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ENVIRONMENTAL INFLUENCES ON THE ^{137}Cs KINETICS OF THE YELLOW-BELLIED TURTLE (*TRACHEMYS SCRIPTA*)[1]

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Abstract. Assessments of ecological risk require accurate predictions of contaminant dynamics in natural populations. However, simple deterministic models that assume constant uptake rates and elimination fractions may compromise both their ecological realism and their general application to animals with variable metabolisms or diets. In particular, the temperature-dependent metabolic rates characteristic of ectotherms may lead to significant differences between observed and predicted contaminant kinetics. We examined the influence of a seasonally variable thermal environment on predicting the uptake and annual cycling of contaminants by ectotherms, using a temperature-dependent model of ^{137}Cs kinetics in free-living yellow-bellied turtles, *Trachemys scripta*. We compared predictions from this model with those of deterministic negative exponential and flexibly shaped Richards sigmoidal models. Concentrations of ^{137}Cs in a population of this species in Pond B, a radionuclide-contaminated nuclear reactor cooling reservoir, and ^{137}Cs uptake by uncontaminated turtles held captive in Pond B for 4 yr confirmed both the pattern of uptake and the equilibrium concentrations predicted by the temperature-dependent model. Almost 90% of the variance in the predicted time-integrated ^{137}Cs concentration was explainable by linear relationships with model parameters. The model was also relatively insensitive to uncertainties in the estimates of ambient temperature, suggesting that adequate estimates of temperature-dependent ingestion and elimination may require relatively few measurements of ambient conditions at sites of interest. Analyses of Richards sigmoidal models of ^{137}Cs uptake indicated significant differences from a negative exponential trajectory in the 1st yr after the turtles' release into Pond B. We also observed significant annual cycling of ^{137}Cs concentrations, apparently due to temperature-dependent metabolism and its influence on ingestion and elimination rates. However, equilibrium concentrations of the radionuclide in the wild population were predictable from negative exponential models based on average annual temperature and its effects on intake and elimination rates, also suggesting that predicting ectotherm responses to long-lived contaminants (such as ^{137}Cs) may be possible without complex ecophysiological modeling.

Key words: biogeochemistry; biotic concentrations; cesium-137; contaminant modeling; diet; kinetics modeling; model sensitivity analysis; physiological ecology; radioecology; radionuclides; Richards sigmoidal model; stochastic models; Testudines; thermal ecology; Trachemys scripta.

INTRODUCTION

Ecological risk assessments attempt to identify negative environmental effects resulting from human activities. One major step in risk assessment involves combining laboratory toxicity data with ecological knowledge of contaminant behavior in the environment to estimate the probability of adverse impacts. To be of any relevance in regulatory or remediation decisions, such assessments require accurate predictions of contaminant behavior in the abiotic and biotic components of ecosystems. This process is complicated by the vast array of species of concern and the number of contaminants involved. There are presently over 100 000 known man-made chemicals (Bartell et al. 1992), and many may have adverse effects on resident biota.

Radionuclides (radioactive elements) are an important class of environmental contaminants. Environmental releases of these substances by nuclear production facilities, reactor accidents, weapons detonations, stored radioactive and mixed waste (Medvedev 1979), abandoned nuclear propulsion systems, and lost or diverted radiotherapy and other radiation sources (A. Nedospasov, Institute of Molecular Genetics, Russian Academy of Sciences, Moscow 123182, Russia, *personal communication*) are an unfortunate reality of modern existence. The accident at the Chernobyl nuclear facility demonstrates graphically the magnitude of ecological, social, and pecuniary damage that can result (Peterson et al. 1986, Anspaugh et al. 1988, Med-

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vedev 1990, Kryshev 1992). When such releases occur, consumption of domestic animals and wildlife inhabiting the contaminated area can become an important pathway for human exposure (Jenkins and Fendley 1968, Jenkins et al. 1969, Whicker 1983, Whicker et al. 1990*a*). As a result, numerous studies have attempted to quantify the uptake, cycling, and distribution of various radionuclides in the environment, as well as to assess their uncertainties in estimating human doses (e.g., Whicker and Kirchner 1987, Anspaugh et al. 1988, Breshears et al. 1989, 1992).

Although environmental releases of radionuclides are not as common as those of other chemical contaminants, radionuclides are of interest because they can produce deleterious effects at low concentrations, because both external and internal exposure can be hazardous, and because many radionuclides can freely substitute for nutrient elements in biochemical reactions. The kinetics of radionuclides can thus yield important insights into the behaviors of chemically similar substances in both ecosystems and in individual species (e.g., when used as tracers in studies of the environmental behaviors of a number of important toxic elements such as Hg or Cd). Moreover, concentrations of radionuclides or radionuclide-labeled contaminants in living organisms can often be determined with greater resolution or lower cost than their stable chemical analogs. If these labeled substances are gamma photon emitters, it is possible to examine the contaminant uptake and loss of the same individuals over time without destructive sampling, through the use of external whole-body counting.

Radionuclide transport modeling for assessing human risk from radionuclide exposure shares the major goals of other risk assessment efforts: to develop reasonable simulations of the behavior of contaminants in the environment, and to translate these simulations into accurate predictions of the effects of such releases on species, populations, or systems of interest (Bartell et al. 1992). However, radionuclide models tend to seek the most precise predictions possible through reconstruction and characterization of *particular* contamination scenarios, whether or not the resulting predictions reflect the general behavior of these substances in the environment. As a result, radionuclide modeling often relies heavily on site- or event-specific data in the formulation of model assumptions and in parameterization. This emphasis is partly due to the necessary trade-off between model accuracy and generality in human exposure/risk assessment models (e.g., Whicker and Kirchner 1987, Whicker et al. 1990*a*). It is also, however, partly a consequence of the relatively poor understanding of the patterns and processes governing the behavior of these contaminants in ecological systems. While large components of certain human dose models center on factors that are under some degree of human control (e.g., agricultural practices, dietary preferences), extension of these models to ecological risk assessments may be problematic because relevant data on abiotic (e.g., chemical availability, climatic information) and biotic factors (e.g., intake and elimination rates, assimilation fractions) may be unavailable or incomplete. In determining the ecological impacts of radiation exposure to biota, there are additional difficulties in converting contamination levels into quantitative dose assessments, and in turn to reasonable risk estimates. There is a potential for introduction of errors and biases at all stages of this assessment, including those that occur when constructing the model, when testing model predictions, and when estimating the probability of adverse effects (Loehle 1987). To partly address these problems, stochastic modeling techniques have been applied to examine the influence of uncertainties in estimates of model parameter values on the subsequent predictions of contamination models (e.g., Whicker and Kirchner 1987, Whicker et al. 1990*a*, Breshears et al. 1992). These techniques employ a "top-down" approach, using model sensitivity analyses to identify areas of model uncertainty where additional research effort may lead to more accurate system-wide predictions. Such techniques have been applied less frequently to studies of contaminant uptake by individual animal species, where the use of simple deterministic models of contaminant uptake and elimination has been more common (but see Evans 1988, Brisbin et al. 1990). These prediction efforts can employ a "bottom-up" approach (i.e., using models with parameters and assumptions derived from the physiology and ecology of the individual species). Predictions from such models may be validated relatively easily, using independent data not used in the model's construction, and model assumptions can then be tested against alternatives.

Unfortunately, simple deterministic models have certain rather restrictive assumptions that may compromise their usefulness in describing the contaminant kinetics of certain animals. For example, because of seasonal differences in metabolic responses, we feel that ectotherms may depart significantly enough from deterministic model assumptions that predictive ability may be compromised. If this is true, then stochastic modeling techniques employed in human risk assessment alone may not in themselves be adequate to make determinations of impacts on entire ecological systems and their inhabitants. Without an understanding of the patterns of ecophysiological responses of a diversity of species, there is the potential danger of inadequately estimating risks on taxa that may be critical components of ecosystems and/or be consumed by humans. It is, therefore, useful to examine the process by which deterministic models are constructed, and consider the influence of model assumptions on the successful simulation of contaminant impacts.

Classical deterministic and related mathematical models

Uptake of radionuclides and other contaminants by animals is frequently represented as a constant rate of

intake coupled with a first-order loss, and may be conceptualized (e.g., Davis and Foster 1958, Whicker and Schultz 1982) as:

$$R \longrightarrow \boxed{q} \xrightarrow{k_{\text{eff}}}$$

and may be expressed as

$$\frac{dq}{dt} = R - k_{\text{eff}}q, \tag{1}$$

where R is the rate of radionuclide intake (in units of activity·time^{-1}), q is the radionuclide body burden (in units of activity), and k_{eff} is a constant (in units of time^{-1}) representing the sum of the loss-rate coefficients of the first-order physical and/or biological losses. This model has the time-dependent solution:

$$q_t = \frac{R}{k_{\text{eff}}}(1 - e^{-k_{\text{eff}}t}) + q_0 e^{-k_{\text{eff}}t}, \tag{2}$$

where q_t is the radionuclide body burden of the animal at time t, R and k_{eff} are as defined above, and q_0 is the initial body burden of the animal at time $t = 0$ (often assumed or measured as zero activity). Under these conditions, the animal comes to radionuclide equilibrium at time $t = \infty$, with the equilibrium body burden (q_{eq}) expressed as:

$$q_{\text{eq}} = \frac{R}{k_{\text{eff}}}. \tag{3}$$

The effective loss-rate coefficient (k_{eff}) is related to the effective half-time (T_{eff}, the time required for half of the quantity present in the organism to be lost through a combination of biological elimination and physical processes) for the substance, such that $\ln(2)/k_{\text{eff}} = T_{\text{eff}}$. After a period of $\approx 5 \times T_{\text{eff}}$, however, the animal is generally considered to be at an effective equilibrium with respect to the contaminant levels in its environment (i.e., the quantities of radionuclide or other contaminant entering and leaving the organism are approximately equal).

The radionuclide intake rate (R) can often be considered a composite parameter, composed of independently measured or modeled constituents. For example, R can be described as the product of the ingestion rate (r), the radionuclide concentration in the food (C_f), and the assimilation efficiency (a), the fraction of ingested radionuclide absorbed by the organism (Whicker and Schultz 1982), such that:

$$\begin{aligned} R \text{ (activity/time)} = {} & r \text{ (mass of food/time)} \\ & \times C_{\text{f}} \text{ (activity/mass of food)} \\ & \times a \text{ (dimensionless)}. \end{aligned} \tag{4}$$

By substitution, differential Eq. 1 above then becomes:

$$\frac{dq}{dt} = rC_f a - k_{\text{eff}}q \tag{5}$$

and

$$q_t = \frac{rC_f a}{k_{\text{eff}}}(1 - e^{-k_{\text{eff}}t}) + q_0 e^{-k_{\text{eff}}t}. \tag{6}$$

The effective loss-rate coefficient (k_{eff}) is also a composite parameter describing multiple processes simulated by independent first-order rate constants that are combined additively, rather than multiplicatively. For example, if the physical half-time of the isotope is short relative to the measurement period (e.g., ^{131}I, with a physical half-time of 8 d), then k_{eff} may be partitioned into two rate constants: k_b and k_p, representing first-order losses from biological elimination and radioactive decay, respectively, with $k_{\text{eff}} = k_b + k_p$. For longer lived radionuclides such as ^{137}Cs, k_p will generally be much smaller than k_b, and $k_{\text{eff}} \approx k_b$. The biological elimination rate constant (k_b) can also be further subdivided into multiple loss rate coefficients representing losses from different body compartments or various routes of elimination of the radionuclide from the body (e.g., Willis and Jones 1977).

The above "negative exponential" model is a special case of the more generalized Richards sigmoid model (Richards 1959), which may be formulated (Brisbin et al. 1990) as:

$$q_t = \left\{ q_{\text{eq}}^{(1-m)} \left[1 - e^{\frac{-k_{\text{eff}}t}{(1-m)}} \right] + q_0^{(1-m)} e^{\frac{-k_{\text{eff}}t}{(1-m)}} \right\}^{\frac{1}{(1-m)}}, \tag{7}$$

where q_t, q_{eq}, and k_{eff} are defined as above, and with an additional shape parameter (m) that allows the simulation of a variety of sigmoidal curves with different inflection points (Richards 1959, White and Brisbin 1980, Brisbin et al. 1986*a*, *b*, 1990). For example, substituting a value of zero for m in Eq. 7, and R/k_{eff} for q_{eq} as in Eq. 3, converts the equation to a negative exponential model that is the same as Eq. 2. A major advantage of the Richards formulation is that it permits the use of nonlinear curve-fitting techniques to obtain a "best fit" to contaminant uptake data and thus produces an unbiased estimate of the trajectory of contaminant uptake without a priori assumptions about model behavior.

