Arch. Environ. Contam. Toxicol. 30, 241–251 (1996)

ARCHIVES OF
Environmental Contamination and Toxicology

A Spatial Energetics Model of Cadmium Accumulation by Diving Ducks

J. R. Lovvorn[1], M. P. Gillingham[2]

[1] Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071, USA
[2] Faculty of Natural Resources and Environmental Studies, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia V2N 4Z9, Canada

Received: 20 June 1995/Revised: 5 September 1995

Abstract. Food-chain transfer of contaminants is often predictable below the level of birds, but relations between contaminant concentrations in birds and their foods are often weak and variable. Much of this variation probably results from the energetics of foraging in fluctuating, heterogeneous environments, which has not been accounted for in past models of contaminant uptake by birds. Because birds are highly mobile with varying lengths of stay in different areas, collecting birds and analyzing their tissues yields unclear information on the importance of local contaminants. Likewise, toxicity assays with captive birds ignore changes in food intake with varying activity and weather experienced by wild birds. Neither of these approaches alone can predict maximum allowable contaminant levels in foods that avoid toxic effects under different field conditions, or what body burdens accumulate during varying lengths of stay that might affect the birds' biology at other places and times. To allow such predictions, an individual-based computer model was developed to simulate the intake of contaminated foods by diving ducks for varying conditions such as weather, water depth, food dispersion, and the size and digestibility of food. Food-intake estimates are combined with laboratory data on contaminant uptake as a function of food consumption and contaminant content. As an example, cadmium uptake is estimated for Canvasback ducks (*Aythya valisineria*) foraging on belowground winter buds of the submerged plant *Vallisneria americana*. Results indicate that relations between cadmium content of food and cadmium uptake by kidneys can be quite different depending on field conditions, and that cadmium content of food can be less important than food dispersion and resulting search costs in determining cadmium uptake. Models that estimate food intake based on energetic profitability can yield very different predictions than models that assume constant daily intake, or assume that food intake simply increases as energy costs of thermoregulation or other factors go up. Such profitability effects might explain much of the confounding variation in deriving bioaccumulation factors for birds.

Studies have shown that the toxicity of given tissue levels of contaminants can vary with an animal's energy balance (Porter *et al.* 1984; Lemly 1993). However, less attention has been paid to the fact that exposure rates of animals eating contaminated foods also vary with energy budgets and associated intake rates. For example, variations in contaminant levels in migratory birds from different sites are often presumed to track different contaminant levels in foods (Vermeer and Peakall 1979; Mora *et al.* 1987; Ohlendorf *et al.* 1991; Vermeer *et al.* 1993). However, contaminant concentrations in tissues often show weak and variable correlations with levels in foods, making it difficult to predict contaminant uptake by predators based only on contaminant content of prey (Kay 1985; Skorupa and Ohlendorf 1991; Ferns and Anderson 1994).

Much of this variation in tissue contaminant levels probably results from the energetics of foraging in fluctuating, heterogeneous environments (Hohman *et al.* 1990a; Belovsky 1994; Pulliam 1994). For example, Skorupa and Ohlendorf (1991) demonstrated that food-chain transfer of selenium to waterbird foods can be predicted rather accurately from selenium concentrations in water, but that concentrations in bird eggs are seldom predictable from selenium levels in bird foods. They stated that avian behavioral ecology, rather than avian physiology per se, appears to be the main source of confounding variation.

Nevertheless, past models of dietary contaminant uptake by birds have assumed constant food intake rates. These rates have been estimated mostly from studies of captive birds or from body-mass allometry over many taxa, and have not considered variability in foraging behavior and energetics under diverse field conditions (DuBowy 1989; Skorupa and Ohlendorf 1991; Peterson and Nebeker 1992). For example, a recent innovative treatment of spatial components of contaminant exposure (Clifford *et al.* 1995) assumed that animals spent equal foraging effort in all parts of their activity range, and were exposed to constant contaminant levels averaged over this range. However, food dispersion in aquatic habitats is commonly associated with varying sediment characteristics (Hicklin and Smith 1984), which often correlate with contaminant content of sediments and foods (Rule and Alden 1990; Holland *et al.* 1993). Thus, models that do not account for the influence of food dispersion

---

Correspondence to: J. R. Lovvorn

on foraging profitability and intake rates will often be poor predictors of tissue contaminant levels of birds in the field (Skorupa and Ohlendorf 1991).

In general, measurements of contaminants in free-ranging birds have included two main approaches: (1) collecting birds and analyzing their tissues (see references below), and (2) collecting and analyzing feathers (Pilastro *et al.* 1993). Effectiveness of these approaches is limited by the fact that birds are highly mobile. One seldom knows, especially during migration or winter, how long an individual bird has been in a certain area (White *et al.* 1983; Henny *et al.* 1990, 1991; Mahaffy *et al.* 1995). If the bird has been there for only a short period, tissue residues might not reflect the full potential for contamination at that site. Conversely, the bird might have acquired contaminants elsewhere, so that high tissue residues have little to do with contaminants at the site where the bird was collected (Boellstorff *et al.* 1985; Henny *et al.* 1991, 1995). It is often desirable to predict contaminant accumulation by birds migrating through or wintering in a contaminated area, uptake which might affect the birds' biology at other places and times (Stickel *et al.* 1977; Boellstorff *et al.* 1985). Because of variable lengths of stay among individual birds, contaminant uptake rates at a given site often cannot be estimated simply by collecting birds or their feathers.

Uptake and toxicity assays with captive birds avoid the above uncertainties, but do not account for changes in food intake with varying activity, weather, and food availability experienced by free-ranging birds. Actual exposure to contaminants depends not only on contaminant concentrations in food, but also on the amount of food eaten (DuBowy 1989; Peterson and Nebeker 1992; USEPA 1993). Thus, studies of captive birds fed diets containing different contaminant concentrations will incompletely reflect contaminant intake that occurs in the field.

Despite these shortcomings, these empirical methods are essential to the modeling approach proposed in this paper. But without quantitatively integrating these disparate kinds of information into a multifactor, ecological context, these methods alone provide limited predictive capabilities for environmental decision-making (Kendall and Lacher 1994). For example, they do not yield predictions of the maximum allowable contaminant levels in foods that avoid toxic effects under different field conditions, such as varying weather, water depth, time spent flying because of human disturbance, or food dispersion as it affects search costs and accessibility of contaminants in foods. Such information is important to predicting contaminant risk to birds under various cleanup scenarios, and to setting regulations for the maximum allowable contaminant levels in water, sediments, or foods (cf. DuBowy 1989; Skorupa and Ohlendorf 1991; Peterson and Nebeker 1992; Clifford *et al.* 1995).

To allow such analyses for diving ducks, a computer simulation model was developed based on experimental and field data (see Lovvorn and Gillingham 1996). The model estimates food intake by ducks for varying combinations of factors that affect their behavior and energetics. Food-intake estimates are then combined with data on tissue uptake by captive ducks as a function of both contaminant content of food and the amount of food eaten. As an example, cadmium uptake is estimated for Canvasback ducks (*Aythya valisineria*) foraging on belowground winter buds of the submerged plant *Vallisneria americana.* This individual-based modeling approach can be used to estimate bioaccumulation factors (BAFs = tissue concentrations/concentrations in food) under different field conditions (cf. Szefer and Falandysz 1987; DuBowy 1989; Skorupa and Ohlendorf 1991; Peterson and Nebecker 1992), as well as variability in BAFs due to differences among individuals in heterogeneous environments (Madenjian *et al.* 1994).

