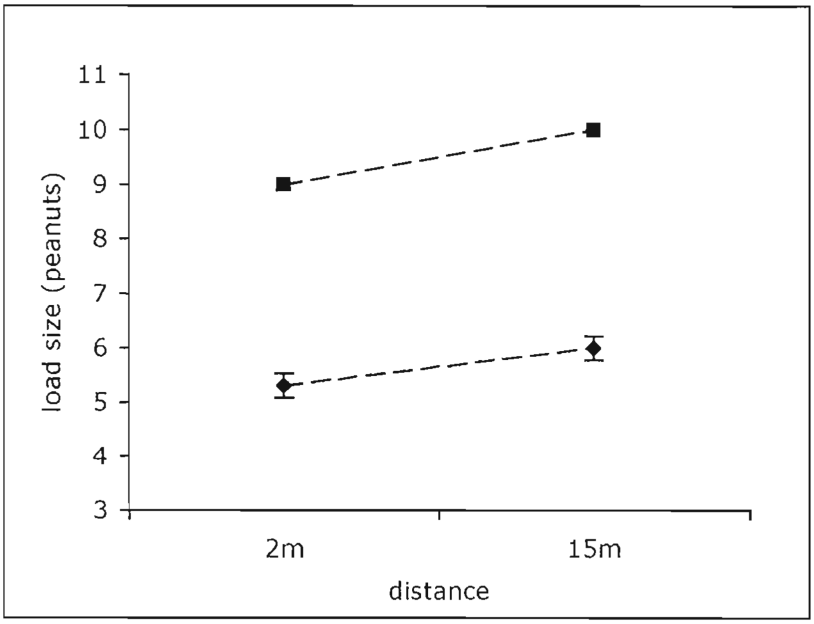

Figure 5. Predicted (squares) and observed (diamonds) load sizes of chipmunks collecting peanut kernels at two distances from their burrow (N=15).

1.5 DISCUSSION

The positive relation of load size and patch time with distance from patch to burrow we observed confirms the many previous reports (reviewed in KRAMER 2001) of this effect of distance. It suggests that chipmunks responded to our artificial food patch in a way that was consistent with more conventional experimental food patches. However, our results also confirm that the quantitative failures of the rate maximizing CPF model with the chipmunk cannot be attributed simply to erroneous extrapolations from imprecisely estimated loading functions. Here we argue that our use of an experimentally generated loading function was appropriate, suggesting a rejection of the rate of food delivery as an appropriate currency of fitness for chipmunk seed hoarding. We also propose modifications that should deal effectively with the CPF model's consistent shortcomings.

The effect of distance was consistent in both years and no interaction was found between distance and year. It is noteworthy, however, that the absolute sizes of loads transported to burrows varied significantly between years. Because the data from both years were collected at different seasons (August 2004 and June 2005) it is difficult to ascertain whether the change in load size over years was due to a season effect or a difference between years. Chipmunk are known to breed at the end of winter (February and March) give birth in early summer and prepare for summer mating (June and July) while simply hoarding seeds in the late summer and fall (ELLIOTT 1978). Assuming that investment in reproductive behavior might hinder maximization of energy gain while foraging, differences in breeding state over the seasons may explain the between year effect observed. Chipmunks are also known to hoard many more seeds daily than required to meet their demands (KRAMER 2001), meaning that they should not be in energetic stress, a factor that is known to increase acceptable risk to foraging animals (KREBS 1980; ROMEY 1995). However, another type of stress may exist in relation to the size of the cumulated hoard before winter hibernation. HOUSTON *et al.* (1993) showed, in the case of potential premature termination of foragin activity by the onset of winter, that the level of foraging should be higher than the level predicted by minimizing the "predation hazard: energy gain" ratio. Given that this stress most probably increases as winter approaches, it is conceivable that chipmunks invest relatively less in predation avoidance later in the season. Therefore, an alternate seasonal explanation could be related to differences in motivation of foraging chipmunks. Although predation is also known to vary between years we have no data to address yearly variation in predation. Nonetheless, the fact that load size changed in response to factors other than those expected strictly from the hypothetical fitness currency suggests that the currency does not capture all the features associated with the evolution of the load size decisions of chipmunks.

It may be argued that the chipmunks did not have the time necessary to learn the exponentially increasing reward function we used. We feel this is unlikely for a number of reasons. First, chipmunks quickly learned to restrict their foraging exclusively to the experimental patch, and waited there during the interval between each individual kernel. Furthermore, closer analysis of the consecutive round-trip replicates after the ten familiarizing round-trips showed no sign of change over time indicating that the behavior of the chipmunk seemed already stable relative to the experimental procedure. Besides, the chipmunk's decision to leave a patch did not appear to depend on the time expected to the next kernel. In a considerable proportion of visits to the patch, when a chipmunk's handling of a kernel was prolonged such that another kernel was delivered while the chipmunk was still at the patch handling the previous item, it never loaded this extra item before leaving. Patch departure, therefore, seems to depend on the interval to the last loaded seed rather than the expected interval to the next seed and so it may not be necessary for the chipmunk to learn the expected intervals.