Negative exponential and Richards models have been applied in a number of studies of contaminant uptake by animals (e.g., Davis and Foster 1958, Fendley et al. 1977, Potter 1987, Brisbin et al. 1990). However, despite the potential inclusion of multiple sources of radionuclide inputs and losses, these models have inherent assumptions that may compromise their realism. Both models assume a constant intake rate, instantaneous and complete mixing of the contaminant within the animal, and a loss rate that is a constant proportion of body burden. However, as the time required to reach effective equilibrium increases, it becomes less likely that these conditions will persist. For example, seasonal changes in food availability, radionuclide concentrations in food, and metabolic status could all alter the trajectory of uptake (Brisbin et al.

1990). Despite this caveat, these models are often very good predictors of body burden when applied to species that achieve a significant fraction of their effective q_{eq} relatively rapidly. One example is endotherms (e.g., Anderson et al. 1976, Fendley et al. 1977, Potter 1987), where the maintenance of a constant body temperature produces energy metabolism rates that are both considerably higher and less variable than those of ectotherms. Maintenance of a higher constant metabolic rate requires a greater amount of food per unit body mass (Peters 1983, Pough et al. 1989). Ingestion rates (r) are, therefore, greater in endotherms, and this increases contaminant intake rates (R). However, a greater ingestion rate also means that food is turned over more rapidly, possibly reducing absorptive efficiency (and thus assimilation, a). The higher overall metabolic rate will also increase element (and contaminant) turnover rates (increasing k_b and thus k_{eff}). This increase in k_b decreases T_{eff}, which in turn decreases the time required to reach effective q_{eq}. Thus, both intake and elimination rates are higher in endothermic animals, suggesting that while endotherms might be expected to achieve a higher q_{eq} due to a higher R, the reciprocal effect of a lower a and higher k_{eff} may reduce q_{eq}. As a result, endotherms and ectotherms inhabiting the same contaminated areas and feeding on similarly contaminated foods may or may not exhibit differences in the magnitude of their equilibrium body burdens that are comparable to the differences in their metabolic rates.

The long biological half-times of several important long-lived radionuclides in ectotherms suggests it is unlikely that many of these animals could attain a significant fraction of q_{eq} during a single active season in the temperate zone (Reichle and Nelson 1970, Staton et al. 1974, Scott et al. 1986, Peters and Brisbin 1988, Mailhot et al. 1989, Hinton et al. 1992, Ugedal et al. 1992). Seasonal changes in intake or loss rates are, therefore, likely to affect the pattern of radionuclide uptake by such ectotherms, perhaps significantly altering it from a negative exponential trajectory. Because the dose commitment to the animal is proportional to the area under the uptake curve (Whicker and Kirchner 1987), assuming an incorrect uptake pattern may not only lead to errors in predicting contaminant body burdens of ectotherms, but also their resulting biological effects. It may, therefore, be desirable to introduce time-variable responses into the models described by Eqs. 2 and 5 above, to more accurately reflect the influence of seasonal temperature changes on the biological processes of ingestion and excretion in these animals.

Ingestion rates (r) of temperate-zone ectotherms are likely to be maximal in warmer months and minimal in winter. If the radionuclide concentration of the food remains constant, and if the time spent ingesting food remains a constant fraction of the total active time, then this seasonality could be modeled by modifying Eq. 4, changing r from a constant to a time-dependent function (r_t). One such function, which changes continually throughout the year, and possesses an annual cycle with a single maximum and minimum is:

$$r_t = \bar{r} - \hat{r} \cos\left[\frac{2\pi}{365.25\ \mathrm{d}}(t + \tilde{t})(\mathrm{d})\right] \tag{8}$$

where r from Eq. 5 is now r_t, composed of $\bar{r}$ (the mean feeding rate), $\hat{r}$ (a coefficient that describes the amplitude of the annual cycle about this mean feeding rate), and $\tilde{t}$ (a coefficient that reflects the times of year when maximum and minimum feeding rates occur). This function is simplistic, in that it assumes that the rules governing feeding behavior are the same at all times of the year.

Other parameters (e.g., a, k_{eff}) are also likely to vary with temperature. Assimilation of radionuclides in the body will be subject to passive and active transport mechanisms that will both be sensitive to the thermal environment. For example, the solubility of a radionuclide in gut contents as well as its diffusion rate across cell membranes will be affected by temperature. Cell membrane proteins acting as ionic "pumps" also perform optimally at specific temperatures (Lehninger 1975), influencing the assimilation of radionuclides that are biochemical analogs of important nutrient elements (e.g., ^{137}Cs as an analog of K, or ^{90}Sr for Ca). These and other physiological factors (e.g., osmotic balance, reproductive output, or somatic growth) may also affect k_{eff}.

Here, we modify the traditional deterministic model often used to predict radionuclide uptake by animals by including temperature-dependent responses such as would be expected of temperate zone ectotherms. We then evaluate the utility of this model compared with simple continuous models in predicting radionuclide uptake by a specific ectothermic resident of a thermally complex environment: the yellow-bellied turtle, *Trachemys scripta*. Using stochastic sampling of model parameters, we analyze the sensitivity of this model to uncertainties in parameter values, describe the factors that are most important in governing the radionuclide kinetics in this species, and discuss those likely to be of importance in modeling the contamination kinetics of ectotherm populations.

Materials and Methods

Study animal

We chose the yellow-bellied turtle, *Trachemys* (=*Pseudemys*, =*Chrysemys*) *scripta*, as our model species for examining the effects of environmental factors on radionuclide kinetics of ectotherms. *Trachemys scripta* is abundant in most lentic and lotic habitats within its range in southern North and Mesoamerica (Ernst 1990, Legler 1990), and there is a wealth of information available on its physiology, life history, and ecology (Gibbons 1990*a*) that may be relevant in

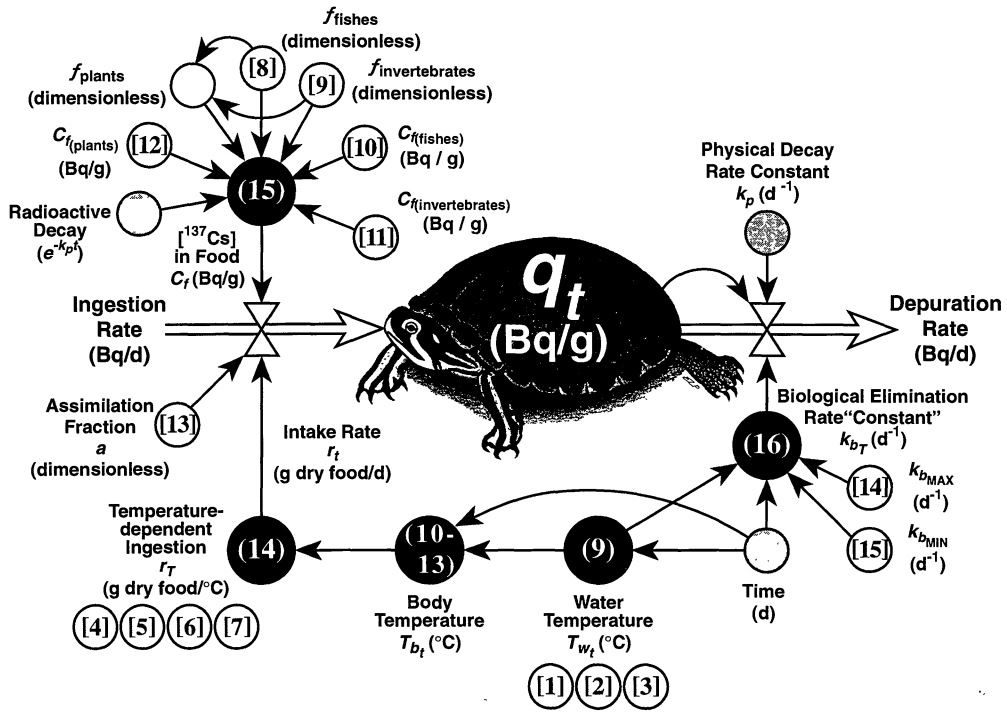

FIG. 1. Conceptual model of ^{137}Cs kinetics of *Trachemys scripta*. Numbered white circles represent model parameters (also see Table 2), with numbers in brackets corresponding to parameters used in the model sensitivity analyses, but with $f_{plants} = 1 - [f_{fishes} + f_{invertebrates}]$. Black circles represent model equations, with numbers in parentheses corresponding to equation numbers. Shaded circles represent other abiotic processes.

predicting its responses to environmental contaminants. This species has also been the subject of intensive radionuclide kinetics research (Scott et al. 1986, Towns 1987, Peters and Brisbin 1988, Brisbin et al. 1990, Hinton and Scott 1990, Hinton et al. 1992). *Trachemys scripta* is an ideal model for examining environmental influences on the radionuclide kinetics of ectotherms because of its complex climate space (Standora 1982), long life-span (Frazer et al. 1990), omnivorous diet (Parmenter and Avery 1990, Schubauer et al. 1990), and home range fidelity (Gibbons et al. 1990).

One population of *T. scripta* inhabits Pond B, an abandoned nuclear reactor cooling reservoir located on the U.S. Department of Energy's Savannah River Site (SRS) near Aiken, South Carolina, USA. During the 1960s, Pond B received significant radionuclide inputs (especially ^{137}Cs and ^{90}Sr) from discharges of contaminated water from one of the SRS' weapons production reactors. As the radioecology of Pond B has been well described (Whicker et al. 1990*b*), we constructed our model using data from this location, and validated it using comparative measurements of ^{137}Cs concentration, [^{137}Cs], of both turtles naturally resident in this reservoir and of experimentally introduced uncontaminated turtles.

We focused our attention on ^{137}Cs for several reasons. As a biochemical analog of potassium, Cs has a ubiquitous distribution within the body (particularly in edible skeletal muscle), and freely participates in important active transport mechanisms of cells, particularly the sodium/potassium adenosine triphosphatase "pump" (Lehninger 1975, Metzler 1977, Nielsen 1986). The characteristic gamma emission of ^{137}Cs permits quantifying body burdens in this species (Towns 1987) without destructive sampling. The long physical half-time (30 yr) of this radionuclide ensures its persistence at measurable levels over the course of long-term experiments. ^{137}Cs is also a high-yield product of nuclear fission, and is present in detectable quantities in a number of contaminated ecosystems, where it is both physically and chemically available to biota (Whicker and Shultz 1982). ^{137}Cs is, for example, the most important long-lived contaminant released during the Chernobyl accident (Peterson et al. 1986, Anspaugh et al. 1988, Medvedev 1990, Kryshev 1992).

Temperature-dependent conceptual and mathematical model

Our conceptual model (Fig. 1) incorporated likely physiological and environmental influences on ^{137}Cs kinetics of *T. scripta*. In particular, we were interested in the effect of a thermally variable environment on ^{137}Cs uptake and seasonal whole-body [^{137}Cs] patterns. Our model considered the effect of temperature on both

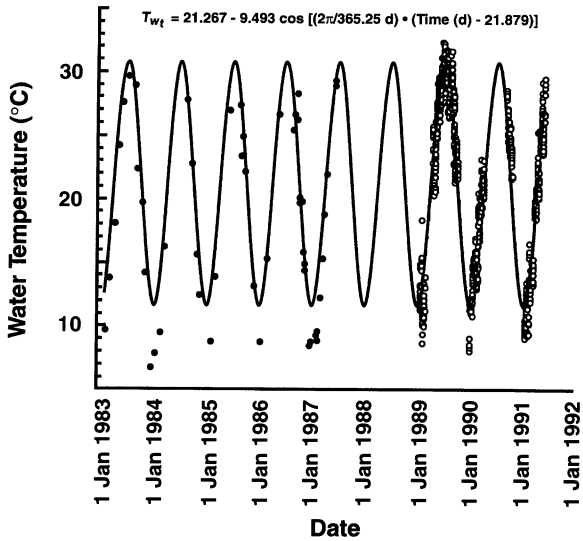

FIG. 2. Pond B water temperatures, showing the periodic regression model (solid line) used to produce time-dependent behavior of the model's intake and elimination functions. The regression fit (see Eq. 9) was to surface water temperatures (●) measured approximately monthly during 1983–1987 (J.E. Pinder III, *personal communication*), combined with temperatures at a depth of 0.31 m (○) measured hourly on discontinuous days during 1989–1991 with an automated system installed at Pond B (Westinghouse Savannah River Laboratory, *unpublished data*). Both sets of measurements were ± 0.1°C.

ingestion and elimination, as well as the effects of variable diet composition and [^{137}Cs] in food.