Methods

For computer simulations, the foraging energetics model described in detail by Lovvorn and Gillingham (1996) was modified. Model food grids of *Vallisneria* winter buds were generated from core samples taken in Lake Mattamuskeet, North Carolina. In the model, written in QuickBasic 4.5 (Microsoft, Redmond, Washington), an individual Canvasback was randomly placed on a food grid and began foraging. A foraging bout (sequence of dives in one or more foraging "loci" as defined below) ended when the duck either filled its esophagus or dropped below a certain energy deficit. Cadmium concentrations in the kidneys were calculated based on model estimates of food intake and equations for cadmium assimilation derived from experiments on captive ducks. We chose cadmium for simulation analyses for several reasons. First, cadmium levels are often elevated in diving sea ducks (Mergini) (Lande 1977; Di Giulio and Scanlon 1984b; Frank 1986; Henny *et al.* 1991, 1995 and refs. therein; Ohlendorf *et al.* 1991), although not in Canvasbacks or other *Aythya* spp. in areas studied to date (White *et al.* 1979; Di Giulio and Scanlon 1984b; Miles and Ohlendorf 1993). Second, experimental data were available on cadmium uptake by duck kidneys as a function of the amount of contaminated food eaten (Di Giulio and Scanlon 1984a). Third, cadmium uptake is dose-dependent and cumulative without significant short-term depuration (elimination from the body) (Scheuhammer 1987), which allows straightforward models relating cadmium intake to kidney concentrations.

With the model, uncertainty analyses were performed to evaluate the relative influence of different environmental, energetics, and assimilation parameters on cadmium levels in the kidneys. Response surfaces were then generated to explore interactions between cadmium content of food and selected environmental variables in determining kidney cadmium uptake.

Energy Expenditure

Field data for energetics modeling were collected at Lake Mattamuskeet, North Carolina, which is <1 m deep throughout and has abundant stands of the submerged plants *Vallisneria americana* and *Potamogeton perfoliatus* (Lovvorn 1989a). Canvasbacks at Lake Mattamuskeet eat almost exclusively the belowground winter buds of *Vallisneria* (Lovvorn 1987). Procedures for observing behavior of Canvasbacks were described in detail by Lovvorn (1989b). During the prewinter fattening period on Lake Mattamuskeet (Lovvorn 1994b), Canvasbacks foraged continuously and did not appear to leave the lake at night, so daytime behavior patterns are assumed to extend through the night (see Lovvorn and Gillingham 1996). Percent time spent by Canvasbacks in activities other than surface-swimming and diving were assumed constant in all model simulations.

Mechanical costs of diving to different depths for different durations were calculated from the model of Lovvorn *et al.* (1991) and Lovvorn and Jones (1991) for diving ducks (*Aythya* spp.). For that model, hydrodynamic drag of ducks frozen in a diving posture was measured in a tow tank. Buoyancy was calculated as the difference between body weight and the weight of water displaced by restrained ducks submerged head-down in a water-filled cylinder. In model calculations, buoyancy was adjusted for compression of respiratory and plumage air spaces with depth. Ducks descending in a tank 2 m deep were filmed at 100 frames/s to determine linear displacement at 0.01-s intervals during a stroke cycle (including power and recovery phases). Work during these intervals was calculated by multiplying drag and buoyancy by displacement, and then adding inertial work done in accelerating the body and the added mass of entrained water. Work during all intervals was then integrated over the power phase to yield work per stroke during descent. Work per stroke at the bottom was calculated by multiplying the buoyant force by the distance the bird would float upward during the time required for a stroke (Lovvorn *et al.* 1991). Counts of strokes needed to reach the bottom and remain there (from video films, see Lovvorn 1994a) allowed calculation of total work during dives.

Stroke rates and speeds of descent and ascent at water depths from 1.2 to 2 m were interpolated from video measurements at those two water depths (Lovvorn 1994a). Stroke rates and speeds for 1.2 m and 2 m were used for shallower and deeper depths, respectively. Work during descent was calculated twice for each depth, once with buoyancy equal to that measured at the surface and once with buoyancy adjusted for hydrostatic pressure at the bottom. These two work values were then averaged for dives to given depths (Lovvorn and Jones 1991).

Water temperature in shallow (<1 m) Lake Mattamuskeet closely tracks air temperature (J. R. Lovvorn, unpubl. data). For simulations, the weighted mean air temperature for all observation days on Lake Mattamuskeet (mean ± 1 SD = 11.4 ± 2.4°C, $n = 9$ days) was used for both air and water temperature.

Mass-specific respirometry data ($\dot{V}O_2$) for congeneric Tufted Ducks (*Aythya fuligula*) were applied to Canvasbacks (see Lovvorn and Gillingham 1996). Costs of sleeping, alert behavior, comfort movements, and passive ascent during dives were assumed equal to that for resting at given water temperatures. For descent and bottom foraging, aerobic efficiencies (η = mechanical power output/aerobic power input) were calculated from the mechanical model described above and respirometry of Tufted Ducks diving to a depth of 0.6 m in water at 7.4°C ($\eta = 0.2337$) and 22.9°C ($\eta = 0.1438$, Bevan and Butler 1992). Aerobic efficiencies were linearly interpolated for water temperatures between these two values, and applied to mechanical work estimates for descent and bottom foraging. The lower $\dot{V}O_2$ (11.59 versus 13.91 W/kg) and resulting higher η during submergence at the lower temperature was offset by higher $\dot{V}O_2$ during pauses between dives. For pauses, values were linearly interpolated between $\dot{V}O_2$ of 17.47 W/kg at 7.4°C and 12.28 W/kg at 22.9°C (Bevan and Butler 1992).

Aerobic cost of surface-swimming in Tufted Ducks, measured only in water at 17.8°C, increased curvilinearly from 6.46 W/kg at 0.40 m/s to 20.99 W/kg at 0.78 m/s (Woakes and Butler 1983). Energy costs of flight were estimated by applying an aerobic efficiency of 0.23 to mechanical costs calculated from the aerodynamic model of Pennycuick (1989; see Lovvorn and Jones 1994). The aerobic power of flying was 230 W at the maximum range speed (V_{mr}) of 23 m/s for the mean (±1 SD) body mass (1.395 ± 0.128 kg) and wingspan (0.873 ± 0.029 m) of 21 adult male Canvasbacks collected on Lake Mattamuskeet in November 1982-83 (Lovvorn 1994b).

Canvasbacks on Lake Mattamuskeet in November 1982 and 1983 gained about 1.66 g of body fat and 0.23 g of body protein per day (all sex-age classes combined, Lovvorn 1994b). Considering digestive and conversion efficiencies, nutrient deposition required an intake of about 4.6 g dry mass of buds per g of body fat, and 14.8 g of buds per g of body protein (Lovvorn 1987:38). At a metabolizable energy of 11.568 kJ/g dry mass of buds (Lovvorn 1987:33), nutrient storage increased the daily energy requirement of Canvasbacks by 127.71 kJ/day.

Energy Intake

Intake of *Vallisneria* winter buds per second spent at the bottom was estimated from a Michaelis-Menten equation fit to the functional response data of Takekawa (1987) (Marquardt method, PROC NLIN; SAS, Inc., Cary, North Carolina). In the equation $I = ax/(b + x)$, I is the number of buds consumed per second at the bottom, x is bud density (number/m^2), and a is the handling time coefficient, or the asymptote for the maximum rate at which Canvasbacks can handle buds regardless of bud density (see Figure 2 in Lovvorn and Gillingham 1996).The search time coefficient b is the bud density at an intake rate of $0.5a$, and thus indicates effects of search time on how quickly the curve for intake rate rises and becomes limited by the asymptotic handling time. For seven bud densities (x) ranging from 10–110 buds/m^2, intake of buds per second at the bottom (I) was estimated by the equation $I = 0.193x/(29.5 + x)$, $R^2 = 0.98$ (see Lovvorn and Gillingham 1996).

The maximum number of *Vallisneria* winter buds a Canvasback could eat in a given foraging bout was taken to be the maximum number of buds found in esophagi among 119 Canvasbacks collected while feeding on Lake Mattamuskeet (see Lovvorn 1994b). For simulations in this paper (early period in Lovvorn and Gillingham 1996), it was estimated that a maximum of 103 buds were ingestable in one foraging bout. Metabolizable energy of *Vallisneria* winter buds (66.7% water) is about 11.568 kJ/g dry mass (Lovvorn 1987:33).

Patch Structure and Computer Simulation of Food Grids

Regarding patch structure, Kotliar and Wiens (1990) defined first-order patchiness as equivalent to "grain," the smallest scale at which an organism differentiates among patches. Second-order patches are made up of clusters of first-order patches (Kotliar and Wiens 1990). The patch structure of winter buds was modeled with grain equal to potential foraging "loci," defined as contiguous circles 1 m in diameter. These loci approximate the area within which a Canvasback makes one or more vertical dives until surface-swimming to a different locus to begin a new series of vertical dives (see Lovvorn and Gillingham 1996).

