

Methodological problems with estimating patch depression during resource depletion

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The Marginal Value Theorem (Charnov 1976) is a widely used paradigm for determining optimal exploitation under conditions of diminishing returns. One requirement for applying this model is estimation of the gain function, which is the cumulative gain as exploitation proceeds. The function is commonly derived from experiments in which one or a number of animals is allowed to deplete food patches either for set durations, set numbers of bites, or until they choose to stop. The cumulative food intake and time taken are then collated from a number of such trials, and some mathematical function is fitted to describe patch depression, which is the term used for an inverse relationship between instantaneous intake rate and elapsed time in the patch. For example, such a procedure was followed by Åström et al. (1990), who analysed intake in relation to exploitation time by moose foraging in an arena of trees varying in size. They derived a function that implicitly assumes patch depletion and depression while foraging, and reported the occurrence of patch depression. Similar or more controlled approaches have been taken with cattle (Laca et al. 1994, Ginnet et al. 1999). Two problems with such an approach are apparent: the unintentional effect of pauses by the animal and averaging across animal-patch combinations.

Animals occasionally pause momentarily during foraging, perhaps because they are disturbed or because they habitually scan for predators whilst foraging. If pauses are randomly distributed during feeding, then the number of pauses will increase with time and will be Poisson-distributed. Depending on how pause length is distributed, the accumulated increase in patch residence time due to pauses will have some form of skewed distribution. Gathering together data on food intake and residence time from a number of trials would

therefore inevitably produce a decelerating cumulative gain function, due to accumulation of pauses rather than resource depression. These points are illustrated by results from simulation, which were implemented using Genstat 5.4.1 (Genstat 5 Committee, 1993).

To clarify the effect of pauses, a linear gain function was simulated, with each prey item having a constant search plus handling time (1 s). Pauses after consuming a prey item were assumed to occur at random with probability $p = 0.05$, and to last for a mean time of 5 s, normally distributed with $sd = 1$, and truncated at zero. The less realistic assumption of pauses lasting a constant 5 s made no difference to the results. Three rules for patch departure were compared, according to the number of food items consumed. These were simulated as either (a) a uniform random deviate between 0 and 100; (b) a normal random deviate with mean = 50 items, $sd = 10$; (c) after exactly 50 items had been taken (Fig. 1a, b and c, respectively). These rules were intended to simulate cases where animals terminate feeding (a) for a variety of unknown reasons; (b) after removing a roughly constant amount of food from each patch; (c) after removing a constant amount. Note that each case has the same expected value. Simulations were repeated for 100 trials, and the accumulated intake and elapsed time (i.e. foraging plus pauses) from each were analysed by non-linear fitting of function 2 of Åström et al. (1990). This gives food eaten in time T as: $E(T) = s\{1 - 1/[1 + (kT/s)]\}$, where s is asymptotic food intake and k is a parameter. Curvilinearity is slight with $0 < k/s < 0.005$ and marked when $k/s > 0.01$.

With random patch departure, data generated were rather similar to those presented by Åström et al. (1990), and parameters of the gain function were $k/s = 0.002$ in the example shown (Fig. 1a). Departure from

the underlying linear foraging rate is evident. It is more marked when patch departure takes place after a mean of 50 items consumed, when $k/s = 0.009$ in the example shown (Fig. 1b). The extreme case of patch departure is shown in Fig. 1c. The curve could not be fitted ($k/s \rightarrow \infty$). It is included mainly to display clearly the skewed distribution of elapsed times. Mean elapsed time was 62 s, with variance 58 s (estimated from 10 replicates). It is this skewness in the independent variable that causes the gain function to bend: data generated with regular pauses instead of random ones resulted in linear gain functions ($k/s < 0.00006$) for patch departure rules (a) and (b). Data from a simulated group of animals, each pausing regularly but with variation between individuals in the number of bites taken between pauses, showed slightly curvilinear gain functions provided that the individual variation was sufficient (e.g. $k/s = 0.001$ and 0.004 for patch departure rules (a) and (b), respectively, given a mean of 20 bites between pauses, with $sd = 5$). The existence of high pausing rates in some animals in a group is sufficient to skew the distribution of patch residence times, due to the accumulation of time spent pausing.

We investigated the effect of reducing the mean pause duration, using the case where a mean of 50 items are removed before patch departure. CV of pause duration

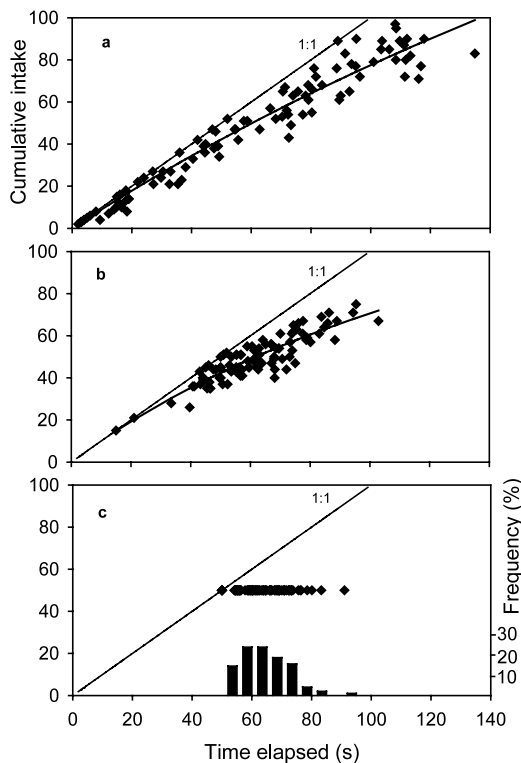


Fig. 1. Gain functions fitted to the endpoints from simulated foraging trials (data points and regression line). A frequency distribution of the elapsed time in patch is shown for the case where exactly 50 items are removed in each trial (c). See text for details.

Table 1. Effect of mean pause duration on curvilinearity of the gain function.

Mean pause duration (s)	mean k/s	Proportion of cases where quadratic term significant at $p < 0.05$
1	0.0001	0.1
2	0.0014	0.5
3	0.0030	1
5	0.0056	1

was maintained at 20%. We tested for departure from linearity of the gain function by assessing the significance of the quadratic regression term. Table 1 shows that, even for cases with mean pause length of 2 s (i.e. twice as long as search plus handling a single item), significant, though slight, curvilinearity was detected in half the simulations run. The phenomenon was not detected with pauses of 1 s mean duration.

It should be noted that the time-course of food intake in each individual trial was essentially linear, being the outcome of an underlying linear pattern of food intake with random pauses inserted. It is when the data from the end-points of many such trials are lumped together for analysis that the opportunity for a curve to best summarise the variation arises. This is a form of multi-collinearity, when a population of straight lines is, erroneously, best summarised by a curve that truly represents neither individual lines nor their functional form. In practice, it is hard to establish depletion curves for an individual feeding on a particular patch, and mean data over a number of animals and patches must be used instead. This must be avoided if random pauses occur during foraging, because curvilinear gain functions can arise even from data generated from trials in which the underlying rate of food intake is constant. Genuine patch depression in the more normal case of patch depletion would tend to be exaggerated by the effect of pauses. Such an effect might be mistaken as a bona fide cause of patch depression, but its origin is distinct from food-related mechanisms and is contingent on the degree of disturbance or other environmental influences such as predation risk.

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