Temperature-dependent intake rate (r_T).—Turtle body temperature was considered to be an important factor governing both ^{137}Cs uptake and elimination. To determine the potential importance of this response, we obtained data on seasonal water temperatures at the Pond B site and combined these data with information on the relationship between ambient temperature and turtle body temperature (Standora 1982), to produce a temperature-dependent (and thus time-dependent) ingestion rate (r_T) similar to Eq. 8. We first constructed a function describing time-dependent water temperatures (T_{w_t}), using data on Pond B surface water temperatures (± 0.1°C) measured approximately monthly during 1983–1987 (J.E. Pinder III, Savannah River Ecology Laboratory, *personal communication*), and water temperatures (± 0.1°C) at a depth of 0.31 m measured hourly at discontinuous intervals during 1989–1991 with an automated system installed at Pond B (Westinghouse Savannah River Laboratory, *unpublished data*). We fitted the regression model

$$T_{w_t} = \bar{T}_w + \hat{T}_w \cos\left\{\frac{2\pi}{365.25\text{ d}}[\text{time(d)} + \tilde{t}]\right\} \quad (9)$$

to the combined temperature data, where $\bar{T}_w$ is the mean annual water temperature (in degrees Celsius), $\hat{T}_w$ is the amplitude (in degrees Celsius) about the mean, and $\tilde{t}$ (in days) is the phase shift of the periodic function relative to the beginning of the year (Fig. 2). This regression was highly significant ($F_{3,10770}$ = 1786.5, P < 0.001), and showed good predictive ability (R^2 = 0.92). We also obtained similar regression parameters from separate fits to the surface and 0.31 m data.

We converted T_{w_t} to time-dependent turtle body temperatures (T_{b_t}) by using regressions for telemetered air/water ambient temperatures (T_a) vs. deep body temperatures (T_b) of free-living *T. scripta* at locations near Pond B (Dick's Pond and Pond C, both on the SRS) during each of four seasons (Standora 1982: Fig. 14A–D):

21 Mar ≤ Spring < 21 Jun (n = 149):

$$T_b = 0.11 + 1.01T_a \quad (r^2 = 0.92), \quad (10)$$

21 Jun ≤ Summer < 21 Sep (n = 450):

$$T_b = 3.70 + 0.89T_a \quad (r^2 = 0.93), \quad (11)$$

21 Sep ≤ Autumn < 21 Dec (n = 382):

$$T_b = 2.25 + 0.88T_a \quad (r^2 = 0.94), \quad (12)$$

21 Dec ≤ Winter < 21 Mar (n = 424):

$$T_b = 0.20 + 1.00T_a \quad (r^2 = 0.97). \quad (13)$$

Because of the close agreement between T_a and T_b, and the relatively narrow range of daily temperatures relative to the daily mean at all seasons (Fig. 2), we considered the effect of mean daily temperature on ingestion only, and did not incorporate thermoregulatory changes in body temperature throughout a given day. For the models, we altered the regression equation to match the intervals described above, substituting T_{w_t} (as calculated above) for T_a.

We estimated a temperature-dependent ingestion rate (r_T) from T_{b_t} from a laboratory study of temperature-dependent ingestion (Parmenter 1980). We converted the ingestion measurements of food consumption over a 14-d period (Parmenter 1980: Fig. 2) into feeding rates, using the original data from which the figure was derived, but including the zero values omitted from the original figure (R. R. Parmenter, Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, *personal communication*). We plotted the resulting ingestion rates, r_T (in grams of dry food per gram turtle per day) vs. temperature, T (in degrees Celsius), and fitted the polynomial model $r_T = r_T(\beta_0) + r_T(\beta_1)T + r_T(\beta_2)T^2 + r_T(\beta_3)T^3$ to the data (Fig. 3). This regression was also highly significant ($F_{3,38}$ = 28.189, P < 0.001), and showed a reasonable degree of predictability (R^2 = 0.69):

$$r_T = 3.1168\cdot10^{-2} - 4.5955\cdot10^{-3}T + 2.1696\cdot10^{-4}T^2 - 3.083\cdot10^{-6}T^3. \quad (14)$$

We used this equation to simulate time-dependent ingestion (r_t) in the model, substituting the values for T_{b_t} calculated using Eqs. 9–13 for T. Ingestion rates increased to a maximum at ≈29°C, very close to the

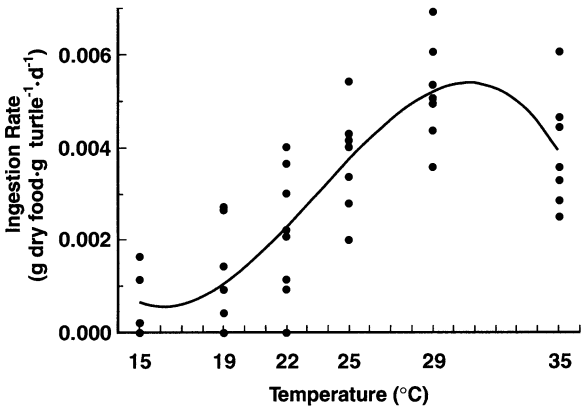

FIG. 3. Temperature-dependent ingestion by *Trachemys scripta* (R.R. Parmenter, Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, *personal communication*). The line indicates the third-order polynomial regression of ingestion rate, r_T (g dry food·g^{-1} turtle·d^{-1}) on temperature, T (°C) from which the parameters $r_T(\beta_0)$, $r_T(\beta_1)$, $r_T(\beta_2)$, and $r_T(\beta_3)$ were estimated (also see Eq. 14, Fig. 1).

28°C body temperature maintained by *T. scripta* during normal thermoregulation (Standora 1982), and declined at lower or higher temperatures. Ingestion was minimal at ≈15°C and we assumed it to be zero below this temperature. This assumption possibly underestimated total annual intake, as stomachs of 17 of 22 *T. scripta* captured in Par Pond during January–February 1978 and December 1979 contained some plants (Schubauer and Parmenter 1981). Turtle body temperatures in the model never exceeded the 35°C upper limit on this equation. It should also be noted that Eq. 14 does not simulate potential ontogenetic decreases in mass-specific food intake rate.

Dietary composition (f) *and radiocesium concentration in food* (C_f).—We estimated the diet of Pond B *T. scripta* from a study (Parmenter 1980) of stomach contents of 29 *T. scripta* inhabiting Par Pond, another large SRS nuclear cooling reservoir located adjacent to Pond B. These turtles' stomachs contained ≈70% plants and 30% animals (14% insects and 16% fish) by dry mass. Stomachs of another southern population of adult *T. scripta* (≈180–220 mm carapace length) contained 60–

TABLE 1. Estimated [^{137}Cs] in the diet of *Trachemys scripta* in the Pond B reservoir. Dry mass of stomach contents and the proportion of each dietary item in the total diet is estimated from data presented in Schubauer and Parmenter (1981). The mean [^{137}Cs] for each major category is the mean of all measured groups (Whicker et al. 1990*b*) within that category. The SD for each major category is the SD of the means of all measured groups (Whicker et al. 1990*b*) within that category.

Taxon	Dry mass of stomach contents (g)		Fraction of diet (f)		[^{137}Cs] (Bq/g)		Mean contribution to C_f (Bq/g food)
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	($f_i \cdot C_i$)
Centrarchid fishes	0.537	1.154	0.162	0.348	25.3	6.4	4.1
All invertebrates	0.499	0.086	0.151	0.026	6.1	4.5	0.9
Gastropods	0.037		0.011		0.9		
Insects							
Coleoptera							
Donacea sp.	0.022		0.007				
Other	0.229	0.010	0.069	0.003			
Odonata							
Anisoptera	0.018		0.005		7.6		
Zygoptera	0.006	0.002	0.002	<0.001	3.4		
Diptera	0.002	<0.001	0.001	<0.001			
Chironomidae					5.5		
Ceratopogonidae					14		
Chrysops sp.					4.9		
Hemiptera	0.071	0.072	0.021	0.022			
Hymenoptera	0.111		0.033				
Orthoptera	0.003	0.001	0.001	<0.001			
All plants	2.278		0.687		15.2	2.7	10.4
Algae	0.004	0.003	0.001	0.001			
Vascular plants							
Bacopa caroliniana	0.725	1.329	0.219	0.401	18		
Brasenia schreberi	0.192	0.071	0.058	0.021	18		
Najas quadalupensis	0.077	0.114	0.023	0.034			
Nymphaea odorata					14		
(seeds)	0.192	0.183	0.058	0.055	14		
(leaves)	0.017		0.005				
Sagittaria sp.	0.003	0.003	0.001	0.001	12		
Utricularia sp.	1.068	1.749	0.322	0.528			

65% vegetation by volume (Hart 1983). We compared (Table 1) the species of known dietary items (Parmenter 1980) to those species for which [^{137}Cs]s were available for Pond B (Whicker et al. 1990*b*). Because few species were represented in both of these studies, we calculated an average for each of the three major taxa (plants, invertebrates, and fishes) and multiplied each by the average [^{137}Cs] in becquerels per gram dry mass for that entire taxon, correcting the wet mass of fish using a 0.22:1.00 dry : wet ratio (Whicker et al. 1990*b*). We calculated C_f as:

$$C_f = \sum_{i=1}^{n} f_i \cdot C_i, \tag{15}$$

where f_i is the contribution of the ith food item to the total diet and C_i is the [^{137}Cs] in becquerels per gram for that item. We estimated relative contributions of each food category (f_i) to the total diet from stomach contents of *T. scripta* from nearby Par Pond (Parmenter 1980). The Pond B [^{137}Cs]s of these food items (C_i) were estimated from collections of plants, benthic invertebrates, and fishes in Pond B (Whicker et al. 1990*b*). Because of the disparate masses and SDs of the invertebrate taxa represented, the SD for the total mass of all invertebrates was calculated as: Σ(mean + SD) $-$ Σ(mean) for all invertebrate taxa. This produced an overall SD weighted by both the mean mass contribution of each taxon and the size of its associated SD. The coefficient of variation (CV) for this estimate [(0.026 $\times$ 100%)/0.151 = 0.17%] was similar to the CV obtained using the variance among groups (Sokal and Rohlf 1969) for the five insect taxa for which SDs were available (0.0036) and the mean (0.0188) of these five taxa [(0.0036 $\times$ 100%)/0.0188] = 0.19%). The mean fraction of diet (f_i) and associated SD for each of the three dietary categories (fishes, invertebrates, and plants) was defined as the mean and SD of the combined mass of each dietary item divided by the 3.314 g average total dry mass of food per turtle stomach (Parmenter 1980). The SDs of plant mass per stomach and fraction of plants in the total diet were not calculated. Instead, the contribution of plants to the total diet was allowed to vary in the model sensitivity runs with shifts in the fraction of intake from animal sources. The average [^{137}Cs] in diet was therefore estimated as:

$$\begin{aligned} C_f = {} & \underset{\text{(plants)}}{0.69 \times 15.2 \text{ Bq/g}} + \underset{\text{(fishes)}}{0.16 \times 25.3 \text{ Bq/g}} \\ & + \underset{\text{(invertebrates)}}{0.15 \times 6.1 \text{ Bq/g}} = \underset{\text{(all food types)}}{15.5 \text{ Bq/g}}. \end{aligned}$$

Our modeling of dietary [^{137}Cs]s did not consider possible differences in the dietary preferences of males and females, nor did it incorporate the ontogenetic progression to an increasingly herbivorous diet that has been observed for this species (Hart 1983).

Radiocesium assimilation fraction (a).—The assimilation of ^{47}Ca by *T. scripta* exceeds 0.5 (Hinton et al. 1992), and we might expect the *a* of ^{137}Cs to be higher than that of Ca due to its lower valence (Ekman 1966). However, this *a* for Ca is unusually high for a vertebrate, and was measured for an aqueous chloride solution at laboratory temperatures (Hinton et al. 1992). As mentioned above, *a* is also likely to increase in proportion to an ectotherm's ability to maintain optimal body temperature, and maintenance of this temperature is probably not possible year-round. We also suspect that not all of the ^{137}Cs ingested by turtles in Pond B is in the same chemical form or state of physical availability. In addition to the ionic form present in living tissue, some ingested ^{137}Cs may be adsorbed to sediments on the surfaces of ingested food, or ingested incidentally during feeding. The availability of adsorbed Cs in the gastric environment of the turtle is unknown, but the strong affinity of Cs ions for sediments appeared to greatly hinder absorption at gastric pHs (Kolehmainen and Nelson 1969). Of the few species for which ^{137}Cs assimilation estimates from natural diets was available, bluegill (*Lepomis macrochirus*) from White Oak Lake appeared to have the greatest degree of dietary and physiological/ecological similarity to Pond B *T. scripta*. We therefore averaged the reported *a* values for this species to obtain a modal value of 0.25, and used a range of values that encompassed the range of those reported by Kolehmainen and Nelson (1969) in our subsequent model sensitivity analyses.