In the fall of 1983, transects for sampling *Vallisneria* winter buds were established in four areas of Lake Mattamuskeet that were heavily used by Canvasbacks the previous fall (see Figure 2 in Lovvorn 1989a). Sediment cores were taken from 20 September to 5 October 1983 before Canvasbacks arrived in early November. Seventy sampling stations were marked with stakes at 50-m intervals along the transects, and three replicate cores (92 cm^2 each) to a depth of 10 cm were taken within 0.5 m of each stake. Water depths at the 70 sampling stations averaged 39 ± 9 cm (±1 SD) (early sample of Lovvorn and Gillingham 1996).

First-order patchiness among individual foraging loci was quantified by using the FORTRAN program NEGBINOM of Krebs (1989:505–513) to fit negative binomial distributions to the above core samples (means of 3 replicate cores per station for 70 stations; see Figure 3 in Lovvorn and Gillingham 1996). These distributions yielded the frequencies of possible loci with different bud densities, *i.e.*, first-order patchiness.

From 18–20 October 1993, additional cores were taken to describe the second-order spatial pattern (as opposed to negative binomial frequencies) of *Vallisneria* buds in Lake Mattamuskeet. Sixteen sampling stations were marked with stakes at 50-m intervals along a transect corresponding approximately (within a few hundred meters) to Transect 3 of the 1983 sample (see Figure 2 in Lovvorn 1989a). At each station, three replicate cores were taken at the transect stake, and at each 1-m increment to a distance of 6 m in a random direction from the transect stake. The distance of 6 m encompassed about 94% of distances moved by Canvasbacks during foraging bouts (see Figure 4 in Lovvorn and Gillingham 1996). Mean ($n = 3$ replicates) number and dry mass of buds at each 1-m increment were then regressed on values at the focal transect stakes ($n = 16$ stations for regressions done separately for each of the six distance increments). None of these regressions were significant for bud numbers (all $r^2 < 0.11$, $P > 0.20$) or bud dry mass (all $r^2 < 0.15$, $P > 0.14$), indicating a lack of predictable spatial pattern at these scales.

Because no second-order patchiness was detected on the scales of 1-m foraging loci and observed foraging movements of Canvasbacks, 40 × 40-m grids of *Vallisneria* winter buds were simulated by rejecting only those randomly-generated coordinates that did not fall within the negative binomial distributions of first-order patchiness (Rejection Method, Press *et al.* 1989; see Figure 5 in Lovvorn and Gillingham 1996).

Giving-Up Rules and Movement Distances

During the study period, aboveground parts of *Vallisneria* had senesced and detached, so Canvasbacks searched for belowground winter buds by touch (see Tome 1988; Ball 1994). In model simulations, Canvasbacks decided when to stop foraging in a given locus and move to a different locus based on their energy balance. After each dive, energy intake was compared to energy expended, including work underwater, surface-swimming between loci, pausing between dives, and the overhead cost of all other daily activities prorated on a per second basis. If expected energy balance on a subsequent dive in the same locus was positive, based on the functional response for the decremented food density and the energy cost of the preceding dive, the duck dove again.

If the expected energy balance from another dive in the same locus was negative, the duck moved to another locus. As noted above, core sampling revealed no second-order patchiness of *Vallisneria* buds at the scale of foraging loci. Thus, in this habitat, Canvasbacks foraging by touch cannot predict how far or in what direction they should move between foraging loci, but rather must search by trial and error for loci with high enough food densities for profitable foraging. In other words, Canvasbacks moving to a new locus had the same negative binomial expectation of food density regardless of direction or distance moved. Any criteria used by Canvasbacks to vary distance moved between loci were unknown, so random samples were drawn from frequency distributions of movement distances observed in the field (see Figure 4 in Lovvorn and Gillingham 1996).

In the model, the duck continued foraging until it (a) filled its esophagus, or (b) accumulated an energy deficit that exceeded one-half the fraction of daily energy requirement that on average must be met during a foraging about [*i.e.*, bout deficit fraction (BDF) = -0.5]. Durations of entire foraging bouts were not measured in the field, but it appeared that Canvasbacks generally engaged in only one bout per half hour. Canvasbacks at Lake Mattamuskeet spent 45% of their time foraging (Lovvorn 1989b), so we estimated the mean duration of foraging bouts as 13.5 min, or 2.02% of daily foraging time (24 h minus time spent in other activities = 11.16 h). Nagy's (1987) allometric equation, based on doubly-labeled water measurements of free-ranging birds, estimates a field metabolic rate of 1120 kJ/day for an average adult male Canvasback on Lake Mattamuskeet in November (Lovvorn 1994b). Thus, a Canvasback must achieve an average profit per foraging bout of 22.62 kJ (0.0202×1120 kJ) to meet its daily energy requirement. When cumulative profit during a bout falls to less than half that value (11.31 kJ), it is unlikely that the duck can achieve positive energy balance by continuing for the average bout duration; hence the choice of BDF = -0.5. The duck should then stop feeding and move to another foraging site, *i.e.*, to another 40×40 grid with a different food regime.

By this scheme, a Canvasback continued feeding in a locus until its energy balance in that locus became negative, regardless of potential for higher net gain at other loci. This decision rule differs from marginal value formulations (Tome 1988; Houston and Carbone 1992), in which an omniscient animal leaves a patch when the net profitability in that patch falls below the average for all patches. However, core samples of winter buds indicated that Canvasbacks sometimes depleted patches to below the habitat average, while higher-than-average densities remained in other patches (Lovvorn 1994a). These patterns probably resulted from high costs of searching for better patches (due to high locomotor costs and tactile foraging of Canvasbacks), constant alteration of food densities by other flock members, and consequent lack of omniscience about the average for all food patches (see also Bernstein *et al.* 1991).

In the model, selection of new loci did not explicitly consider effects of foraging aggression, or of predation risk and related flocking behavior (Thompson *et al.* 1974; Lovvorn 1989b; Hyman *et al.* 1990). Such factors might influence the direction or distance moved, although the negative binomial expectation of food density was independent of direction or distance. Such effects on search costs were accounted for implicitly by sampling from the frequencies of distances moved in the field.

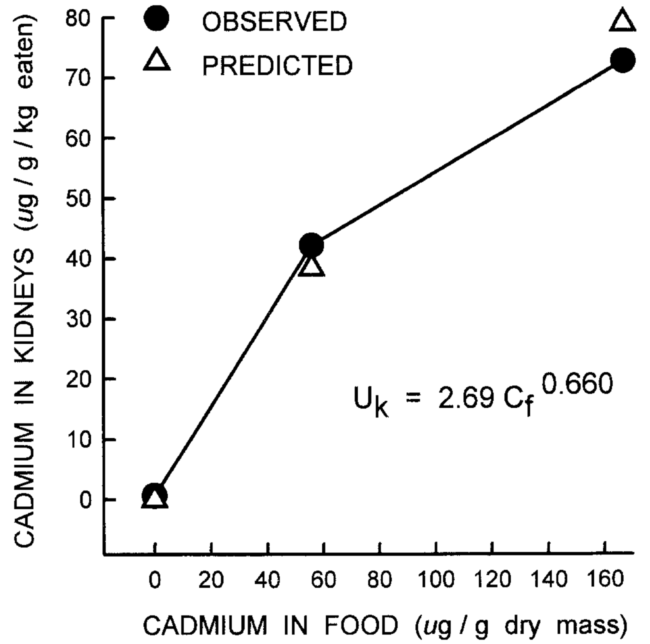

Fig. 1. Mean cadmium uptake by kidneys per kg of food consumed (U_k) by adult Mallards after eating commercial ration containing different cadmium levels (C_f) for 42 days (see Table 1). Both observed values and values predicted from an equation fit to these data (linear regression on log-transformed values) are shown. All values are on a dry mass basis. In the equation, the "cadmium uptake exponent" is 0.660

Cadmium Assimilation from Food

Cadmium assimilated by kidneys per kg of food consumed was estimated from the data of Di Giulio and Scanlon (1984a). Based on 42-d trials with adult Mallards (*Anas platyrhynchos*), cadmium uptake by kidneys (μg/g) per kg of food consumed (U_k) was related to cadmium concentration in the food (C_f) by the equation $U_k = 2.69C_f^{0.660}$ (fitted by linear regression on log-transformed values, $r^2 > 0.99$, $P = 0.001$, all values on a dry mass basis, Table 1, Figure 1). In Mallards fed 2, 15, and 210 μg Cd/g fresh mass of commercial ration, kidney cadmium concentrations continued to increase from 30 to 60 to 90 days on the food, except for a decrease at 90 days on the 210 μg/g treatment (White and Finley 1978). Data of White and Finley (1978) and Di Giulio and Scanlon (1985b) suggest that, for a range of 2-50 μg Cd/g fresh mass of food, kidney cadmium concentrations are at no more than 50% of maximum after 42 days, and continue to increase monotonically for at least 90 days (Figure 2). Therefore, in the model, cadmium uptake by the kidneys was allowed to increase monotonically according to the above allometric equation relating kidney uptake per kg of food consumed to cadmium concentration in food. The model assumed no avoidance of contaminated food by Canvasbacks (Heinz and Sanderson 1990).

