

## Evaluation of Two Models for Predicting Elemental Accumulation by Arthropods<sup>1</sup>

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### ABSTRACT

Two different models have been proposed for predicting elemental accumulation by arthropods. Parameters of both models can be quantified from radioisotope elimination experiments. Our analysis of the 2 models shows that both predict identical elemental accumulation for a whole organism, though differing in the accumulation in body and gut. We quantified both models with experimental data from <sup>134</sup>Cs and <sup>86</sup>Sr elimination by crickets. Computer simulations of radioisotope accumulation were then compared with actual accumulation experiments. Neither model showed exact fit to the experimental data, though both showed the general pattern of elemental accumulation.

Radioisotope tracers have proved to be powerful tools in ecosystem-level research on nutrient cycling. Tracer techniques are one of the few methods available for evaluating the rate parameters essential for describing nutrient dynamics in ecosystems. Radioactive tracer measurements of parameters such as nutrient ingestion, accumulation, and turnover in arthropod food chains have recently been used in several nutrient cycling studies in ecosystem contexts (Gist and Crossley 1975, Webster 1975). These applications of the tracer technique depend on models describing tracer behavior in the organisms under study.

The 1st models used in ecological radiotracer studies were single-component exponential decay equations (Fig. 1), analogous to models of physical radioactive decay (e.g., Davis and Foster 1958, Crossley and Pryor 1960). These models were supplanted by others using 2 or more components. Reichle and Crossley (1965) developed a 2-compartment model for radioisotope elimination by arthropods (Fig. 1). They estimated model parameters from single ingestions of isotopes using procedures analogous to those used for estimating equilibria in radioactive decay series and for separating mixtures of radioisotopes with different decay rates (Chase and Rabinowitz 1962). This model has been widely used in analysis of radioisotope elimination by arthropods (Reichle and Crossley 1965, Reichle 1967, Van Hook and Crossley 1969, Moulder et al. 1970, Van Hook 1971, Crossley et al. 1971, Gist 1972, Webster 1975).

To avoid some of the biologically unrealistic assumptions of the Reichle-Crossley (R-C) model, Goldstein and Elwood (1971) and Kowal (1971) developed a model which uses the same experimental data with a different interpretation (Fig. 1). In the R-C model, assimilation is treated as an instantaneous fraction of ingestion. In the Goldstein-Elwood (G-E) model, assimilation is more realis-

tically treated as an uptake rate. The G-E model has been used in several ecological studies (Elwood and Goldstein 1975, Elwood and Eymann 1976).

The purpose of the research reported here was to compare the Reichle-Crossley and Goldstein-Elwood models for their ability to describe accumulation curves for radioactive tracers. In laboratory experiments, accumulations of 3 different radioisotopes were followed in house crickets (*Acheta domesticus*). Results were compared with predictions from the G-E and R-C models, using as parameters values obtained from single-ingestion retention experiments with the insects.

### Materials and Methods

House crickets (*Acheta domesticus*) obtained as young adults from a commercial supplier were used in radioisotope accumulation and elimination experiments. General rearing procedures followed those recently suggested by Clifford et al. (1976). Food used was a commercial cricket mixture.

Food containing radioisotopes was prepared by mixing 30 g food with 30 g water containing ca. 70  $\mu$ Ci of <sup>51</sup>Cr, <sup>86</sup>Sr, or <sup>134</sup>Cs. Food was dried overnight (40°C), ground with mortar and pestle, and given to crickets in petri dishes. Food consumption was measured gravimetrically.