Unshelled kernels were chosen as food items on the basis of their ideal size for the experimental procedure we used. The smaller sized sunflower seeds that are normally used with chipmunks are loaded so quickly, that a human experimenter could not distribute them at a similar pace with the required level of precision. On the other hand, larger seeds like acorns allow only a few seeds (two to three) to be loaded simultaneously, considerably reducing the information that can be obtained from this three step loading function. The load sizes we observed (5,3±0,20 and 6,0±0,25 kernels for 2 m and 15 m respectively) were not constrained by the animal's cheek pouch volumes because during the trials used to generate the loading function chipmunks could collect larger loads (mean 7,8 ± 1,68 peanut kernels) some individuals collecting up to 12 kernels. It may be objected that peanut kernels are perishable items, unlike most items usually used in chipmunk hoarding experiments. However, chipmunks also hoard perishable items in their burrows such as plant bulbs and mushrooms (ELLIOTT 1978). Since we are strictly interested in the hoarding behavior and not the management of food reserves, we are confident that the use of unshelled kernels was appropriate.

The mean of each individual's minimum travel times for each distance was used to predict load size for a given distance using the tangent method because minimum travel times are less influenced by disturbances that are not relevant to the animal's actual foraging rate (KRAMER & NOWELL 1980). In any case, using mean travel times would increased the disparities between observations and predictions, making the use of the mean of each individual's minimum travel times the most conservative.

Other studies reported disparities between observations and predictions of the CPF model and in some of these cases, qualitative modifications to the model have provided a better fit between predictions and observations. For example, longer than optimal patch times and larger than optimal load sizes have been observed in the great tit (*Parus major*) (Cowie 1977) and the house martin (*Delichon urbica*) (Bryant & Turner 1982). This disparity between predictions and observations can be explained by the existence of a higher foraging cost during transit time, which involves active flight, than during actual foraging at the patch where flight is not involved (Kacelnik & Houston 1984). This difference was confirmed by Nudds & Bryant (2000) who showed that flight was indeed metabolically more expensive than foraging at the patch; short flights requiring up to 28 times the basal metabolic rate for zebra finches (*Taeniopygia guttata*). This type of explanation involving higher travel costs, however, cannot account for the smaller than expected load sizes we observed with the chipmunk. To reconcile observations and predictions in chipmunks one needs to argue for a higher cost during foraging at the patch rather than during transit between burrow and patch (Kacelnik & Houston 1984).

Energetic factors that could make loading in the patch relatively more costly than traveling may be invoked. For example, Schmidt-Hempel *et al.* (1985) showed that including the metabolic costs of transport of nectar by honeybees (*Apis mellifera*) between flowers in a patch (patch cost) leads to models that predicts partial crop-loading which is the observed foraging behavior. However, loading and running expenditure in the chipmunk (0.020 and 0.035 kcal/min, respectively) do not differ much and are negligible relative to the energetic gain of a medium load (~12 kcal/3g of sunflower seeds). Therefore, the net rate of food delivery to the burrow (rate of food delivery – energetic expenditures) will not differ much from the gross rate of food delivery (Kramer 2001). This leads us to think that the currency of fitness used up to now, gross rate of food delivery to the burrow, may ignore an important non-energetic cost that is spread irregularly across the foraging activities of the chipmunk (Giraldeau & Kramer 1982; Giraldeau *et al.* 1994).

An important component of fitness in most species is predator avoidance. There is good reason to believe this is also the case for chipmunks. In fact, Bowers & Ellis (1993) showed that chipmunks appeared to employ a patch exploitation strategy that minimized the "predation hazard: energy gain" ratio. When predation hazards are important, which seems to be the case in nearly all behavioral field studies (Lima & Dill 1990), it implies that foraging decisions must involve a tradeoff between anti-predation behaviors and maximization of energy gain (Bowers 1990; Lima & Dill 1990).

Predation hazards would be a good candidate explanation for the consistent disparity between predicted and observed values in chipmunk CPF if its intensity was demonstrably greater at the patch than while traveling between patch and burrow. We feel such a difference is likely. During patch time, the animal's behavior is devoted to searching for seeds and loading and so its attention is often directed towards the ground, a situation that could very well interfere with its efficiency of predator detection and hence lead to higher predation hazard while at the patch (LIMA & DILL 1990). In addition, *T.striatus* shows intermittent locomotion while traveling between burrow and patch (MCADAM & KRAMER 1998), meaning that chipmunks pause regularly while traveling. Theses pause locations are under the chipmunk's control, and seem often to correspond to strategic locations such as on a log or a rock, which provide good vantage points for predator detection, and may provide potentially rapid refuges given a predation event (personal observations). On the other hand, patch location is out of the chipmunk's control, potentially making it a less strategic location for a rapid escape. Hence we believe perceived predation hazard to be higher at the patch. This interpretation could be consistent with the pattern of premature termination of loading or with differential yearly predation hazards. The lower mean load sizes observed in the spring of 2005 compared to those observed in the late summer of 2004 could result from a change in predation avoidance only if the hazard was higher in the patch. Otherwise, if the hazards were equal regardless of the position, maximization of energy gain would always be the best behavior since it minimizes the time spent exposed to predation (outside the burrow).