Uncertainty Analyses

Effects of variation in selected parameters (Table 2) on model estimates of cadmium uptake by the kidneys were evaluated. Uncertainty analyses

Table 1. Food intake and kidney cadmium concentrations of adult Mallards after eating commercial ration containing different cadmium levels (C_f) for 42 days, and mean cadmium uptake by kidneys per kg of food consumed (U_k) (based on data from Di Giulio and Scanlon 1984a). All values are on a dry mass basis (food contained 10% water). Based on these data, $U_k = 2.69C_f^{0.660}$ ($r^2 > 0.99$, $P = 0.001$; see Figure 1)

Cd in food (μg/g)	Mean daily food intake (kg)	Total food intake (kg)	Cd in kidneys (μg/g)	Mean Cd uptake (μg/g/kg of food)
0	0.120	5.04	2.9	0.58
56	0.118	4.96	208.8	42.10
167	0.110	4.62	335.2	72.55

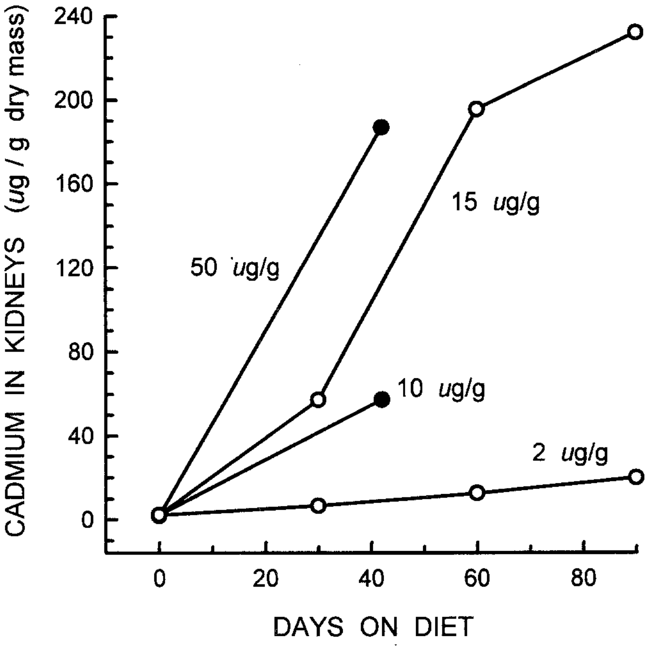

Fig. 2. Cadmium concentrations in kidneys (μg/g dry mass) of adult Mallards as a function of days eating commercial rations containing different concentrations of cadmium (μg/g fresh mass). Solid circles are data from Di Giulio and Scanlon (1985b); open circles are data from White and Finley (1978). Kidney concentrations from White and Finley (1978) were converted from fresh to dry mass based on a dry-mass fraction of fresh kidneys of 23.44% (Scanlon 1982)

considered ranges of values likely to occur in areas where Canvasbacks forage on winter buds of *Vallisneria*, such as Lake Mattamuskeet, the Chesapeake Bay region, Long Point Bay of Lake Erie, and the upper Mississippi River. In these analyses, the concern was not with sampling from normal or similar distributions around particular means, but rather with variation between observed endpoints. Thus, all parameters were considered uniformly distributed within ranges in Table 2 (see Lovvorn and Gillingham 1996 for further details on range selection).

No data were available on the range of variability in bud dispersion as measured by the negative binomial parameter *k*. At Lake Mattamuskeet in 1983, values of *k* ranged from 1.504 in October to 0.930 after Canvasbacks left the lake in December. In Simulations 1 and 2, *k* was varied from 1 to 5 and from 1 to 10, respectively.

Mean cadmium concentrations in whole plants of *Vallisneria americana* (μg/g dry mass) ranged from 0.63 in northern Currituck Sound, Virginia to 1.15 and 3.64 at two sites in the Potomac River halfway between Washington, D.C. and Chesapeake Bay (Di Giulio and Scanlon 1985a). We found no higher concentrations reported for *Vallisneria*, but values as high as 32.33 μg/g dry mass were reported for the submerged plant *Elodea canadensis* grown in the field on soils from a highly contaminated site (Mayes *et al.* 1977), and an extreme (and probably very rare) value of 89.6 μg/g in *Potamogeton crispus* at another contaminated area (McIntosh *et al.* 1978). In Simulations 1 and 2, cadmium concentrations in *Vallisneria* were varied from 0 to 10 and 0 to 30 μg/g dry mass, respectively. Only one data set, that of Di Giulio and Scanlon (1984a), was available for deriving the "cadmium uptake exponent." This is the exponent for the rate of kidney cadmium uptake per kilogram of food consumed depending on cadmium concentration in food (Table 1, Figure 1). This exponent was varied by ±5% in Simulation 1 and ±20% in Simulation 2.

Uncertainty Simulations 1 and 2 each included 150 foraging bouts. In a Latin hypercube design (Swartzman and Kaluzny 1987), the uniform distributions (Table 1) were divided into 150 equal intervals, and for each bout, values for each parameter were randomly selected from intervals chosen randomly without replacement. After simulations, all variables were ranked and the dependent variable (kidney cadmium concentration) was regressed against the independent variables (randomly chosen parameter values) for each bout. Relative partial sums of squares (RPSS) for ranked data indicated the variance in kidney cadmium concentration explained by variation of individual parameters, with effects of the other parameters statistically removed. This method revealed which parameters should be measured more accurately and precisely to improve estimates of kidney cadmium concentration. For ease of comprehension, partial coefficients of determination (partial r^2) are also reported; however, parameters can show high correlation (partial r^2) but account for small residual variances as indicated by RPSS.

Response surfaces were also generated to explore interactions between cadmium content of food and selected environmental variables in determining kidney cadmium uptake. These simulations assumed that Canvasbacks spent 45% of their time foraging throughout the diel period, based on field observations (Lovvorn 1989b, see above). For each combination of parameter levels, one entire days' foraging was simulated for ten individual Canvasbacks.

Results

In Canvasbacks feeding for 45% of 24-h periods, simulated uptake of cadmium by the kidneys varied directly with cadmium levels in *Vallisneria* winter buds (Figure 3). As influenced by the uptake equation in Figure 1, kidney cadmium levels increased more rapidly at higher concentrations in buds (Figure 3). For a cadmium concentration (30 μg/g dry mass) that is very high relative to values likely to be observed in submerged plants in the field (Eisler 1985), the highest kidney uptake over 90 days was about 300 μg/g.