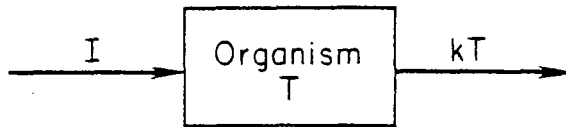
Experimental units consisted of 20 female crickets housed in a 2-gal ice cream carton, supplied with food and water, and maintained at 30°C. Free access to radioactive food was given in accumulation experiments. At ca. 48-h intervals all crickets were removed from the cartons and counted individually for radioactivity with a Packard multichannel analyzer system equipped with a 4-in (10.2 cm) diam crystal containing a 1-in (2.54 cm) well. Following counting, crickets were returned to the carton. All counts were corrected for radioactive decay. For estimates of elimination rates, access to radioactive food was limited to one h, after which nonradioactive food was substituted. Kolehmainen (1972) showed there was no significant difference in elimination of <sup>137</sup>Cs between bluegill fed a single dose and bluegill in

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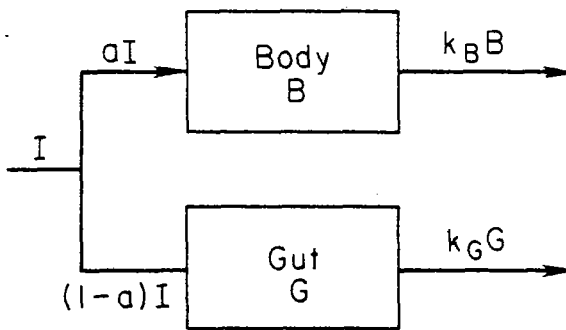
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### Single Component Model



### Reichle - Crossley Model



### Goldstein - Elwood Model

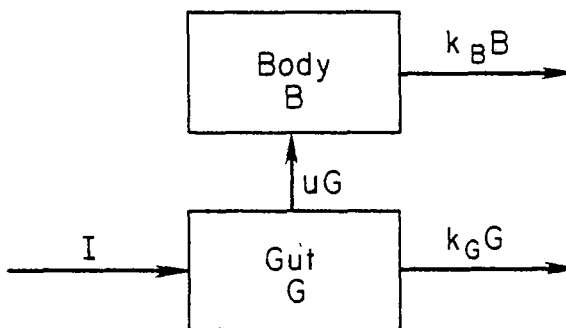


FIG. 1.—Compartment models for 3 conceptualizations of elemental transfer through arthropods. Symbols explained in text. Modified from Goldstein and Elwood (1971).

equilibrium with respect to  $^{137}\text{Cs}$ . More frequent counting intervals were used in turnover experiments.

#### Results

For a single component model of radioisotope dynamics within an individual animal we can use a mass balance relationship to write

$$\frac{dT(t)}{dt} = I(t) - E(t), \quad (1)$$

where  $T(t)$  is the total radioisotope content or body burden,  $I(t)$  is ingestion, and  $E(t)$  is elimination. Assuming elimination is directly proportional to total radioisotope content,  $E(t) = kT$ , where  $k$  is the elimination rate, the solution to the differential equation is

$$T(t) = I_0 e^{-k(t-t_0)}, \quad t \geq t_0. \quad (2)$$

This solution is for an "acute" feeding where it is assumed  $I(t) = I_0 \delta(t)$ , where  $I_0$  is the total amount ingested and  $\delta(t)$  is the impulse function (dirac delta function). For a "chronic" feeding,

$$I(t) = \begin{cases} f(t) & , t < t_0, \text{ feeding period} \\ 0 & , t \geq t_0, \text{ counting period,} \end{cases}$$

the solution for  $t \geq t_0$  is the same as for the acute feeding except the initial value may not be  $I_0$  as some of the ingested material may have already been eliminated. Using a logarithmic transformation of equation 2,  $\ln T(t) = \ln I_0 - kt$ ,  $t_0 = 0$ ,  $k$  can be evaluated from the results of a tagging experiment by least squares regression.

For radioisotopes which are either not assimilated or are rapidly and completely assimilated, radioisotope elimination data fit this model quite well. Chromium is generally not assimilated or very poorly assimilated by insects (Crossley and Van Hook 1970). Elimination of  $^{51}\text{Cr}$  by crickets does conform very well to this single component elimination model (Fig. 2).