A way to test the hypothesis of greater predation danger at the patch would be to modify the chipmunk's perceived predation hazard experimentally and see how the load sizes change; lower apparent predation hazard in the patch should produce observations closer to rate maximizing predictions and vice versa. Similar results have been obtained with multimammate mice (*Mastomys natalensis*) by providing a cover over a patch (MOHR *et al.* 2003). If predation turns out to be responsible for the discrepancy between predictions and observations, then it will be important to consider modification of the currency of fitness to take this into account. However, predation hazards and rate of food delivery to the burrow are difficult to convert into a single common currency. One way around this problem would be to use numerical models of dynamic optimization in order to predict the load sizes while taking both predation hazard and rate of food delivery into account (MCNAMARA & HOUSTON 1986).

Repeated quantitative failures of earlier tests of the CPF model with chipmunks were weakened by uncertainty in the estimated shape of the loading function. In particular, given that chipmunks leave patches before they collect an optimal load, it follows that the predicted optimal values are almost always beyond most of the observations used to estimate the loading functions. By using experimentally generated loading functions our study increases the confidence we have that the disparity between observed and predicted load sizes imply a real shortcoming of the currency of fitness that is commonly used with chipmunks. We suggest that a currency that allows for a higher cost during patch time compared to travel time could explain this behavior, and we predict that predation hazard is the most likely candidate for this cost. We are confident that future experimental work will show that reduction of predation hazards at the patch could eventually produce a quantitative fit to the rate maximizing CPF model in chipmunks.

1.6 APPENDIX I

MEAN VALUES OF LOAD SIZE OBSERVED AND OPTIMAL VALUES PREDICTED FROM THE CPF MODEL USING MINIMUM TRANSIT TIME OBSERVED CORRESPONDING TO THE TWO TREATMENTS.

Overall mean values observed are shown in units ± standard error.

	Minimum transit time (s)		Mean load size (peanuts)		Predicted load size (peanuts)	
Ind.	2 m	15 m	2 m	15 m	2 m	15 m
1	12	47	5,1	7,6	9	10
2	28	63	7	7,9		
3	27	71	5,6	6,9		
4	19	35	6,3	6,7		
5	23	66	5,3	6,2		
6	32	59	5,6	5,9		
7	27,4	76,7	5,1	4,5		
8	13,1	92,3	4,4	5,8		
9	50,1	77,5	5,5	5		
10	35,4	67	4,7	5,2		
11	16,8	49,3	4,7	5,4		
12	33,8	64,9	3,7	5,4		
13	17,2	62,8	5,3	6,1		
14	25,2	40,5	5,2	5		
15	26	57,6	5,8	6		
mean (n=15)	25,7 ±2.5	62,0 3.9	5,3 ±0,2	6,0 ±0,2		

CONCLUSION

Les échecs répétés des tests quantitatifs du modèle d'AC sont associés à une incertitude considérable relativement à la forme réelle de la courbe de chargement aux alentours des valeurs optimales, car les tamias arrêtent de prélever des graines avant d'atteindre ces valeurs. Notre étude augmente la confiance pouvant être investi dans la courbe de chargement utilisée pour générer les tailles de charges optimales issues du modèle actuel, car nous avons utilisé une méthode permettant de faire des prédictions plus fiables. Ainsi, la différence souvent raportée entre les tailles de charges observées et prédites semble confirmée.

Pour produire le patron observé avec les tamias, soit des charges plus petites que prédites, un coût plus élevé durant l'approvisionnement à la parcelle est requis (KACELNIK & HOUSTON 1984). Ceci porte à croire que la devise de conversion utilisée jusqu'ici pourrait être incomplète dans le sens qu'elle ne prend pas en compte certains coûts répartis irrégulièrement au travers des activités d'approvisionnement du tamia rayé (GIRALDEAU & KRAMER 1982; GIRALDEAU *et al.* 1994).
Le risque de prédation semble être un coût potentiel intéressant, car ce risque est reconnu comme déterminant dans la majorité des études comportementales de terrain (LIMA & DILL 1990), et les décisions en approvisionnement impliquent souvent un compromis entre les comportements anti-prédation et la maximisation des gains énergétiques (BOWERS 1990; LIMA & DILL 1990). En fait, BOWERS & ELLIS (1993) ont identifié le risque de prédation comme un coût réel à l'approvisionnement du tamia. De plus, durant le temps de parcelle, l'attention de l'animal étant partiellement vouée à l'approvisionnement, la capacité de détection de prédateur est réduite, ce qui mène à un risque de prédation plus grand durant l'approvisionnement à la parcelle (LIMA & DILL 1990).

Nous sommes donc confiant que l'inclusion de coûts appropriés à l'approvisionnement à la parcelle dans le modèle d'AC générera des prédictions quantitatives en accord avec les observations. Pareillement, une manipulation du risque de prédation apparent pour le tamia devrait modifier les tailles de charges observées; une réduction du risque apparent provoquant des tailles de charges plus importantes et donc plus proches des prédictions initiales du modèle d'AC.

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