In uncertainty analyses in which all parameters (Table 2) were varied simultaneously, only four parameters explained significant variation in kidney cadmium uptake by Canvasbacks foraging on *Vallisneria* buds. These variables were aerobic efficiency, bud dispersion as quantified by the negative binomial parameter *k*, cadmium concentration in buds, and bud metabolizable energy (Table 3). By far the most influential parameter

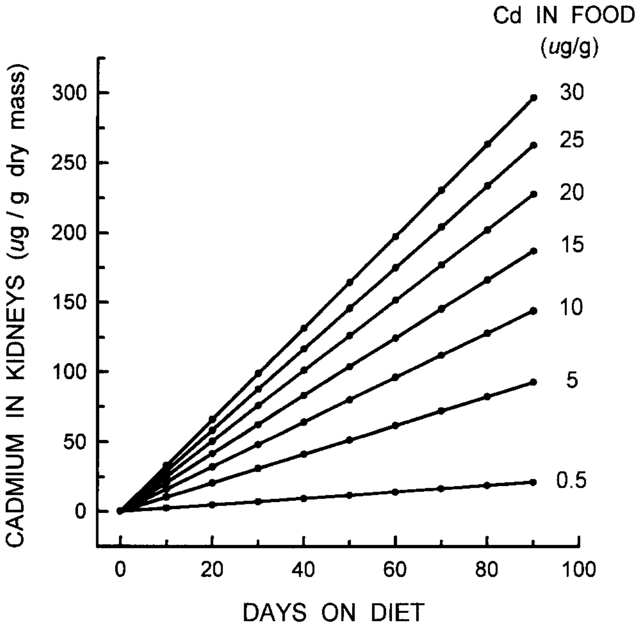

Fig. 3. Simulated cadmium uptake by the kidneys of Canvasbacks, depending on numbers of days eating *Vallisneria* winter buds containing different cadmium concentrations (μg/g dry mass). Each line represents mean results from simulations for 150 individual Canvasbacks, each feeding for 45% of a 24-h period

Table 3. Relative partial sums of squares (RPSS for rank-transformed data) from uncertainty analyses of the model of kidney cadmium uptake by Canvasbacks eating *Vallisneria* winter buds. In Simulation 1, negative binomial k varied from 1 to 5, cadmium concentration in food varied from 0–10 μg/g dry mass, and the cadmium uptake exponent (see Figure 1) varied by ±5%. In Simulation 2, k varied from 1 to 10, cadmium concentration in food varied from 0–30 μg/g, and the cadmium uptake exponent varied by ±20% (see Table 1). Both simulations included 150 foraging bouts, each bout with parameter values randomly selected from ranges in Table 1 by the Latin hypercube method. RPSS indicate the variance in kidney cadmium concentration (μg/g dry mass) explained by variation in each parameter, with effects of the other parameters statistically removed. $R^2 = 0.85$ for Simulation 1 and 0.73 for Simulation 2, $P < 0.001$

	Simulation 1		Simulation 2	
Parameter	RPSS	Partial r^2	RPSS	Partial r^2
Aerobic efficiency	53.67	0.752[a]	180.87	0.493[a]
Negative binomial k	32.53	0.648[a]	60.08	0.244[a]
Cadmium level in buds	2.30	0.115[a]	87.29	0.320[a]
Water depth	0.25	0.014	0.23	0.001
Bud metabolizable energy	0.07	0.004	26.19	0.124[a]
Dry mass/bud	0.05	0.003	2.20	0.012
Water temperature	0.04	0.002	0.36	0.002
Mean number of buds/m^2	0.03	0.002	0.24	0.001
Cadmium uptake exponent	0.02	0.001	4.69	0.025

[a] $P < 0.05$

Table 2. Parameters and their ranges used in uncertainty analyses of the model for kidney cadmium uptake by Canvasbacks eating *Vallisneria* winter buds. For parameters having two specified ranges, the second range was used in a second set of simulations (Simulation 2 in Table 3) in which ranges for other parameters were unchanged

Parameter	Range
Water depth (m)	0.5–3.5
Water temperature (°C)	1–25
Aerobic efficiency, η[a]	$\eta \pm 0.07$
Dry mass/bud (g)	0.030–0.18
Bud metabolizable energy (kJ/g dry mass)	11.568 ± 5%
Mean number of buds/m^2	111–366
Negative binomial k of bud dispersion	1–5, 1–10
Cadmium level in buds (μg/g dry mass)	0–10, 0–30
Cadmium uptake exponent (see Figure 1)	0.660 ± 5%, ±20%

[a] Calculated for different temperatures from the data of Bevan and Butler (1992), see text

in both Simulations 1 and 2 was aerobic efficiency, the factor for converting mechanical energy costs of locomotion to actual food requirements. At lower cadmium concentrations in food that are typical of field conditions (Simulation 1), the cadmium content of food per se was much less important than food dispersion and resulting search costs in determining cadmium uptake by the kidneys.

Response surfaces from varying only two parameters in the model at a time demonstrate effects of environmental variation on kidney cadmium uptake for given concentrations in *Vallisneria* winter buds (Figure 4). These environmental variables influence cadmium uptake by their effects on foraging energetics. Water depth had little effect on cadmium uptake at low levels of cadmium in *Vallisneria* buds, but for high cadmium levels in buds, uptake was over twice as high at shallow depths (Figure 4A). This trend results from the fact that Canvasbacks consume more food relative to time and energy spent searching when water is shallow. Water temperature had no effect on food or cadmium intake (Figure 4B). Higher mass/bud also increased food intake rate, which raised cadmium uptake as concentrations in food increased (Figure 4C). When no other parameters were allowed to vary, food dispersion as measured by the negative binomial parameter k had no effect on cadmium uptake at any level in *Vallisneria* buds (Figure 4D).

Comparing results of two-parameter perturbations (Figure 4) with results from sensitivity analyses in which all parameters varied simultaneously (Table 3) suggests that effects of single parameters (water depth and mass/bud) can be masked if some other parameters vary (aerobic efficiency, negative binomial k), and that food dispersion becomes important only in concert with variation in other parameters (cf., Figure 4C, Table 3). It is obvious, however, that the relationship between cadmium content of food and cadmium uptake by kidneys can be quite different depending on field conditions that alter the energetics of foraging.

Discussion

Results of the model address several important questions that are often difficult to examine with field data alone. Such questions include

1. How is contaminant uptake by birds affected by varying lengths of stay in a contaminated area?
2. How is contaminant uptake affected by interactions between

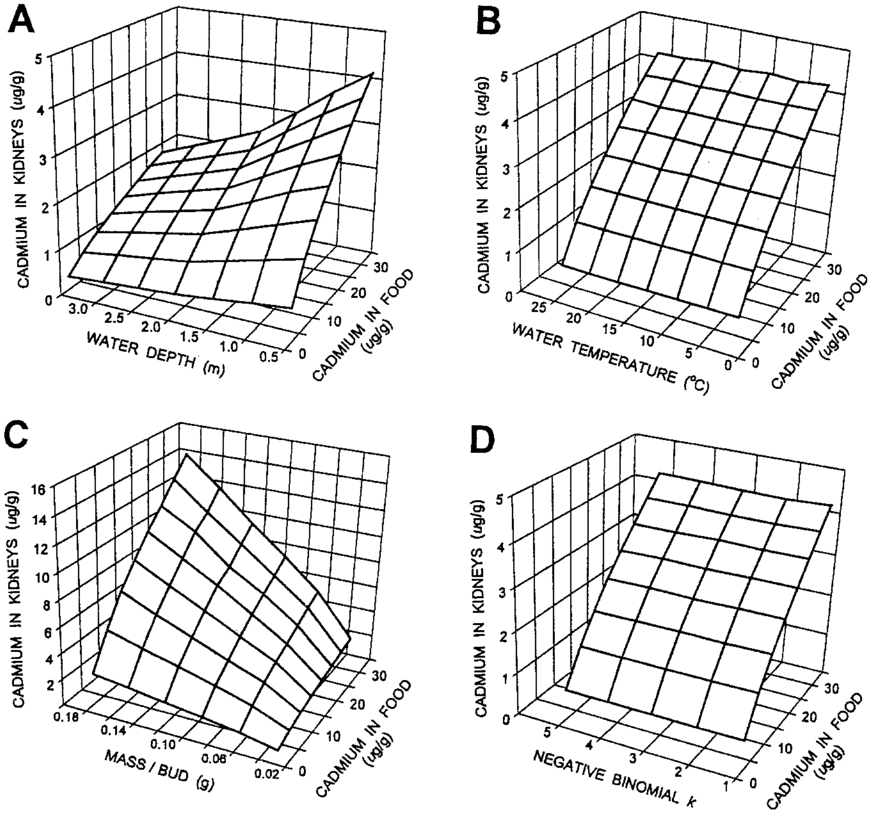

Fig. 4. Simulated effects of variation in single environmental parameters on the relation between cadmium content of *Vallisneria* winter buds and cadmium uptake by the kidneys of Canvasbacks, when no other parameters are allowed to vary. Each point in the response-surface grid represents the mean for 10 individual Canvasbacks foraging 45% of the time for one day

contaminant content of food and both spatial and temporal changes in environmental conditions?