The equilibrium body burden accumulated by an organism feeding continuously on food tagged with a nonassimilated radioisotope such as  $^{51}\text{Cr}$  can be predicted with this model. The equilibrium (or steady state) solution to this model is

$$T(ss) = \frac{I}{k}, \quad (3)$$

where  $I$  is the constant rate of feeding. Model prediction of  $^{51}\text{Cr}$  accumulation by crickets based on a measured elimination rate and gravimetric estimation of the feeding rate is compared to experimental data in Fig. 2. Data conform nicely to a single-component retention (elimination) curve, but show considerable scatter around the single-component accumulation model generated from the retention rate. The model gives the general picture but not the vagaries of discontinuous feeding and elimination by individual crickets.

Data from most radioisotope elimination experiments do not fit a straight line, rather a semi-logarithmic plot shows 2 straight line components. Elimination of  $^{134}\text{Cs}$  and  $^{85}\text{Sr}$  by crickets illustrates this point (Fig. 3). The 2 components are usually attributed to a rapid rate of elimination of non-assimilated material and a slower rate of assimilated material elimination.

#### Reichle-Crossley Model

Simulation of 2-component elimination behavior can be achieved by dividing the total organism,  $T$ , into 2 components, body,  $B$ , and gut,  $G$ ,

$$T(t) = B(t) + G(t). \quad (4)$$

The model assumes that a fraction,  $a$ , of ingestion is assimilated instantaneously from the gut and goes directly into the body component. The remainder,  $(1-a)I$ , stays in the gut. Loss of assimilated materials, excretion, is directly proportional to the radioisotope content of the body,

$$Ex(t) = k_B B(t). \quad (5)$$

Similarly, loss of non-assimilated materials, defecation, is proportional to gut content,

$$F(t) = k_G G(t). \quad (6)$$

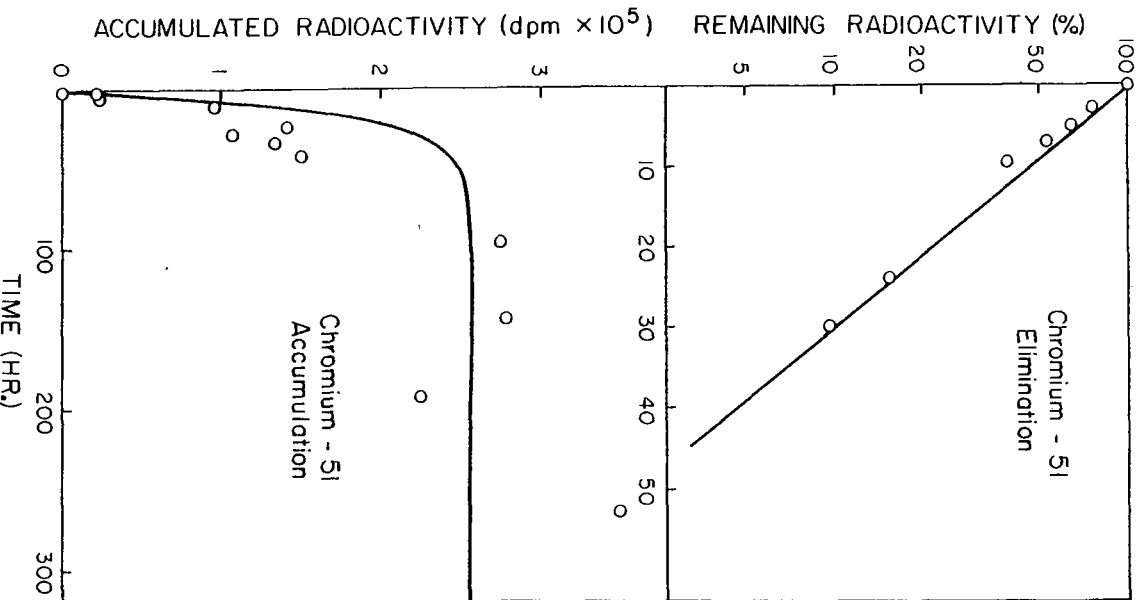


Fig. 2.—Elimination (above) and accumulation (below) of Chromium-51 by crickets (*Acheia domestica*). Each point represents mean radioactivity of several crickets; number varies. Upper line fitted by least-squares regression of log<sub>e</sub> percent radioactivity on time. Lower line generated by single-component model (explained in text).