Temperature-dependent elimination rate fraction (k_{b_T}) *and elimination rate coefficients.*—We assessed the temperature dependence of the biological elimination rate constant (k_b) from two studies (Scott et al. 1986, Peters and Brisbin 1988) of ^{137}Cs elimination by *T. scripta* kept in an outdoor holding pond at the SRS's Savannah River Ecology Laboratory (SREL). Measurements of whole-body [^{137}Cs]s at 65-d intervals throughout the year (Scott et al. 1986) showed a wide range of seasonal values for k_b, notably an abrupt increase in k_b in the early spring (31 March–11 June) that was 4 times higher than the summer value and 10 times the winter value. However, weekly measurements of ^{137}Cs k_b of turtles under identical conditions from 1 April to 30 August (Peters and Brisbin 1988) showed very constant values for k_b throughout the active season, with no evidence of discontinuities in elimination curves that would suggest exceptionally high loss rates in early spring. We therefore assumed a constant (and maximal) loss rate during the active season (1 April–30 September), $k_{b_{\text{MAX}}}$, averaging 0.0076 d^{-1} (Peters and Brisbin 1988). This assumes that turtles can maintain optimal body temperature (and thus associated digestive and turnover rates) by thermoregulation during this portion of the year. For the remainder of the year, we simulated a temperature-dependent loss rate (k_{b_T}) based on $k_{b_{\text{MAX}}}$ and on an annual minimum estimate ($k_{b_{\text{MIN}}}$) of 0.0020 d^{-1} (Scott et al. 1986), using a function similar to Eq. 9:

$$k_{b_T} = \bar{k}_b + \hat{k}_b \cos\left\{\frac{2\pi}{365.25\ \mathrm{d}}[\mathrm{time(d)} + \tilde{t}]\right\}, \quad (16)$$

where $\bar{k}_b$ (d^{-1}) is the average biological elimination rate constant (= $[(k_{b_{\mathrm{MAX}}} - k_{b_{\mathrm{MIN}}})/2 + k_{b_{MIN}}]$), $\hat{k}_b$ (d^{-1}) is the amplitude about that average (= $[\hat{T}_w/\bar{T}_w]\bar{k}_b$), and $\hat{T}_w$, $\bar{T}_w$, and $\tilde{t}$ are defined as for Eq. 9.

Model construction

The simulation model was constructed and run using the STELLA II simulation modeling software package (version 2.2.2, High Performance Systems, Hanover, New Hamphsire) on an Apple Macintosh microcomputer, using a fourth-order Runge-Kutta algorithm with a time step of 1 d. Conditional statements were used to modify seasonally dependent values for intake and loss rates (i.e., in applying Eqs. 10–13 and 16), and continuous functions were used as described above to estimate water temperatures and associated intake and elimination rates (Eqs. 9, 14, and 16). Because of the time dependence of certain parameter values and model equations, the initial time for the model runs was set at the 120th calendar day of the 1st yr to correspond with the date at which a cohort of uncontaminated turtles was released into an enclosure in Pond B to provide comparative data for model validation. A 5-yr period was used for each simulation run. Simulations of ^{137}Cs TBB (total body burden) were made on a mass-specific basis, i.e., [^{137}Cs] (in becquerels per gram), and no corrections were made for changes in [^{137}Cs] due to somatic growth, or for potential reproductive losses of ^{137}Cs. We also did not estimate ^{137}Cs uptake from routes other than ingestion, both because the [^{137}Cs] of Pond B water is low (Whicker 1990*b*) and because these sources appear to contribute only slightly to the ^{137}Cs TBB of fishes (Evans 1988), where additional uptake from water appears to be primarily through the gills.

Model validation

We evaluated our model's predictions by comparing the modeled time-dependent uptake patterns with the actual ^{137}Cs uptake of a group of uncontaminated *T. scripta* released into an enclosure in the Pond B reservoir, and by comparing the modeled effective equilibrium [^{137}Cs]s after 5 yr with the [^{137}Cs]s of "wild" (free-living native) *T. scripta* residing in the Pond B reservoir. Neither of these data sets were used in the construction of the temperature-dependent model or in estimating its parameter values. Live turtles were whole-body counted on a 15.2 cm wide × 10.2 cm high NaI(Tl) solid scintillation detector/photomultiplier and a Canberra 8100 multichannel analyzer, and counts were converted to ^{137}Cs activities according to procedures described elsewhere (Peters 1986, Scott et al. 1986, Towns 1987, Peters and Brisbin 1988).

Radiocesium uptake by uncontaminated turtles.–We constructed two 7.6 × 15.2 m enclosures (Enclosures 1 and 2) in shallow water at the northwestern end of Pond B. Ten adult female *T. scripta* were collected by hand from an uncontaminated lake in Aiken County, South Carolina. The turtles were whole-body counted to determine initial background levels of ^{137}Cs. We also assessed the contribution to the ^{137}Cs background from natural background radionuclides of similar energies. Because the skeleton comprises up to 40% of the body mass in this species (Towns 1987), and because naturally occurring Ra isotopes can substitute for Ca in the skeleton (Hinton et al. 1992), we were particularly concerned about radionuclides in the Ra decay series at secular equilibrium with Ra in the skeleton. One such radionuclide (^{214}Bi) has a similar gamma photon energy (609 keV) to ^{137}Cs (662 keV). We therefore also obtained initial whole-body counts from each of these turtles on a lithium-drifted reverse-electrode germanium semiconductor detector, coupled with a Canberra Series 85 multichannel analyzer. This instrument allowed us to distinguish the separate energy peaks for background ^{137}Cs and ^{214}Bi, and to develop correction factors for the presence of this radionuclide in each turtle (Peters 1986). After these initial counts were made, the turtles were fitted with radio transmitters to assist in recapture, and released into Enclosure 1 on 1 May 1986. During the 2nd yr of the study, Enclosure 2 was constructed nearby, and five of the turtles were moved into it from Enclosure 1. Additional aquatic macrophytes and fish collected from Pond B were provided several times each week during the first 4 mo after release to replace those destroyed during construction of the enclosure or consumed by the turtles.

Turtles were removed from the enclosures at periodic intervals, transported back to the SREL for whole-body counting, and returned to the enclosures the same day. Radiocesium concentrations were corrected for physical decay of the radionuclide, using the date of release into Enclosure 1 (1 May 1986) as the initial time.

^{137}Cs concentrations of free-living pond B turtles.–We live-trapped *T. scripta* from 12 locations around the perimeter of Pond B using hoop traps baited with canned sardines (holes were punched in the cans to provide an attractive odor, but not permit the turtles to consume a significant amount of bait). We captured turtles mostly during July–August 1987–1990, except for 5 captured in March 1987, 13 in September 1989, and 16 in May 1990. Captured turtles were transported to the SREL where they were weighed, sexed, whole-body counted, marked by filing or drilling notches in the marginal scutes of the carapace (Gibbons 1990*b*) to permit identification of recaptured individuals, and released the next day. Over the 4-yr study period, an ≈9% decrease in each turtle's TBB would be expected due to physical decay of the radionuclide, independent of biological elimination. Similar decreases would also be expected to occur in all other environmental ^{137}Cs levels. ^{137}Cs concentrations of the turtles were therefore corrected for physical decay of the radionuclide, using 7 March 1987 (the date when the first wild turtles were

TABLE 2. Parameters used in sensitivity analyses of ^{137}Cs kinetics of *Trachemys scripta*. At the beginning of each run, all parameters were randomly sampled from simulated normal distributions by a Monte Carlo technique, except for assimilation (a), which was sampled from a triangular distribution. Means and SDs for the other parameters were calculated from values estimated in Table 1 (parameters [8] through [12]), from literature estimates (parameters [14] and [15], Scott et al. 1986, Peters and Brisbin 1988), or from regression analysis estimates (parameters [1] through [3], Eq. 9; parameters [4] through [7], Eq. 14). Distributions containing parameter values less than zero were truncated at zero. For sensitivity analyses, these parameters were used as independent variables in a multiple regression with the square root of the time-integrated [^{137}Cs] (daily [^{137}Cs] (Bq/g) summed over a 5-yr period (Bq d/g)) as the dependent variable. Parameter numbers in brackets correspond to the conceptual model (Fig. 1).

Parameter	Description	$\bar{X}$ (SD)
[1] $\bar{T}_w$	Mean annual water temperature (in degrees Celsius)	21.267 (0.088)
[2] $\hat{T}_w$	Amplitude about mean annual water temperature (in degrees Celsius)	9.493 (0.129)
[3] $\tilde{t}$	Phase shift of annual maximum and minimum temperature (in days)	21.879 (0.769)
[4] $r_T(\beta_0)$	Intercept of temperature-dependent ingestion equation (in grams dry food per gram turtle per day)	0.031 (0.012)
[5] $r_T(\beta_1)$	Slope (T) of temperature-dependent ingestion equation (in grams dry food per gram turtle per day)	0.005 (0.002)
[6] $r_T(\beta_2)$	Slope (T^2) of temperature-dependent ingestion equation (in grams dry food per gram turtle per day)	2.17×10^{-4} (6.36×10^{-5})
[7] $r_T(\beta_3)$	Slope (T^3) of temperature-dependent ingestion equation (in grams dry food per gram turtle per day)	3.08×10^{-6} (8.44×10^{-7})
[8] f_{fishes}	Contribution of fishes to total diet (dimensionless)	0.162 (0.348)
[9] $f_{\text{invertebrates}}$	Contribution of invertebrates to total diet (dimensionless)	0.151 (0.026)
[10] $C_{f(\text{fishes})}$	[^{137}Cs] in Pond B fishes (in becquerels per gram dry fish)	25.3 (6.4)
[11] $C_{f(\text{invertebrates})}$	[^{137}Cs] in Pond B invertebrates (in becquerels per gram dry invertebrates)	6.1 (4.5)
[12] $C_{f(\text{plants})}$	[^{137}Cs] in Pond B plants (in becquerels per gram dry plants)	15.2 (2.7)
[13] a	Fraction of intake absorbed into body tissues (dimensionless)	Lower: 0.070 Mode: 0.250 Upper: 0.700
[14] $k_{b_{\text{MAX}}}$	Annual maximum effective biological elimination rate constant per day	0.0076 (0.0033)
[15] $k_{b_{\text{MIN}}}$	Annual minimum effective biological elimination rate constant per day	0.0020 (0.0004)

captured) as the initial time. All turtles were released at the capture sites by the following day.

Comparisons of model validation data with predictions of continuous uptake models

In addition to the temperature model described above, we also compared the observed [^{137}Cs]s of the wild and enclosure turtles to predictions of simpler continuous models. Because other studies (e.g., Potter 1987, Brisbin et al. 1990) have demonstrated significant deviations from negative exponential ^{137}Cs uptake, we tested whether a negative exponential model was appropriate for describing ^{137}Cs uptake in the 1st yr following release. We fitted the ^{137}Cs uptake data of the enclosure turtles to continuous models in which the Richards shape parameter (m) was both fixed at zero and permitted to vary and used an F test (White and Brisbin 1980) to determine whether m differed significantly from zero. These fits were made using nonlinear least squares regression, using only the [^{137}Cs] data collected within the 1st yr after the turtles were released into Enclosure 1, beginning from the 1 May release date, continuing through the following winter, and ending with the resumption of ^{137}Cs uptake the following spring (t = 0 to 354 d). Richards model fits were made to data from each enclosure turtle individually, as well as to the combined data for all enclosure turtles for this period. Finally, we examined whether reasonable predictions of long-term (multiyear) equilibrium [^{137}Cs] were possible using average estimates of intake and loss rates. For this, we used two deterministic negative exponential models with parameter values based on the mean value for ingestion (i.e., the estimated ingestion rate at the average annual temperature: $\bar{T}_w$ = 21.267°C), the mode of the estimated assimilation fraction (0.25), the mean C_f (15.5 Bq/g), and either (1) the average annual k_b value (0.0048 d^{-1}) or (2) the average active season k_b value (0.0076 d^{-1}).