3. How do spatial variations in the contaminant content of food affect variability in tissue contaminant levels among individual birds?
4. How do the above effects influence the maximum allowable contaminant concentrations in food under varying field conditions?

Effects of Varying Lengths of Stay

After 90 days of foraging on *Vallisneria* winter buds containing a high concentration of cadmium (30 μg/g dry mass), simulated cadmium levels in Canvasback kidneys were about 300 μg/g (Figure 3). In 90-day experiments with captive Mallards, kidney concentrations of about 230 μg/g had no significant effects on body mass or food consumption (White and Finley 1978), and marginal to no effects on kidney and testis histology and spermatogenesis (White *et al.* 1978). Captive ducks are not subject to a multitude of additional energy costs such as having to search for food, or frequent flying due to human disturbance. However, the model does account for many of these additional factors, and suggests that kidney cadmium levels for very high concentrations in plant foods might have minimal adverse effects on adult ducks exposed for several months during the nonbreeding period. Note that cadmium accumulates continually in the renal cortex with very little excretion, so that older animals generally have higher levels than younger individuals in the same environment (Scheuhammer 1987; Henny *et al.* 1991). Thus, long-term accumulation on the scale of years might eventually result in toxic effects.

In invertebrate foods of diving ducks, cadmium concentrations are seldom higher than the maximum of 30 μg/g dry mass examined in our computer simulations. For example, the major food of Canvasbacks in Pamlico Sound, North Carolina after they leave Lake Mattamuskeet, as well as in Chesapeake Bay, is bivalves of the genus *Macoma* (Lovvorn 1987; Perry and Uhler 1988). Reported cadmium content (μg/g dry mass) of *Macoma* spp. (without shells) ranged from 0.13–0.33 (White *et al.* 1979) and 0.23–0.63 (Di Giulio and Scanlon 1985a) in Chesapeake Bay, where kidney cadmium levels (μg/g dry mass) in Canvasbacks averaged 9.81 (White *et al.* 1979) and 6.00 (range 0.16–23.68) (Di Giulio and Scanlon 1984b). Mean cadmium concentrations (μg/g dry mass) in bivalve prey (without shells) and in kidneys of locally collected diving ducks have been reported as 1–5 in *Mytilus edulis* versus 25 in Common Eiders (*Somateria mollissima*) (Lande 1977), and 0.61 in *Mytilus edulis* and 0.08 in *Macoma balthica* versus 5.15 (range 1.5–8.3) in Greater Scaup (*Aythya marila*) (Szefer and Falandysz 1987). At a site contaminated with cadmium, levels in *Mytilus edulis* varied from 12 to 37 μg/g dry mass (Cossa 1988). Field and laboratory studies suggest that only the upper end of the latter range might result in kidney cadmium levels in ducks that are associated with kidney lesions or hematological effects (see review by Scheuhammer 1987).

In estimating contaminant risk to migratory birds, an important question is whether contaminant uptake by transient birds at a certain site affects their survival or reproduction at other places and times. Such analyses require data on depuration rates (rates of contaminant elimination from the body), which are nonexistent for all but a few contaminants. Liver selenium concentrations in captive Mallards declined almost linearly over 42 days after termination of trials on contaminated diets (Heinz *et al.* 1990). However, White and Finley (1978) found no significant declines in kidney cadmium concentrations after a 30-d post-treatment period in Mallards previously fed 15 and 210 μg Cd/g fresh mass of food for 90 days. Blomqvist *et al.* (1987) estimated the mean half-life of renal cadmium in Dunlins (*Calidris alpina*) as about 1 yr, with an implied maximum of 2.5 yr. Future experimental studies on contaminant uptake by birds should include measurements of post-treatment depuration rates, which would allow model estimation of long-term effects on reproduction due to exposure of transient birds to contaminants at given sites.

Relative Effects of Environmental Variables and Contaminants in Food

At concentrations of cadmium in *Vallisneria* buds likely to be found in the field (Simulation 1), uncertainty analyses (Table 3) indicated that cadmium content of buds was much less important than bud dispersion and resulting search costs in determining cadmium uptake by the kidneys. Thus, differences in kidney cadmium levels between birds collected at different sites might result more from differences in food dispersion and search energetics than from differences in contaminant levels in foods. The cadmium uptake exponent, from the equation for cadmium uptake per kilogram of food consumed (Figure 1), was not significant, and had less influence on cadmium uptake than did a variety of other ecological factors (Table 3). These results suggest that obtaining exact measurements of cadmium uptake rates in captive birds is less important than accounting for environmental parameters that usually are not considered in captive studies.

By far the most important variable in the model was aerobic efficiency, the factor for converting mechanical energy costs of locomotion to actual food requirements. This result emphasizes that accurate measurements of oxygen consumption under different controlled conditions are critical to estimates of food consumption and contaminant intake in the field (Lovvorn 1994a; Lovvorn and Gillingham 1996).

When other environmental variables were constant, dry mass/bud strongly influenced kidney cadmium levels (Figure 4C), although this effect was masked when other parameters varied (Table 3). For bivalve foods, prey size would probably exert greater effects on kidney cadmium uptake because cadmium concentrations in bivalves generally increase with age and size, sometimes dramatically (Kay 1985).

Simulated patterns of cadmium uptake with changes in environmental factors might at first seem counter-intuitive, *i.e.*, as energy costs increase, food and cadmium intake decrease (Figure 4). These trends result from the constraints of foraging profitability on food intake. In the model, ducks continue to forage as long as their energy intake exceeds energy costs as affected by environmental conditions. That Canvasbacks often are fatter in areas where food and weather conditions are more favorable (Lovvorn 1994b) supports the idea that free-ranging Canvasbacks generally continue to feed as long as foraging is profitable. By this scheme, higher energy costs do not simply increase the duration of foraging. Rather, higher costs require that energy intake per time be higher for foraging to remain profitable.

In the model, Canvasbacks will not continue feeding in a locus or at a general site where foraging is unprofitable. Higher energy costs mean that they will spend more time searching for loci or sites where food density is high enough to support profitable foraging. If many loci have inadequate food densities, increased energy costs do not necessarily result in Canvasbacks eating more, and they will often have higher food and contaminant intake when conditions are favorable than when they are unfavorable. In the latter case, they will forage only where food availability is high enough or else will give up and leave the area entirely. Moreover, adequacy of a certain energy intake depends on energy expended to acquire that food, which changes the minimum intake needed; thus, when viewed from the standpoint of profitability, the concept of a constant daily food requirement is not meaningful. Models that estimate food intake based on energetic profitability can therefore yield very different predictions than models that assume constant daily intake, or assume that food intake simply increases as energy costs of thermoregulation or other factors go up. Such profitability effects might explain the poor performance of the latter models in predicting contaminant uptake (Skorupa and Ohlendorf 1991). A major challenge to improving the accuracy of profitability models is determining the time scale over which birds balance their energy budgets (Lovvorn and Gillingham 1996).

Effects of Spatial Variations of Contaminants in Food

Large variations in contaminant content of sediments on the scale of several meters (Holland *et al.* 1993), and corresponding differential uptake of contaminants by invertebrates (Rule and Alden 1990), might result in unusually high contaminant levels in individual birds depending on their foraging response to bivalve dispersion. Data on dispersion of bivalve prey and contaminant concentrations needed for our model are not currently available. Once this information is obtained, simulations can be readily performed to provide estimates of maximum contaminant intake by individual birds.

A major advantage of individual-based models is that they allow consideration of differences among individuals in their activity ranges and resulting contaminant exposures. Individual Canvasbacks move among sites in a general area (Howerter 1990), and food grids can be generated to represent conditions at these different sites. If data for among-site movements are available, effects of localized contamination at different sites within a bird's activity range can be simulated by allowing model birds to forage in different grids for different lengths of time. An excellent effort toward such an approach is presented by Clifford *et al.* (1995); however, their formulation does not consider effects of foraging profitability on the accessibility of contaminants within an animal's foraging range. Such effects could be readily integrated into their scheme, which uses a Geographic Information System.