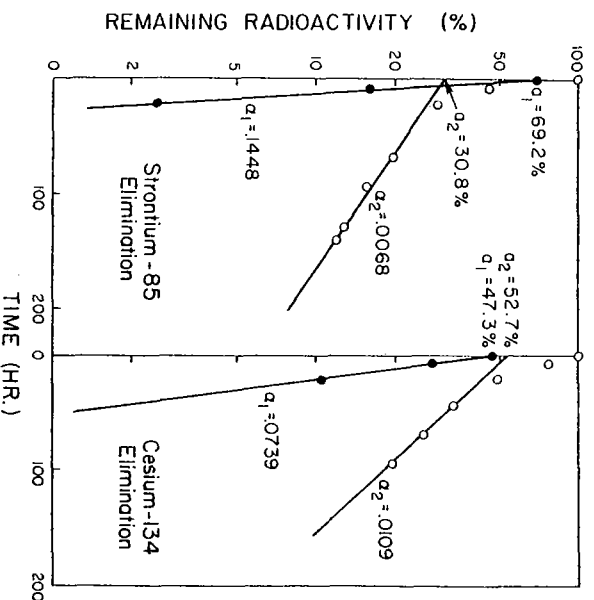


Fig. 3.—Elimination of radioactive tracers by crickets (*Acheia domestica*). Each point represents a mean of several crickets; number varies. Lines fitted from least-squares regressions of log<sub>e</sub> percent radioactivity on time, following stripping of long components by eye. Symbols explained in text.

Mass balance equations for the R-C model are then,

$$\frac{dB(t)}{dt} = aI(t) - k_B B(t), \quad (7)$$

and

$$\frac{dG(t)}{dt} = (1-a)I(t) - k_G G(t).$$

The solution for elimination dynamics following an acute or chronic feeding ( $I = 0$  for  $t \geq t_0$ ) are

$$B(t) = B_0 e^{-k_B(t-t_0)}, \quad (8)$$

$$G(t) = G_0 e^{-k_G(t-t_0)},$$

and  $T(t) = B_0 e^{-k_B(t-t_0)} + G_0 e^{-k_G(t-t_0)}$ ,  $t \geq t_0$ ,

where  $B_0$  is the initial body content ( $B_0 = B(t)$ ,  $t = t_0$ ) and  $G_0$  is the initial gut content ( $G_0 = G(t)$ ,  $t = t_0$ ). For an acute feeding,  $B_0 = aI_0$  and  $G_0 = (1-a)I_0$ . The predicted equilibrium for a continuous feeding experiment can be found by setting the derivatives (equation 7) equal to zero,

$$B(ss) = \frac{aI}{k_B},$$

$$G(ss) = \frac{(1-a)I}{k_G}, \quad (9)$$

and

$$T(ss) = \frac{ak_B + (1-a)k_B}{k_G k_B} I.$$

#### Goldstein-Elwood Model

One assumption of the Reichle-Crossley model is that assimilated material is absorbed by the body

immediately after ingestion ( $B_0 = aI_0$ ). In the Goldstein and Elwood model, all ingested food is passed immediately to the gut ( $G_0 = I_0$ ,  $B_0 = 0$ ) and assimilation takes place at a rate proportional to gut contents,

$$A(t) = uG(t), \quad (10)$$

where  $u$  is the assimilation rate. In other respects the G-E model is identical to the R-C model. The mass balance equations are,