Model sensitivity analyses

To assess the sensitivity of the temperature-dependent model to uncertainties in the estimates of its parameter values, the model was run using 1000 sets of parameters, using a Monte Carlo technique to randomly sample each parameter from its expected distribution (Table 2). The individual regression coefficients and associated standard deviations for Eqs. 9 and 14 were included as separate parameters in the model runs, but it was not possible to determine the errors on the regression coefficients for Eqs. 10–13. However, the high r^2 values for each of these equations suggested that the errors of these coefficients were small relative to their respective means. Because the mean values of all other model parameters were derived from data where normal distributions were observed (or tested for, in the case of parameters based on regression coefficients), all were sampled from simulated normal distributions for the sensitivity runs, with parameter distributions that enclosed zero constrained to values greater than zero. When estimating model uncertainty, parameter distri-

butions should be selected to minimize bias (Rose 1983). Sampling from distributions based on the variances of parameters appears to yield better estimates of parameter sensitivity (in at least some situations) than does sampling from distributions based on percentages of parameter means (Breshears et al. 1992). We made an exception for assimilation (a) because little information was available on the nature of this parameter's distribution. For this parameter, we used a triangular distribution with a mode as described above for bluegill, and a range enclosing the upper and lower limits of ^{137}Cs a values observed for bluegill (Kolehmainen and Nelson 1969). We allowed the [^{137}Cs]s of all three food categories and the fractions of the two animal components in the diet to vary, using the means and standard deviations as shown in Table 1. For each model run, the plant intake fraction (f_{plants}) was fixed at $[1 - (f_{\text{invertebrates}} + f_{\text{fishes}})]$, and the large standard deviation of the estimate for f_{fishes} produced some model runs where diet was composed almost entirely of plants (i.e., when sampled values for $f_{\text{invertebrates}}$ and f_{fishes} were both from the low ends of their distributions). The values for f_{plants} were not included in the sensitivity analysis regression models because of this collinearity with the animal components of diet. This allowed us to simulate the effect of an increased contribution by plants to the overall diet on ^{137}Cs levels. The plant component of the *T. scripta* diet increases with increasing age (Clark and Gibbons 1969, Hart 1983), and the diets of at least some individuals during some seasons is composed largely of plants (Schubauer and Parmenter 1981, Parmenter and Avery 1990). We also modeled $k_{b_{\text{MAX}}}$ and $k_{b_{\text{MIN}}}$ as independent parameters, and used conditional statements within the model to always constrain $k_{b_{\text{MAX}}}$ to $\geq k_{b_{\text{MIN}}}$.

Runs meeting the parameter criteria described above, i.e., those not leading to unrealistic simulations (e.g., negative model output values, O'Neill et al. 1982) were used in estimating the effects of parameter uncertainty on model output. The time-integrated [^{137}Cs] (in becquerel-days per gram) for the 5-yr period, i.e.,

$$\text{time-integrated}[^{137}\text{Cs}](\text{Bq-d/g}) = \sum_{t=0}^{1825\ \text{d}} q_t, \quad (17)$$

was used as the dependent variable in a multiple regression analysis of the effect of variation in each parameter on the modal output. We examined the squares of the partial correlation coefficients (R^2) of each model parameter as a measure of the strength of the linear relationship between that parameter's value and the model output, after controlling for the linear effects of the other parameters (Kleinbaum et al. 1988). Partial R^2 values are appropriate for this purpose (rather than F statistics) because of the deterministic nature of the model: a specific set of model parameter values will always yield the same model output value, with an expected residual mean square of zero. Nonzero values of the residual mean square thus reflect the appropriateness of a particular linear model in fitting the output data, rather than errors in measuring the dependent variable (Rose 1983, MacNeil et al. 1985).

We also assessed the collective significance of groups of related model parameters (T_{w_t}, r_T, f, C_f, a, and k_{b_T}) in predicting the model output values, by comparing the R^2 values of "Reduced" models (with these parameter groups omitted as predictors of model output) to the R^2 values of "Full" models containing all model parameters (White et al. 1983). We tested two different "Full" models. Full Model I contained all parameters listed in Table 2 regressed on time-integrated [^{137}Cs]. Full Model II contained these same parameters plus the 18 first-order interaction terms between the three temperature parameters (T_{w_t}: $\bar{T}_w$, $\hat{T}_w$, and $\tilde{t}$) and the parameters associated with temperature-dependent intake (r_T: $r_T(\beta_0)$, $r_T(\beta_1)$, $r_T(\beta_2)$ and $r_T(\beta_3)$) and elimination (k_{b_T}: $k_{b_{\text{MAX}}}$ and $k_{b_{\text{MIN}}}$). We used an F test of the multiple-partial correlation coefficients (Kleinbaum et al. 1988), where:

$$F = \frac{\dfrac{[R^2_{(\text{Full Model})} - R^2_{(\text{Reduced Model})}]}{[\text{Regression df}_{(\text{Full Model})} - \text{Regression df}_{(\text{Reduced Model})}]}}{\dfrac{[1 - R^2_{(\text{Full Model})}]}{\text{Residual df}_{(\text{Full Model})}}}. \quad (18)$$

This F statistic (with df = (Regression $\text{df}_{(\text{Full Model})}$ − Regression $\text{df}_{(\text{Reduced Model})}$), Residual $\text{df}_{(\text{Full Model})}$) tests whether the addition of each group of model parameters significantly improves the prediction of model output, given that the other groups of model parameters are already in the regression model (Kleinbaum et al. 1988). For example, removal of the two k_{b_T} parameters ($k_{b_{\text{MAX}}}$ and $k_{b_{\text{MIN}}}$) tests H_0: $\beta k_{b_{\text{MAX}}} = \beta k_{b_{\text{MIN}}} = 0$, and gives an indication of the relative importance of this parameter group in predicting the output from a given set of model runs.

RESULTS

Model predictions and validation

^{137}Cs concentrations of free-living pond B turtles.— We made 287 captures of 245 naturally resident *T. scripta* (112 ♂, 103 ♀, and 30 too immature to determine by morphological sexual characteristics). Most captures were made during July-August 1987–1990, except for five that were captured in March 1987, 13 in September 1989, and 16 in May 1990. Covariate analysis of the total ^{137}Cs body burden (TBB, in becquerels) as a function of body mass (W, in kilograms), using the model TBB = aW^b, revealed no difference in either the slope ($F_{3,\,279} = 2.14$, $P = 0.10$), or the intercept ($F_{3,\,279} = 0.36$, $P = 0.79$) of this relationship across years. A separate covariate analysis of the 42 turtles captured during two or more years also revealed no difference in either the slope ($F_{3,84} = 0.49$, $P = 0.69$) or the intercept ($F_{3,84} = 0.53$, $P = 0.66$), so we

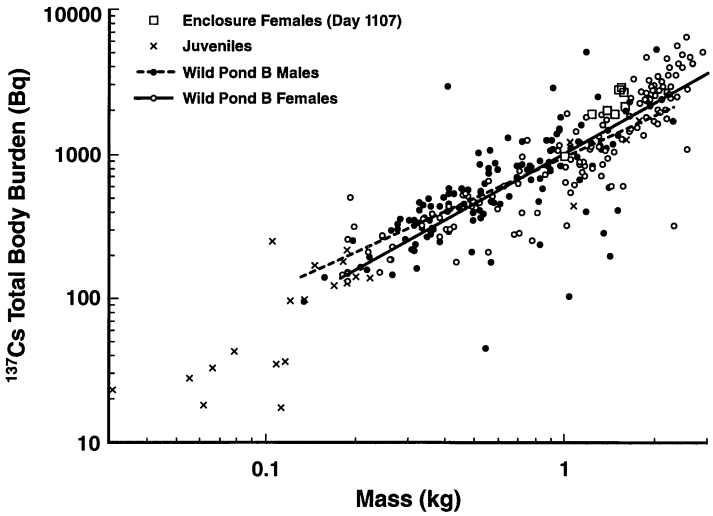

FIG. 4. ^{137}Cs total body burdens (TBB) of resident ♀ (○), ♂ (●), and juvenile (×) Pond B *Trachemys scripta* measured during four consecutive years. The model TBB (Bq) = *a*Mass (kg)*b* was fit to both ♀♀ (solid line) and ♂♂ (dashed line). The slope of the line fit to the ♀♀ was significantly >1, indicating that total body [^{137}Cs] also increased with increased body mass. TBBs of eight uncontaminated ♀♀ measured 1107 d after release into enclosures on Pond B (□) are also shown.

combined the data from all individuals (including recaptures). The [^{137}Cs]s of the wild turtles were lognormally distributed, with a geometric mean ($\bar{x}_G$) of 0.96 Bq/g (95% CI of 0.90–1.02 Bq/g). The range of [^{137}Cs]s was much broader (0.09–7.64 Bq/g), probably reflecting different residence times in Pond B and immigration by turtles from other more or less contaminated localities on the SRS. The equilibrium [^{137}Cs]s predicted by the model for June–August (≈1.5–1.7 Bq/g) were slightly higher than the average observed for Pond B turtles, but were well within the range. The mean whole-body [^{137}Cs] we observed for the Pond B turtles was about half that reported for muscle tissue alone (Whicker et al. 1990*b*). The TBB of the wild turtles increased as a power function of increased body mass (Fig. 4), with TBB = $997.2W^{1.121}$ ($F_{1,285}$ = 978.9, $P < 0.001$, $r^2 = 0.77$). The slope of this regression was significantly greater than 1, (95% CI 1.051–1.192), indicating that (unlike muscle) whole-body [^{137}Cs] increases with increasing mass. Covariate analysis of the model TBB = aW^b with sex as a factor revealed no difference between the intercepts of the two sexes ($F_{1,261}$ = 0.57, P = 0.45), but did reveal a significant difference in slopes ($F_{1,261}$ = 4.35, P = 0.04). The slope of the relationship between TBB and mass differed significantly from unity in ♀♀ (TBB = $995.4W^{1.151}$, 95% CI for the slope = 1.048–1.253, $F_{1,134}$ = 496.4, $P < 0.001$, $r^2 = 0.79$), but not for ♂♂ (TBB = $939.5W^{0.949}$, 95% CI for the slope = 0.779-1.118, $F_{1,127}$ = 122.6, $P < 0.001$, $r^2 = 0.49$). This relationship for female *T. scripta* was also true of the enclosure turtles (Fig. 4): on day 1107 after release (the last day on which all eight of the surviving turtles were captured), TBB = $1084.7W^{1.974}$ ($F_{1,6}$ = 29.2, $P < 0.002$, $r^2 = 0.83$, 95% CI for the slope = 1.081-2.863). Covariate analysis revealed no difference between the ♀♀ of the wild population and the enclosure turtles in either the slope ($F_{1,140}$ = 0.62, P = 0.43) or the intercept ($F_{1,140}$ = 0.05, P = 0.82) of this relationship, indicating that differences in [^{137}Cs] of the two groups probably reflected body mass differences, as most enclosure turtles were within the upper 25% of the size range of the wild population (Fig. 4).

There appeared to be substantial fidelity by the resident turtles to their individual sites within Pond B: of the 42 turtles captured in more than one year, 35 of 50 recaptures were at the same trap location where the turtle was first collected, and 14 of the remaining 15 recaptures were in the nearest adjacent traps. We therefore tested for the differences in the relationship between ^{137}Cs TBB and W due to location within Pond B by comparing the data by trap location. Nearly all of the differences in ^{137}Cs TBBs at different locations proved to be the result of differences in the body masses and/or the sex ratios of turtles trapped at each site. However, we observed one exception: ^{137}Cs TBBs of ♀ turtles collected on the west shore of Pond B (near the entrance to the cove where the radionuclides entered Pond B) were significantly lower (Scheffe's S: Difference = 0.735, Critical Difference = 0.616, P = 0.021) than ♀♀ collected in a cove on the northernmost end of the pond (furthest from the point of radionuclide entry). This was true even after correction for differences in body mass: covariate analysis of TBB = aW^b using trap site as a factor, indicated that the ♀♀ from these two locations differed in the slope ($F_{1,39}$ = 13.15, $P < 0.001$), but not the intercept ($F_{1,39}$ = 2.97, P = 0.093) of that regression. We observed no other relationships between trap location and ^{137}Cs TBB.

Radiocesium uptake by uncontaminated turtles.— Two of the 10 uncontaminated turtles released into the Pond B enclosures died at end of the second summer following release (early September 1987). The remaining eight turtles survived for at least 3 yr in the enclosures, and seven were still alive when the experiment was concluded (4 yr after release).