Maximum Allowable Contaminant Concentrations

Skorupa and Ohlendorf (1991) noted that concentrations of selenium at trophic levels below birds can be predicted rather accurately from waterborne concentrations, but that variations in bird behavior apparently confound prediction of selenium levels in bird eggs. Application of foraging models such as ours might allow better predictions of contaminant levels in birds. Bivalve prey of many diving ducks often accumulate contaminants, and are important species in many monitoring programs (Fischer 1988; Cain and Luoma 1990). However, energetics-based models require that studies of captive birds document contaminant uptake as a function of the amount of food eaten, which is often not reported. Moreover, extrapolations of captive feeding trials to field situations need to account for contaminants assimilated from substantial amounts of sediment ingested by benthic-feeding birds along with their food (Beyer *et al.* 1994; J. R. Lovvorn, pers. observ.). Probably most importantly, adverse effects of given tissue levels of contaminants are usually unknown, and appear to be quite different even among closely related taxa such as sea ducks (Mergini) versus dabbling and bay ducks (Anatini and Aythyini) (Henny *et al.* 1995). Much work on the pathological effects of different tissue contaminant levels is needed before either direct monitoring or model estimates can be interpreted in terms of contaminant risk.

Model Applications to Other Species

Among aquatic vertebrates, benthivores are often the most impacted by chronic pollution of nearshore sediments and foods (Vermeer and Peakall 1979; Di Giulio and Scanlon 1984b, 1985a; Smith *et al.* 1985). For example, in Commencement Bay, Washington, Surf Scoters (*Melanitta perspicillata*) with a sediment-associated diet contained 50 times more cadmium in their kidneys than did Western Grebes (*Aechmophorus occidentalis*) eating fish in the same area (Henny *et al.* 1991). Benthic foods of most diving ducks occur in stationary, 2-dimensional patterns that are more easily described, experimentally manipulated, and mathematically modeled than are mobile prey in the water column (Sjoberg, 1988; Tome 1988; Breck 1993; Ball 1994; Lovvorn and Gillingham 1996). Costs of locomotion of diving ducks under varying conditions of water depth, water temperature, and food dispersion have also been thoroughly studied and modeled (Lovvorn 1994a; Lovvorn and Gillingham 1996). Similar models would be valuable for diving birds such as cormorants in areas where they feed mainly on bottom fishes that are highly susceptible to contamination (Mallins *et al.* 1984; see refs. on diets in Derby and Lovvorn 1996), and where the abundance and wide distribution of cormorants make them especially good species for contaminant monitoring (Fox *et al.* 1991).

Implications for Future Research and Modeling

Quantitative predictions of computer models should always be viewed with healthy skepticism. However, the model in this paper serves useful purposes in addition to quantitative prediction. First, it helps identify what parameters are most important in determining contaminant uptake under diverse field conditions, knowledge that is useful in designing laboratory studies that are relevant to field situations. Second, toxicity tests on relatively large, warm-blooded animals are very expensive, and increasingly have animal rights implications. Thus, investigators need to have very focused ideas about what levels of exposure really need to be tested, and what environmental factors will alter the generality of the results under actual field conditions. For example, at high cadmium levels in plant foods, simulated cadmium uptake by ducks in the field (Figure 3) is not expected to affect body mass or food intake (cf. White and Finley 1978). Consequently, experiments on captive ducks should focus on reproductive effects of cadmium levels in foods ≤ 30 μg/g dry mass. Such preliminary modeling helps to avoid spending scarce dollars on experimental treatments that are less relevant, or that have limited value unless critical ancillary data are collected at the same time.

The model in this paper also shows that bioaccumulation factors that do not account for environmental variations might give erroneous results under many circumstances. Thus, there needs to be a shift in emphasis of empirical research away from isolated investigations and toward empirical studies that validate and test the assumptions of integrative models.

Acknowledgments. Field and laboratory work by JRL was supported primarily by the Delta Waterfowl and Wetlands Research Station, a Rackham Graduate Fellowship at the University of Michigan, a Dean's Fellowship at the University of Wisconsin, and a National Science Foundation-NATO Postdoctoral Fellowship at the University of British Columbia. Additional funds were provided by a U.S. Department of Energy grant to W. P. Porter and a grant from the Natural Sciences and Engineering Research Council of Canada to D. R. Jones. T. W. Arnold provided excellent field assistance. We appreciate the aid and encouragement of B. D. J. Batt, R. D. Drobney, J. Y. Takekawa, W. P. Porter, D. R. Jones, R. W. Blake, and staff of the Mattamuskeet National Wildlife Refuge.

References

Ball JP (1994) Prey choice of omnivorous Canvasbacks: Imperfectly optimal ducks? Oikos 70:233–244

Belovsky GE (1994) Modeling avian foraging: Implications for assessing the ecological effects of pesticides. In Kendall RJ, Lacher TE (eds) Wildlife toxicology and population modeling. Lewis Publishers, Boca Raton, FL, pp 123–137

Bernstein C, Kacelnik A, Krebs JR (1991) Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. J Anim Ecol 60:205–225

Bevan RM, Butler PJ (1992) The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the Tufted Duck *Aythya fuligula.* J Exp Biol 163:139–151

Beyer WN, Connor EE, Gerould S (1994) Estimates of soil ingestion by wildlife. J Wildl Manage 58:375–382

Blomqvist S, Frank A, Petersson LR (1987) Metals in liver and kidney tissues of autumn-migrating Dunlin *Calidris alpina* and Curlew Sandpiper *Calidris ferruginea* staging at the Baltic Sea. Mar Ecol Prog Ser 35:1–13

Boellstorff DE, Ohlendorf HM, Anderson DW, O'Neill EJ, Keith JO, Prouty RM (1985) Organochlorine chemical residues in White Pelicans and Western Grebes from the Klamath Basin, California. Arch Environ Contam Toxicol 14:485–493

Breck JE (1993) Foraging theory and piscivorous fish: Are forage fish just big zooplankton? Trans Am Fish Soc 122:902–911

Cain DJ, Luoma SN (1990) Influence of seasonal growth, age, and environmental exposure on Cu and Ag in a bivalve indicator, *Macoma balthica,* in San Francisco Bay. Mar Ecol Prog Ser 60:45–55

Clifford PA, Barchers DE, Ludwig DF, Sielken RL, Klingensmith JS, Graham RV, Banton MI (1995) An approach to quantifying spatial components of exposure for ecological risk assessment. Environ Toxicol Chem 14:895–906

Cossa D (1988) Cadmium in *Mytilus* spp.: Worldwide survey and relationship between seawater and mussel content. Mar Environ Res 26:265–284

Derby CE, Lovvorn JR (1996) Predation on fish by cormorants and pelicans in a coldwater river: A field and modeling study. Can J Fish Aquat Sci (in press)

Di Giulio RT, Scanlon PF (1984a) Sublethal effects of cadmium ingestion on mallard ducks. Arch Environ Contam Toxicol 13:765–771

———, ——— (1984b) Heavy metals in tissues of waterfowl from the Chesapeake Bay, USA. Environ Pollut (Ser A) 35:29–48

———, ——— (1985a). Heavy metals in aquatic plants, clams, and sediments from the Chesapeake Bay, U.S.A. Implications for waterfowl. Sci Total Environ 41:259–274

———, ——— (1985b) Effects of cadmium ingestion and food restriction on energy metabolism and tissue metal concentrations in Mallard ducks (*Anas platyrhynchos*). Environ Res 27:433–444

DuBowy PJ (1989) Effects of diet on selenium bioaccumulation in marsh birds. J Wildl Manage 53:776–781

Eisler R (1985) Cadmium hazards to fish, wildlife, and invertebrates: A synoptic review. US Fish Wildl Serv Biol Rep 85(1.2)

Ferns PN, Anderson JI (1994) Cadmium in the diet and body tissues of Dunlins *Calidris alpina,* from the Bristol Channel, UK. Environ Pollut 86:225–231