$$\frac{dB(t)}{dt} = uG(t) - k_B B(t) \quad (11)$$

and

$$\frac{dG(t)}{dt} = I(t) - (u+k_G) G(t).$$

For an acute feeding,  $I(t) = I_0\delta(t)$ , the solution equations for  $t \geq t_0$  are

$$G(t) = I_0 e^{-(u+k_G)(t-t_0)},$$

$$B(t) = \frac{I_0 u}{u+k_G-k_B} \left[ e^{-k_B(t-t_0)} - e^{-(u+k_G)(t-t_0)} \right], \quad (12)$$

and

$$T(t) = I_0 \left[ \frac{k_G-k_B}{u+k_G-k_B} e^{-(u+k_G)(t-t_0)} + \frac{u}{u+k_G-k_B} e^{-k_B(t-t_0)} \right]$$

(Goldstein and Elwood 1971).

Predicted equilibrium values on continuous feeding are

$$G(ss) = \frac{I}{u+k_G},$$

$$B(ss) = \frac{uI}{k_B(u+k_G)},$$

and

$$T(ss) = \frac{k_B+u}{k_B(u+k_G)} I. \quad (13)$$

#### Evaluation of Model Parameters

Solution equations for total animal activity after an acute feeding,  $T(t)$ ,  $t \geq t_0$ , involve the sum of 2 exponential decay terms in both models. Using regression, data from an elimination experiment can be fit to a similar equation,

$$T_{ex}(t) = a_1 e^{-\alpha_1 t} + a_2 e^{-\alpha_2 t} \quad (14)$$

where  $\alpha_1 > \alpha_2$  and  $a_1 + a_2 = 1$  (obtained by normalizing data). By equating terms, coefficient values of this regression equation can be used to evaluate the parameters of the 2 models.

For the R-C model, assuming  $k_G > k_B$  and letting  $I_0 = 1$  by normalization,  $k_G = \alpha_1$ ,  $k_B = \alpha_2$ , and  $a = a_2$ . In the G-E model it is assumed that  $u + k_G > k_B$  so that  $u + k_G = \alpha_1$ , and  $k_B = \alpha_2$ . Also

$$\frac{u}{u+k_G+k_B} = a_2,$$

so that

$$u = (\alpha_1 - \alpha_2) a_2,$$

and

$$k_G = (1-a_2)\alpha_1 + \alpha_2 a_2.$$

These relationships are summarized in Table 1. For the G-E model assimilation efficiency is found by dividing the integrated assimilation by ingestion,

$$\frac{1}{I_0} \int_0^\infty uG(t) dt = \frac{u}{u+k_G} \quad (15)$$

(Goldstein and Elwood 1971). Note that in all cases the assimilation efficiency estimated from the G-E model will be smaller than the R-C model estimate. Both models predict the same equilibrium values,  $T(ss)$ , for radioisotope accumulation for total organisms (Table 1).

Using the regression coefficients from Fig. 3, and gravimetrically estimated ingestion rates, both the R-C model and the G-E model were quantified and used to predict radioisotope accumulation (Table 2). Simulations were performed on a CDC Cyber 70 computer using the Runge-Kutta method of integration. The 2 models showed identical accumulation curves. Mathematically the 2 models have identical zero-initial condition solutions for  $T(t)$ . While the total organism radioactivity,  $T(ss)$ , is the same for the 2 models, the relative proportions in gut and body differ significantly. The R-C model predicts larger fractions of total radiotracer in the body than does the G-E model.

Simulations of strontium-85 elimination and accumulation (Fig. 4) indicate the 2 models exhibit different behavior for gut and body contents of radio-

Table 1.—Relationships of Reichle-Crossley and Goldstein-Elwood model parameters to the coefficients of the 2-component regression model.