Radiocesium uptake by the enclosure turtles corresponded closely with the predictions of the tempera-

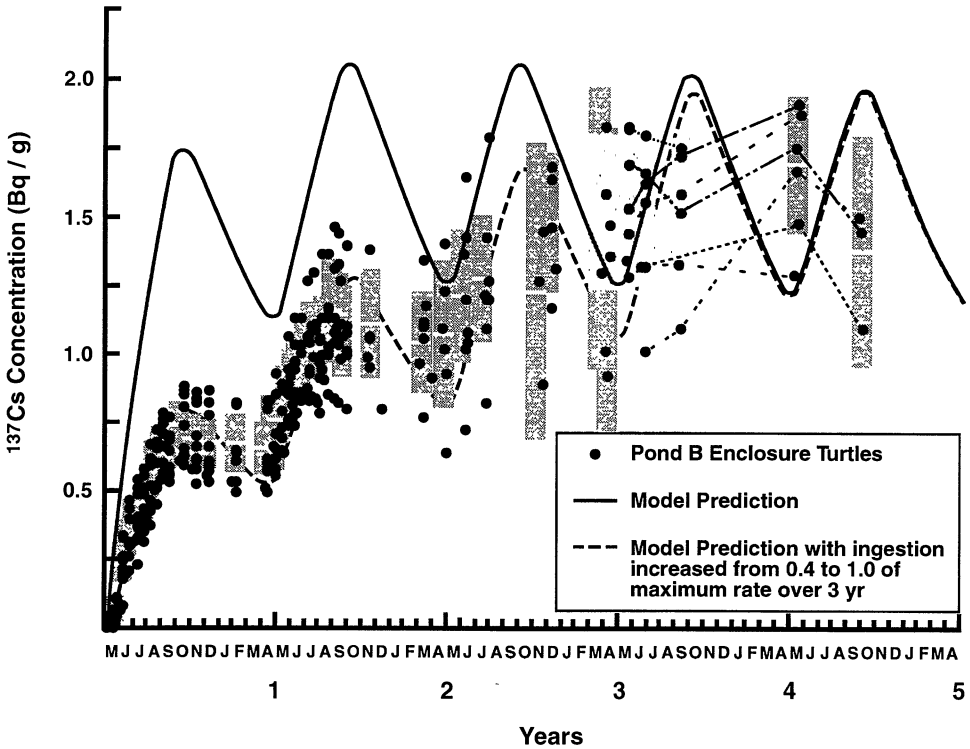

FIG. 5. Five-year ^{137}Cs uptake by *Trachemys scripta* in Pond B. Symbols (●) indicate measured [^{137}Cs]s of uncontaminated turtles released into enclosures on Pond B, with [^{137}Cs]s of individual turtles connected with dotted lines after 3 yr. The solid line indicates [^{137}Cs]s predicted by the temperature-dependent model. The dashed line shows the prediction by the temperature-dependent model when ingestion was initially set to 0.4 of the maximum rate and increased linearly to the maximum rate over 3 yr. The shaded bars indicate the 95% CIs for the mean [^{137}Cs] of the enclosure turtles at the time of each recovery effort (with all turtles inside each bar recovered within 1 wk). The mean [^{137}Cs] for turtles recaptured in each recovery effort is indicated by a horizontal white line within each shaded bar. Date of initial release of uncontaminated turtles was 1 May 1986.

ture-dependent model (Fig. 5). Uptake was rapid during the first two active seasons, reaching an annual maximum in late summer. Lesser but significant losses occurred during the first two winters, and elimination rates decreased compared with summer. During the first 2.5 yr, the model and enclosure turtles showed very similar dates of annual [^{137}Cs] maxima and minima, and both the model and these data indicated that at least 90% of effective equilibrium was reached in ≈2–3 yr, compared with estimates of 1.0–2.6 yr using warm-season k_b estimates alone (Peters and Brisbin 1988). There was some indication, however, that the model predictions were becoming "out of phase" after 2.5 yr, with annual maximum and minimum [^{137}Cs]s of the enclosure turtles (Fig. 5). This may have been due to the fact that we recaptured the turtles much less frequently as they approached their asymptotic [^{137}Cs]s, and recaptured fewer individuals during each recovery effort after this time. This could have resulted in less accurate estimates of the 95% CIs of the mean [^{137}Cs]s. We therefore could not determine whether this was truly representative of a long-term trend, or an artifact of smaller and less frequent samples.

The temperature-dependent model predicted that a greater fraction of effective equilibrium [^{137}Cs] would be attained in the 1st yr than we observed for the enclosure turtles (Fig. 5). One possible explanation for this is that the enclosure turtles might not have attained their maximal ingestion rates until some time after release, perhaps because of a lack of available food due to destruction of aquatic vegetation within the enclosures during their construction or during recapture efforts. Although we supplemented the food supply during the first active season, this may not have permitted normal feeding. Evidence for this is shown by the masses of the enclosure turtles. Covariate analysis of the model W (in kilograms) $= a + b$ time (in days), with individual turtle as the factor showed no significant growth for the 1st yr after release ($F_{9, 149} = 0.67$, $P = 0.73$), but masses increased significantly after this time ($F_{9, 155} = 4.19$, $P < 0.001$). Slopes of individual regressions of time on body mass for each turtle were also indistinguishable from zero ($P > 0.05$) in the 1st yr, but were significantly greater than zero for 7 of the 10 turtles after 1 yr. Of the three turtles showing insignificant increases in body mass, two were the turtles that died at the end of the second summer after release. To test the effect of a time-dependent increase in in-

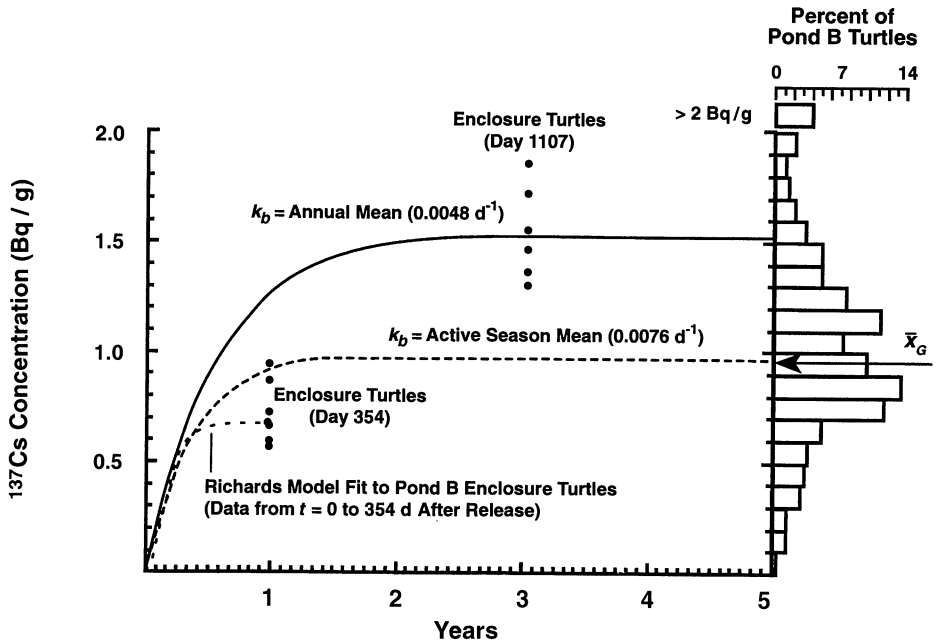

FIG. 6. Continuous models of ^{137}Cs uptake by Pond B *Trachemys scripta*. The solid line corresponds to negative exponential uptake when k_b is the estimated average for the entire year (0.0048 d^{-1}). The dashed line corresponds to negative exponential uptake when k_b is the average measured during the active season (0.0076 d^{-1}) only. The dotted line corresponds to a flexible-shaped Richards model fitted to the combined uptake data from the 10 Pond B enclosure turtles, using [^{137}Cs] data collected between 1 May and the end of the first winter (t = 0 to 354 d) after release only (also see Table 3 fit to all turtles). Symbols (●) indicate [^{137}Cs]s of uncontaminated turtles released into enclosures on Pond B, measured on days 354 and 1107 following release. The histogram shows the distribution of [^{137}Cs]s of 287 captures of 245 wild Pond B turtles. The geometric mean ($\bar{x}_G$) indicated on the histogram is the mean [^{137}Cs] for all wild Pond B turtles (including recaptures).

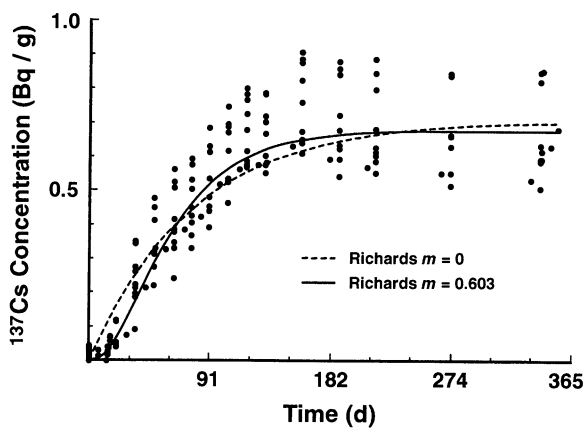

FIG. 7. Continuous models of ^{137}Cs uptake by Pond B *Trachemys scripta*. Symbols (●) indicate measured [^{137}Cs]s of turtles between their 1 May release into Enclosure 1 and the end of the first winter after release (t = 0 to 354 d). The curves show the results of nonlinear least squares regressions of Richards sigmoidal models fit to the combined [^{137}Cs] data for all turtles. The solid line indicates the curve fit using a stochastic Richards model (where the Richards shape parameter m was allowed to vary). The dashed line indicates the curve fit using a negative exponential model (i.e., a Richards model with m constrained at zero).

gestion rate, we also incorporated a linearly increasing ingestion function into the model, in which ingestion was increased from 0.4 to 1.0 of maximum over a 3-yr period. The resulting prediction (Fig. 5, dashed line) more closely matched both the magnitude and pattern of the observed uptake. Such a correction might not be necessary in simulating radionuclide uptake by free-ranging turtles already occupying the site and accustomed to feeding within it at the time of the radionuclide contamination event.

Simpler negative exponential and Richards models (Figs. 6 and 7, Table 3) also showed good correspondence with observed [^{137}Cs]s. The equilibrium [^{137}Cs] (0.97 Bq/g) predicted by the model with k_b equal to the estimated average for the active season (0.0076 d^{-1}, dashed line of Fig. 6) was extremely close to the geometric mean [^{137}Cs] of wild Pond B turtles (0.96 Bq/g). The equilibrium prediction (1.54 Bq/g) by a model with k_b equal to the estimated annual average (0.0048 d^{-1}, solid line of Fig. 6), although ≈50% greater, was very similar to the average annual [^{137}Cs]s of the enclosure turtles (≈1.6 Bq/g, with the mean annual average occurring during midsummer). Eight of the 10 enclosure turtles showed statistically significant de-

TABLE 3. Results of nonlinear least squares regressions of a Richards sigmoidal model fit to uptake data from the Pond B enclosure turtles (t = 0 to 354 d, with n indicating the number of measurements of each turtle). The estimated [^{137}Cs]s, biological elimination rate constants (k_b), and Richards shape parameters (m) during this period are shown, together with the coefficients of determination (R^2) for the regression fits, and the F statistics and significance levels for the tests of $m > 0$.

		Day 354 [^{137}Cs] (Bq/g)		Estimated k_b		Richards shape parameter (m)			Significance test of $m > 0$*	
Turtle	n	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	R^2	F	P
1	16	0.585	0.019	0.011	0.002	0.552	0.138	0.98	17.81	<0.005
2	16	0.647	0.019	0.010	0.001	0.566	0.094	0.98	21.49	<0.001
3	16	0.713	0.027	0.008	0.002	0.763	0.115	0.96	17.11	<0.005
4	17	0.863	0.018	0.011	0.001	0.573	0.068	0.99	41.97	<0.001
5	15	0.583	0.021	0.015	0.002	0.463	0.145	0.96	7.26	<0.025
6	16	0.608	0.023	0.007	0.001	0.760	0.094	0.97	23.21	<0.001
7	17	0.956	0.025	0.012	0.001	0.237	0.183	0.98	0.74	NS
8	15	0.675	0.021	0.010	0.002	0.692	0.116	0.97	16.34	<0.005
9	17	0.585	0.018	0.011	0.001	0.577	0.114	0.97	13.70	<0.005
10	15	0.878	0.032	0.013	0.001	0.302	0.167	0.97	2.79	NS
All	160	0.678	0.028	0.010	0.002	0.603	0.148	0.88	44.62	<0.001

* df = 1, $n - 4$.
NS = not significant at the $P = 0.05$ level.

partures from a negative exponential uptake pattern (Table 3) during the first 354 d after release into the enclosures, illustrating the greater utility of the Richards model in estimating ^{137}Cs in this species. The average equilibrium predicted by the Richards model fit to the combined uptake data from all Pond B enclosure turtles (dotted line of Fig. 6, solid line of Fig. 7) was approximately two-thirds of the geometric mean [^{137}Cs] of wild Pond B turtles, but direct comparisons of the Richards model to other models must consider that this fit was made to uptake data from the 1st yr after release only, with the asymptote reflecting decreased winter intake and elimination rates, rather than attainment of equilibrium [^{137}Cs]s.