	R-C model	G-E model
Egestion rate	$k_G = \alpha_1$	$k_G = a_1\alpha_1 + a_2\alpha_2$
Excretion rate	$k_B = \alpha_2$	$k_B = \alpha_2$
Assimilation rate		$u = (\alpha_1 - \alpha_2)a_2$
Assimilation efficiency	$a = a_2$	$\frac{u}{u+k_G} = \frac{(\alpha_1 - \alpha_2)a_2}{\alpha_1}$
Equilibrium values for continuous feeding		
$G(ss)$	$\frac{a_1 I}{\alpha_1}$	$\frac{I}{\alpha_1}$
$B(ss)$	$\frac{a_2 I}{\alpha_2}$	$\frac{(\alpha_1 - \alpha_2)a_2}{\alpha_1\alpha_2} I$
$T(ss)$	$\frac{a_1\alpha_2 + a_2\alpha_1}{\alpha_1\alpha_2} I$	$\frac{a_1\alpha_2 + a_2\alpha_1}{\alpha_1\alpha_2} I$



for cesium-134 accumulation reached a steady-state equilibrium more rapidly than the models predicted. Observed equilibrium for cesium-134 was reasonably close to predicted values,  $T(ss)$  (Table 2). For strontium-85, observed values were only ca. 65% of model predictions in later stages of experiments.

### Discussion

All 3 models considered in this study showed the general accumulation behavior—uptake of radioisotopes to a steady state. At lower levels of resolution the models were less successful. None showed the type of behavior attributable to individual cricket behavior. The models assume continuous feeding and elimination, but individual crickets eat and eliminate in discrete units. During elimination experiments for parameter estimation, feeding irregularities are not so important and elimination data for numbers of individuals show little scatter (Fig. 2 and 3). The discrete aspects of feeding and elimination introduced considerable variation into accumulation experiments, especially for the radioactive tracer with rapid turnover (Chromium-51, Fig. 2). Less point-to-point variation was found for radioisotopes with slower turnovers (Fig. 5). Thus, the models appear to yield satisfactory predictions at gross levels of resolution, and less satisfactory predictions at finer levels of resolution.

Reasons for the deviations of experimental results from the model predictions using 2 component systems (Fig. 5) are not understood at this time. Every attempt was made to stabilize environmental factors in the elimination and accumulation experiments. Experiments were started with young adults, whose life expectancy was ca. 30 days, and experiments were terminated well before senescence. Nonetheless, aging phenomena cannot be excluded. Counting times for radioactivity determinations were kept brief and frequencies of counting were kept to a minimum. Still, the procedure may produce unmeasured physiological effects. In all, we see no reasonable improvements for procedures to reduce these possible effects.

Both 2-component models, the Reichle-Crossley model and the Goldstein-Elwood model, exhibit identical behavior for total radioactivity in crickets. At that level of resolution the choice of model is a matter of preference. The models differ in their prediction of relative contents of gut and body components. Here more resolution is possible. Current models of arthropod food webs do not separate body and gut contents (Gist and Crossley 1975). For vertebrates, such resolution might be essential if separate body and gut data are involved (Goldstein and Elwood 1971). The G-E model seems more attractive at this level of resolution, but it doubtless oversimplifies the assimilation process. We did not attempt to dissect cricket guts to measure gut contents separately, and doubt that such measurements would be a valid evaluation anyway. Arthropod guts are major excretory organs for some

radioactive tracers (Crossley and Pryor 1960). The instantaneous assimilation assumed by the R-C model is clearly an oversimplification. Still, the model does permit separation of ingested tracer into 2 pools, assimilated and nonassimilated, which is conceptually useful. In some applications the more realistic concept of assimilation rate represented by the parameter  $\mu$  in the G-E model may be more useful than assimilation efficiency.

We conclude that either model would be useful in evaluating elemental movement in trophic systems. Current state-of-the-art does not seem to require high resolution. Both models interpret elemental accumulation from retention data, and use parameters in relatively similar ways. It would appear to us that, from an ecological viewpoint, more value would accrue from improving the modeling of linkage to food resources than from improving the modeling of internal dynamics of the organisms.

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