The predictions of the time-integrated [^{137}Cs]s for the temperature-dependent and the negative exponential models based on the annual average k_b (the areas under the solid lines of Figs. 5 and 6, respectively) differed only slightly. The negative exponential model prediction of annual integrated [^{137}Cs] was 2492 Bq-d/g for the first 5 yr after release, compared with 2196 Bq-d/g for the temperature-dependent model (13% difference). This would suggest that the simpler negative exponential model represents a conservative estimate of integrated [^{137}Cs]. However, the situation changed as the two models approached equilibrium. When model runs were extended beyond 5 yr, the negative exponential model's prediction of integrated [^{137}Cs] was $\approx$ 562 Bq-d/g for each year after the initial five, while the temperature-dependent model prediction was $\approx$ 580 Bq-d/g ($\approx$3% greater) each year. The prediction of annual integrated [^{137}Cs] by a negative exponential model based on the estimated average active season k_b (dashed line of Fig. 6) was considerably less than that of the temperature-dependent model (1649 Bq-d/g for the first 5 yr, and 355 Bq-d/g each year thereafter), suggesting that the accurate estimation of elimination rates, including their changes during different seasons, is important in successfully predicting cumulative ^{137}Cs exposure in this species.

Sensitivity analysis of the temperature-dependent model

We found a significant relationship between the model parameters described in Table 2 and the 5-yr time-integrated [^{137}Cs] output values predicted by the temperature-dependent model. However, there was a relationship between the regression residuals and the untransformed model output values. A square-root transformation was therefore applied to stabilize the variance of the dependent variable and prevent violation of the assumption of homoscedasticity (Kleinbaum et al. 1988). These $\sqrt{\text{time-integrated [}^{137}\text{Cs]}}$ values were regressed against the parameters described in Table 2 ($F_{15, 258} = 137.4$, $P < 0.001$). The overall coefficient of determination for the regression model was high ($R^2 = 0.89$), indicating that nearly 90% of the variance in model results related linearly to variation in the model parameters, with nonlinear interactions among model parameters accounting for the remaining model variance (Bartell et al. 1992). Table 4 shows the squares of the partial correlation coefficients (R^2) for the model parameters, ranked in order of the magnitudes of their linear correlations with the model output values. Parameters associated with assimilation, with the temperature-dependent ingestion rate (r_T), and with the maximum effective biological elimination rate constant ($k_{b_{MAX}}$) showed the highest partial correlations with $\sqrt{\text{time-integrated [}^{137}\text{Cs]}}$.

Multiple-partial F tests (Table 5) of the R^2 values of the reduced models compared with Full Model I also indicated that the r_T, a, and k_{b_T} parameters contributed most to the prediction of model output values, with $r_T > a > k_{b_T} > C_f > f > T_{w_t}$. We obtained similar results for Full Model II, with $a > r_T > k_{b_T} > C_f > f > T_{w_t}$.

TABLE 4. Squares of partial correlation coefficients for parameters used as independent variables in a multiple regression on $\sqrt{\text{time-integrated [}^{137}\text{Cs]}}$, ranked by the magnitude of their linear correlations with the model output values. Numbers in brackets correspond to parameters of the conceptual model (Fig. 1). Parameter descriptions are given in Table 2.

Parameter	Partial R^2
[13] a	0.9420
[5] $r_T(\beta_1)$	0.8534
[7] $r_T(\beta_3)$	0.5599
[4] $r_T(\beta_0)$	0.4172
[14] $k_{b_{MAX}}$	0.4083
[6] $r_T(\beta_2)$	0.1043
[12] $C_{f(\text{plants})}$	0.0639
[10] $C_{f(\text{fishes})}$	0.0465
[8] f_{fishes}	0.0357
[1] $\bar{T}_w$	0.0039
[2] $\hat{T}_w$	0.0024
[9] $f_{\text{invertebrates}}$	0.0008
[3] $\tilde{t}$	0.0008
[11] $C_{f(\text{invertebrates})}$	0.0007
[15] $k_{b_{MIN}}$	0.0002

However, when we included the interactions between the T_{w_t} parameters and the parameters associated with r_T and k_{b_T} in the regression model, there were only trivial improvements in predictive ability (Full Model II: $F_{33, 240} = 62.05$, $P < 0.001$, $R^2 = 0.90$) despite the addition of 18 additional independent variables. A multiple-partial F test of both Full models (No T_{w_t} Parameter Interactions regression, Full Model II, Table 5) showed no significant improvement in predictability as a result of the combined addition of the interaction terms for $\bar{T}_w$, $\hat{T}_w$, and $\tilde{t}$. In fact, neither Full model showed significant improvement in predictability from the combined addition of the T_{w_t} parameters (Table 5). This result agreed with the low proportion of model variance explained by nonlinear interactions among model parameters and suggests that our model is relatively insensitive to uncertainties in the estimates of water temperature as a function of time of year. Our regression model of T_{w_t} (Eq. 9) appeared to be a better predictor of higher temperatures across years than it was for some of the extreme winter lows (Fig. 2), but we also assumed no ingestion at $\leq 15°C$. As mentioned above, we estimated similar temperature parameters from the two available data sets (Fig. 2), one of which contained many more data points. Thus, adequate estimates of temperature-dependent ingestion and elimination may require relatively few measurements of ambient conditions at sites of interest.

Our results also indicated that our model was relatively insensitive to uncertainties in diet composition, and in estimates of [^{137}Cs]s within dietary components, compared with the effects of a, r_T, and k_{b_T}, but both f and C_f contributed significantly to the predictive ability of both Full regression models (Table 5). In both Full model tests, the model showed greater sensitivity to uncertainties in estimating [^{137}Cs] in food than to uncertainties in estimating dietary composition, but all R^2 values for these variables were < 0.07.

DISCUSSION

The metabolic status of an animal at the time of contaminant release may greatly affect the importance of the various exposure pathways and their contribution

TABLE 5. Results of parameter sensitivity analysis, showing multiple-partial F statistics (Kleinbaum et al. 1988, also see Eq. 17) calculated for the effects of the removal of groups of model parameters from multiple regressions on $\sqrt{\text{time-integrated [}^{137}\text{Cs]}}$. Full Model I is a multiple regression of the 15 model parameters listed in Table 2 on $\sqrt{\text{time-integrated [}^{137}\text{Cs]}}$. Full Model II is a multiple regression of the same 15 model parameters, but includes the 18 first-order interactions of the three temperature parameters, T_{w_t}: $\bar{T}_w$, $\hat{T}_w$, and $\tilde{t}$, with the four temperature-dependent ingestion, r_T: $r_T(\beta_0)$, $r_T(\beta_1)$, $r_T(\beta_2)$, and $r_T(\beta_3)$, and two biological elimination rate, k_{b_T}: $k_{b_{MAX}}$, and $k_{b_{MIN}}$, parameters.

Model	R^2	df	Multiple-partial F	P
Full Model I (no T_{w_t} parameter interactions)	0.8887	15, 258		
Reduced Models				
No T_{w_t} parameters	0.8879	3, 258	0.63	NS
No r_T parameters	0.1972	4, 258	400.82	<0.001
No k_{b_T} parameters	0.8117	2, 258	89.31	<0.001
No f parameters	0.8845	2, 258	4.89	<0.005
No C_f parameters	0.8744	3, 258	11.06	<0.010
No a parameter	0.8116	1, 258	178.74	<0.001
Full Model II (with T_{w_t} parameter interactions)	0.8951	33, 240		
Reduced Models				
No T_{w_t} parameters	0.8949	3, 240	0.13	NS
No T_{w_t} parameter interactions	0.8887	18, 240	0.81	NS
No T_{w_t} parameters or T_{w_t} parameter interactions	0.8879	21, 240	0.78	NS
No r_T parameters or r_T parameter × T_{w_t} parameter interactions	0.2082	16, 240	98.21	<0.001
No k_{b_T} parameters or k_{b_T} parameter × T_{w_t} parameter interactions	0.8262	8, 240	19.70	<0.001
No f parameters	0.8907	2, 240	5.02	<0.010
No C_f parameters	0.8814	3, 240	10.43	<0.001
No a parameter	0.8244	1, 240	161.79	<0.001

to the total radiation dose. The annual cycling of [^{137}Cs]s that we observed in Pond B *T. scripta* appeared to be the result of temperature-dependent metabolism and its influence on uptake and elimination rates. Our model indicated a strong relationship between temperature and both contaminant uptake and loss in this species, suggesting that the responses of such ectotherms to contaminants with short ecosystem residence times may be dependent on the time (season) of contaminant release. This relationship was in fact predictable from annual temperature patterns and their relationships to ingestion and elimination rates. However, covarying seasonal influences on dietary composition and in the [^{137}Cs]s of food species may also play a role in such cycling. The dose effects from uptake of short-lived radionuclides seem particularly likely to be sensitive to such seasonal differences in food consumption rate, food type, and availability. For example, some species may feed during certain seasons on uncontaminated food stored before the time of the radionuclide release. In our model, ingestion was the major route of radiocesium intake, but similar results might be expected when inhalation would be a major exposure pathway (e.g., radionuclide gases or aerosols). A release of the same radionuclide in winter would likely have less effect on ectotherms than in the summer because ectotherm temperature-dependent respiration, feeding, and excretion rates would all be depressed relative to their levels in the warmer seasons. However, even endotherms may hibernate or overwinter in refugia (as *T. scripta* does [Standora 1982]), thus avoiding all but minimal contact with winter-released radionuclides.

Long-term equilibrium [^{137}Cs]s of the resident Pond B population were predictable from average annual temperatures, suggesting that responses by ectotherms to long-lived contaminants may not differ substantially from those of endotherms, and may be predictable without complex modeling of the thermal environment. However, we emphasize that the ingestion rate used in our two negative exponential models (Fig. 6) was derived from knowledge of temperature-dependent ingestion patterns and elimination rates. Although the difference in the predictions of cumulative exposure by these two models was small, the cumulative effect of these differences on predictions of lifetime risk should be evaluated. *Trachemys scripta* require 7 yr to reach reproductive age, and can live a further 10–15 yr as adults (Frazer et al. 1990).

The use of the Richards model with a flexible m value was clearly preferable to a model with a fixed m value (negative exponential model) in describing initial ^{137}Cs uptake in this species. The values for m calculated for most of the individual turtles (Table 3), as well as the value calculated for all turtles combined ($m = 0.603$) indicated an uptake curve shape that more closely resembled the trajectory that would be produced by a von Bertalanffy model (where $m = 0.667$) than the trajectory of a negative exponential model. This deviation from negative exponential kinetics confirms a general pattern observed for other contaminants and in other species (Potter 1987, Brisbin et al. 1990). In our study, the enclosure turtles were restricted in their access to the food resources of the entire pond, yet these deviations from a negative exponential uptake still occurred despite the fact that food availability was maximal during the first days of uptake (when supplemental contaminated food was provided). Similar deviations from negative exponential uptake have also been observed when transplanted American coots were permitted unrestricted movement on Pond B (Potter 1987, Brisbin et al. 1990). This might be considered to represent a "travel lag" effect (Brisbin et al. 1990), in which organisms stressed from capture and introduction into a new habitat exhibit initial intake rates that are reduced relative to the eventual maximum attained after they acclimate to new conditions and diets. However, these same uptake patterns have also been observed to occur in mosquitofish (*Gambusia affinis*) when uptake of mercury was via absorption from water, with the mercury being introduced after the fish were already acclimated (Brisbin et al. 1990). These patterns may be a result of TBBs representing the summation of the contaminant contents of different body compartments (e.g., gut contents, soft tissues, and bone), which differ in the rates at which they accumulate and/or eliminate contaminants (Matis et al. 1991). The underlying mechanism of these deviations may therefore relate to physiological processes, such as different rates of formation of complexes between contaminants and the active transport enzymes of cell membranes, as well as to the time required for such exchange sites to reach saturation.

The 95% CI for [^{137}Cs] of the wild Pond B turtles collected in the active season was less (±6% of the mean) than the interval between annual maximum and minimum concentrations predicted by our temperature-dependent model (± 30% of the mean). Samples of *T. scripta* taken throughout the year might therefore be expected to exhibit detectable cycling. However, the collective range of average annual [^{137}Cs]s of all enclosure turtles was also greater than the annual range of concentrations of each individual enclosure turtle, and appeared to represent a size-dependent pattern similar to that observed for the wild population. The different relationships between [^{137}Cs] and mass for the two sexes may complicate detection of cycling patterns if seasonal samples contain differing proportions of individuals of different body sizes or sexes, unless corrections are made for these effects. *Trachemys scripta* are sexually size dimorphic (♀♀ larger than ♂♂), and a number of collection methods have been observed to yield sex-biased results in different seasons (Gibbons 1990*b*). The ♂:♀ sex ratio we observed (1.09) was close to unity, but other population estimates of Pond B *T. scripta* have shown greater ratios of ♂♂ to ♀♀. An independent estimate of the Pond B *T. scripta* pop-

ulation made during 1987–1990 (J. Greene, Savannah River Ecology Laboratory, *personal communication*) indicated a ratio of 1.83, with 249 individuals captured (143 ♂, 78 ♀, and 28 immature). An earlier estimate (Gibbons 1990*c*) was 2.37 for all adults, or 1.41 for adults > 100 mm plastron length. Differences in the sex ratios obtained in the collection of validation data may therefore influence the statistical descriptions of contaminant concentrations in other modeling efforts.

We observed only a weak association between capture location and [^{137}Cs] for the wild Pond B turtles. Pond B mosquitofish also showed a general lack of a relationship between location and [^{137}Cs] (Newman and Brisbin 1990), except that ♂♂ collected near the entrance to the R canal (through which the radionuclides were discharged into Pond B, and which is much more highly contaminated than the reservoir) had mean [^{137}Cs]s ≈40% greater than ♂♂ collected at the spillway or the northern end of the pond (farthest from the R canal). However, our closest trap location to the R canal was over 300 m from the R canal entrance, at the edge of the main lake basin. The topography of the Pond B is such that the main flow of water moves directly past this location, across the main channel, and over the spillway. There is also considerable wind-induced wave action at this site, which may scour away contaminated sediments. In contrast, we observed that the turtles with the highest [^{137}Cs]s were from the northern end of the reservoir, farthest from the R canal. However, the sediments in this location are protected from erosion by a dense growth of aquatic macrophytes, and these sediments have the highest [^{137}Cs]s (Whicker et al 1990*b*).

The wild Pond B turtles showed no indication of decreasing ^{137}Cs body burdens over the 4 yr that measurements were taken. On the basis of removal by radioactive decay alone, ≈91% of the total ^{137}Cs present in Pond B in 1987 should still have been present in 1990. Our predicted estimates of mass-dependent turtle body burdens had 95% confidence limits that were too broad to reveal a decrease of this magnitude (with lower and upper CL ranging from approximately ± 7 to 11% of the mean TBB). Future measurements may reveal that ^{137}Cs TBBs of Pond B *T. scripta* are decreasing with time, but several decades may have to elapse before these decreases become statistically significant. This result also suggests that any other physical and/or biological processes that may be acting to decrease ^{137}Cs availability to Pond B *T. scripta* (e.g., progressive burial of ^{137}Cs-contaminated sediments by detritus and sedimentation, removal of aqueous $^{137}Cs^{+}$ via drainage) are isolating or removing the radionuclide at a collective rate that is even slower than the rate of radioactive decay.

Although we made allowances for the uncertainty of [^{137}Cs] in food between model runs, we made no attempt to simulate potential seasonal changes in the dietary concentration of [^{137}Cs] within model runs. However, the model was relatively insensitive to changes in the dietary parameters, and this may be due to the fact that although the average $C_{f(\text{fishes})}$ was higher (25.3 Bq/g) and the average $C_{f(\text{invertebrates})}$ was lower (6.1 Bq/g) than the average $C_{f(\text{plants})}$ (15.2 Bq/g), the relative contributions of these three categories to the total diet resulted in an average overall C_f (15.5 Bq/g) that was nearly identical to that of plants alone (Table 1). Our sensitivity analyses suggest that diets would have to include substantially different proportions of invertebrates or fish to significantly affect the average C_f. However, the low correlation coefficients for these parameters (Table 4) suggest that more detailed studies of diet composition and [^{137}Cs] are unlikely to greatly improve the accuracy of model predictions of ^{137}Cs uptake in this species.

Our estimates of [^{137}Cs]s in food were based on samples primarily collected during the winter (Whicker et al. 1990*b*), and both plant and animal populations may change in [^{137}Cs] throughout the year (Kelly 1988, Whicker 1990*b*). Pond B aquatic macrophytes have been shown to vary in [^{137}Cs] due to seasonal changes in leaf production and senescence rates and to changes in ^{137}Cs physical and/or chemical availability (Kelly 1988). Pond B invertebrates and fish fed upon by *T. scripta* might also show seasonal variations in [^{137}Cs] similar to that observed for the turtles. Such cycles have been observed in several species of fishes from White Oak Lake, Tennessee (Kolehmainen and Nelson 1969, Nelson 1969), although bluegill from Par Pond (Harvey 1964) and largemouth bass from Pond B (Whicker et al. 1990*b*) did not so vary. Again, variation in [^{137}Cs]s of fish samples collected in different seasons may be obscured by similar factors as for turtles (e.g., size-dependent TBB), as annual extremes in the fish populations showing such cycling have only been approximately ± 25% of the mean (Kolehmainen and Nelson 1969, Nelson 1969). If this relatively narrow range in annual concentration extremes of both fish and turtles is typical of contaminant behavior in ectotherms, this may simplify the prediction of concentration levels and assessments of ecological risk in these animals.

The most important areas of model uncertainty appear to be seasonal changes in food intake rates and the assimilation rates actually achieved by turtles in Pond B. As is obvious from our results, finding suitable predictive functions for ingestion rates can be difficult, particularly when extrapolating from laboratory estimates. However, our results suggest that reliable estimation of ingestion rate is of critical importance in determining [^{137}Cs]s in *T. scripta,* and this agrees with the results of a similar study of plaice (*Pleuronectes platessa*), in which food intake explained ≈70% of [^{137}Cs] (Evans 1988).

We found difficulty in estimating the ^{137}Cs assimilation fraction (*a*) for *T. scripta*: most studies of alimentary assimilation of ^{137}Cs by animals are for free ions in aqueous solution, which may not reflect chem-

ical availability of the radionuclide in natural diets, especially for incidentally ingested soils or sediments. In the bluegill (*Lepomis macrochirus*), assimilation efficiency changed with the type of dietary item (Kolehmainen and Nelson 1969), and with body size (possibly due to differences in gut turnover rates). The ^{137}Cs assimilation from a particular dietary item also depended on its assimilation state within that item. For example, the a of *L. macrochirus* was only 0.07 when fed insect larvae reared on ^{137}Cs-contaminated sediments, but increased to 0.69 when fed insect larvae reared on ^{137}Cs-contaminated algae (Kolehmainen and Nelson 1969). The a from ingested detritus (0.03), was similar to that for sediment-contaminated insects, while the a from algae (0.69) matched that from algae-fed insect larvae. This indicates that for this species at least, ^{137}Cs adsorbed to sediments was much more refractory to dietary assimilation than was ^{137}Cs associated with body tissues. A better understanding of the potential effects of diet and the physiochemical environment on radionuclide assimilation is thus clearly desirable for this model. However, measurement of assimilation for complex natural diets at different temperatures may be difficult. Nevertheless, even given the possibility of an exaggerated effect on the model through the broad range of a values we assumed, our model results indicated that assimilation may be one of the most important site- or species-specific parameters for the predictive modeling of ectotherm contaminant uptake. The importance of k_{b_T} (especially $k_{b_{MAX}}$) in our model indicates that obtaining a better predictive relationship between temperature and radionuclide elimination would also be desirable.

There is a 6- to 30-fold difference in the expected metabolic rates of endotherms and ectotherms of equal body sizes, depending on temperature (Peters 1983, Pough et al. 1989). American Coots (*Fulica americana*) and yellow-bellied turtles (*Trachemys scripta*) have significant overlap in both body mass and diets in Pond B (Parmenter 1980, Potter 1987), which suggests that the q_{eq}s of these species might differ by a similar magnitude to the difference in their metabolic rates. However, the whole-body ^{137}Cs concentrations ($\pm$ SE) of populations of these species in Pond B were 3.7$\pm$0.4 Bq/g for coots (Potter 1987), and 0.96$\pm$0.04 Bq/g for turtles (this study), a less than fourfold difference. Both our time-dependent model and the data from the introduced enclosure turtles indicate that the time required to reach 0.9 of q_{eq} is $\approx$2 yr, $\approx$30 times longer than the $\approx$24 d required for American Coots (Potter 1987). When estimates of time to 0.9 q_{eq} are made using negative exponential models, the range is from 302 d (when k_b is the average we measured during the active season [=0.0076 d^{-1}]) to 479 d (when k_b is our estimated average for the entire year [=0.0048 d^{-1}]), a 13–20 fold difference. Thus, the net effect of the differences in r, a, and k_{eff} between endotherms and ectotherms may be best represented by the *time* required to achieve an effective q_{eq} (rather than by the q_{eq} levels themselves). This perhaps reflects integrated metabolic output, and may therefore be a potential means of comparing relative metabolic rates of species sharing similar habitats and diets. The annual cycling of [^{137}Cs]s also suggests that a correlation may exist between feeding rates and ^{137}Cs turnover in the body. Measurements of the turnover of other Group IA alkali metals (^{22}Na and ^{86}Rb) have been used to estimate ingestion rates in the field (e.g., Gallagher et al. 1983, Green et al. 1986). Our validation of the predicted temperature-dependent ingestion rates of *T. scripta* by predicting [^{137}Cs] behavior in the field suggests that radionuclides of other alkali metals (e.g., ^{134}Cs or ^{86}Rb, both with shorter physical half-times) may also be useful for this purpose (Peters et al. 1995).

Several questions persist concerning the ^{137}Cs kinetics of *T. scripta*. The positive relationship between turtle mass and [^{137}Cs] for both the wild and enclosure female turtles is the opposite of the trend observed for Pond B mosquitofish (Newman and Brisbin 1990) and the trend expected from a decline in mass-specific ingestion rate with increasing mass (Peters 1983). Assuming constant exposure for all members of the population, departures from a slope of 1 in the TBB = aW^b relationship suggest the possibility of size-dependent behaviors (e.g., ingestion rates, activity) or in the number of tissue-binding sites, which would influence ^{137}Cs assimilation, retention, and excretion (Newman and Brisbin 1990). Paradoxically, we have observed (Peters and Brisbin 1988) that ^{137}Cs biological half-time *decreases* significantly with increased mass in *T. scripta* (which other factors being equal, should also decrease equilibrium [^{137}Cs]s), again in contrast with other vertebrates (Reichle and Nelson 1970, Mailhot et al. 1989). An increase in [^{137}Cs] with increasing size might be partly explained in *T. scripta* by an ontogenetic shift away from a juvenile diet containing a greater proportion of invertebrates of lower [^{137}Cs] to one containing a greater proportion of plants (Hart 1983), or by changes in dietary potassium due to this shift. However, our results suggest that dietary [^{137}Cs] alone is unlikely to influence greatly equilibrium [^{137}Cs] levels (Table 4). The differences in assimilation efficiency due to the longer gut passage times of adults (Parmenter 1981) and the possible influence of the alimentary environment on ^{137}Cs assimilation may be more important in explaining this pattern.

Although the [^{137}Cs]s of Pond B *T. scripta* are, on a mass basis, quite low (averaging $\approx$300 pg/kg turtle) the combined internal and external exposure from ^{137}Cs and other radionuclides in Pond B appears to be sufficient to produce measurable biological effects in this species. Flow cytometric analyses of *T. scripta* inhabiting seepage basins on the SRS containing chemical and radiological contaminants have revealed increased variation in the DNA content of the turtles' red blood cells, as well as multiple DNA peaks in some specimens that

suggest aneuploid mosaicism (Bickham et al. 1988). These types of genetic damage are also evident in the Pond B population (Lamb et al. 1991), where radionuclide levels are much lower. Moreover, the genetic anomalies observed in the Pond B population cannot be attributed to the turtles having been exposed to chemical contaminants released into the pond along with the radiological waste.

Our results demonstrate the importance of considering the physiological ecology of animal species when developing predictive models of contaminant uptake in an environmental context. Although this paper has focused on ^{137}Cs kinetics in an ectotherm, we believe that many of the features of the model we have described should be true also for other types of contaminants. Also, other taxa that display environmentally dependent metabolic rates or activity patterns (e.g., invertebrates) may also exhibit similar deviations from continuous uptake patterns. Our results suggest that important knowledge of the patterns and processes of contaminant cycling in natural systems can be gained by developing predictive models based on knowledge of the interactions between animals and their environment, and testing such models against independent validation data from native and experimentally introduced animals. Stochastic modeling techniques can aid in identifying those factors that explain the greatest proportion of model variation, and can aid in planning further research efforts to reduce these uncertainties and improve model predictions. Manipulative laboratory experiments can allow further exploration of the patterns of contaminant kinetics in animal species and their responses to changes in physiological or environmental conditions. A logical next step in our modeling efforts would be to develop the relationships necessary to convert internal body burdens and external exposure rates into quantitative dose estimates. Comparisons of such estimates with information on genetic responses should yield important information on the effects of chronic low-level radiation exposure on this species, and may lead to radionuclide risk assessments that are based on mechanistic, rather than correlative processes.

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