Fischer H (1988) *Mytilus edulis* as a quantitative indicator of dissolved cadmium. Final study and synthesis. Mar Ecol Prog Ser 48:163–174

Fox GA, Weseloh DV, Kubiak TJ, Erdman TC (1991) Reproductive outcomes in colonial fish-eating birds: A biomarker for developmental toxicants in Great Lakes food chains. I. Historical and ecotoxicological perspectives. J Great Lakes Res 17:153–157

Frank A (1986) In search of biomonitors for cadmium: Cadmium content of wild Swedish fauna during 1973-1976. Sci Total Environ 57:57–65

Heinz GH, Pendleton GW, Krynitsky AJ, Gold LG (1990) Selenium accumulation and elimination in Mallards. Arch Environ Contam Toxicol 19:374–379

Heinz GH, Sanderson CJ (1990) Avoidance of selenium-treated food by Mallards. Environ Toxicol Chem 9:1155–1158

Henny, CJ, Blus LJ, Grove RA (1990) Western Grebe, *Aechmophorus occidentalis,* wintering biology and contaminant accumulation in Commencement Bay, Puget Sound, Washington. Can Field-Nat 104:460–472

Henny CJ, Blus LJ, Grove RA, Thompson SP (1991) Accumulation of trace elements and organochlorines by Surf Scoters wintering in the Pacific Northwest. Northwestern Nat 72:43–60

Henny CJ, Rudis DD, Roffe TJ, Robinson-Wilson E (1995) Contaminants and sea ducks in Alaska and the circumpolar region. Environ Health Perspect 103 (Suppl 4):41–49

Hicklin PW, Smith PC (1984) Selection of foraging sites and invertebrate prey by migrant Semipalmated Sandpipers, *Calidris pusilla* (Pallas), in Minas Basin, Bay of Fundy. Can J Zool 62:2201–2210

Hohman WL, Pritchert RD, Pace RM, Woolington DW, Helm R (1990a) Influence of ingested lead on body mass of wintering Canvasbacks. J Wildl Manage 54:211–215

Holland PT, Hickey CW, Roper DS, Trower TM (1993) Variability of organic contaminants in inter-tidal sandflat sediments from Manukau Harbour, New Zealand. Arch Environ Contam Toxicol 25:456–463

Houston AI, Carbone C (1992) The optimal allocation of time during the diving cycle. Behav Ecol 3:255–265

Howerter DW (1990) Movements and bioenergetics of Canvasbacks wintering in the upper Chesapeake Bay. MS thesis, Virginia Polytech Inst and State Univ, Blacksburg, VA

Hyman JB, McAninch JB, DeAngelis DL (1990) An individual-based simulation model of herbivory in a heterogeneous landscape. In: Turner MG, Gardner RH (eds) Quantitative methods in landscape ecology. Springer-Verlag, New York, pp 443–475

Kay SH (1985) Cadmium in aquatic food webs. Residue Rev 96:13–43

Kendall RJ, Lacher TE (eds) (1994) Wildlife toxicology and population modeling. Lewis Publishers, Boca Raton, FL

Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59:253–260

Krebs CJ (1989) Ecological methodology. Harper Collins Publishers, NY

Lande E (1977) Heavy metal pollution in Trondheimsfjorden, Norway, and the recorded effects on the fauna and flora. Environ Pollut 12:187–198

Lemly AD (1993) Metabolic stress during winter increases the toxicity of selenium to fish. Aquat Toxicol 27:133–158

Lovvorn JR (1987) Behavior, energetics, and habitat relations of Canvasback ducks during winter and early spring migration. Ph.D thesis, Univ of Wisconsin, Madison, WI

——— (1989a) Distributional responses of Canvasback ducks to weather and habitat change. J Appl Ecol 26:113–130

——— (1989b) Food defendability and antipredator tactics: Implications for dominance and pairing in Canvasbacks. Condor 91:826–836

——— (1994a) Biomechanics and foraging profitability: An approach to assessing trophic needs and impacts of diving ducks. Hydrobiologia 279/280:223–233

——— (1994b) Nutrient reserves, probability of cold spells and the question of reserve regulation in wintering Canvasbacks. J Anim Ecol 63:11–23

Lovvorn JR, Gillingham MP (1996) Food dispersion and foraging energetics: A mechanistic synthesis for field studies of avian benthivores. Ecology 77:in press

Lovvorn JR, Jones DR (1991) Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can J Zool 69:2879–2887

———, ——— (1994) Biomechanical conflicts between adaptations for diving and aerial flight in estuarine birds. Estuaries 17: 62–75

Lovvorn JR, Jones DR, Blake RW (1991) Mechanics of underwater locomotion in diving ducks: Drag, buoyancy and acceleration in a size gradient of species. J Exp Biol 159:89–108

Madenjian CP, Carpenter SR, Rand PS (1994) Why are the PCB concentrations of salmonine individuals from the same lake so highly variable? Can J Fish Aquat Sci 51:800–807

Mahaffy MS, Bennett CR, Parson W (1995) Puget Sound waterbirds as contaminant monitors. Proc Puget Sound Research '95 Conf, Puget Sound Water Qual Author, Olympia, WA, pp 927–935

Mallins DC, McCain BB, Brown DW, Chan S-L, Myers MS, Landahl JT, Prohaska PG, Friedman AJ, Rhodes LD, Burrows DG, Gronlund WD, Hodgins HO (1984) Chemical pollutants in sediments and diseases of bottom-dwelling fish in Puget Sound, Washington. Environ Sci Technol 18:705–713

Mayes RA, McIntosh AW, Anderson VL (1977) Uptake of cadmium and lead by a rooted aquatic macrophyte (*Elodea canadensis*). Ecology 58:1176–1180

McIntosh AW, Shephard BK, Mayes RA, Atchison GJ, Nelson DW (1978) Some aspects of sediment distribution and macrophyte cycling of heavy metals in a contaminated lake. J Environ Qual 7:301–305

Miles AK, Ohlendorf HM (1993) Environmental contaminants in Canvasbacks wintering on San Francisco Bay, California. Calif Fish and Game 79:28–38

Mora MA, Anderson DW, Mount ME (1987) Seasonal variation of body condition and organochlorines in wild ducks from California and Mexico. J Wildl Manage 51:132–141

Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol Monogr 57:111–128

Ohlendorf HM, Marois KC, Lowe RW, Harvey TE, Kelly PR (1991) Trace elements and organochlorines in Surf Scoters from San Francisco Bay, 1985. Environ Monit Assess 18:105–122

Pennycuick CJ (1989) Bird flight performance. Oxford University Press, Oxford UK

Perry MC, Uhler FM (1988) Food habits and distribution of wintering Canvasbacks, *Aythya valisineria,* on Chesapeake Bay. Estuaries 11:57–67

Peterson JA, Nebeker AV (1992) Estimation of waterborne selenium concentrations that are toxicity thresholds for wildlife. Arch Environ Contam Toxicol 23:154–162

Pilastro A, Congiu L, Tallandini L, Turchetto M (1993) The use of bird feathers for the monitoring of cadmium pollution. Arch Environ Contam Toxicol 24:355–358

Porter WP, Hinsdill R, Fairbrother A, Olson LJ, Jaeger J, Yuill T, Bisgaard S, Hunter WG, Nolan K (1984) Toxicant-disease-environment interactions associated with suppression of immune system, growth, and reproduction. Science 224:1014–1017

Press WH, Flannery BP, Teukolsky SA, Vetterling WT (1989) Numerical recipes: The art of scientific computing (FORTRAN Version). Cambridge University Press, NY

Pulliam HR (1994) Incorporating concepts from population and behavioral ecology into models of exposure to toxins and risk assessment. In: Kendall RJ, Lacher TE (eds) Wildlife ecology and population modeling. Lewis Publishers, Boca Raton, FL, pp 13–26

Rule JH, Alden RW (1990) Cadmium bioavailability to three estuarine animals in relation to geochemical fractions to sediments. Arch Environ Contam Toxicol 19:878–885

Scanlon PF (1982) Wet and dry weight relationships of Mallard (*Anas platyrhynchos*) tissues. Bull Environ Contam Toxicol 29:615–617

Scheuhammer AM (1987) The chronic toxicity of aluminum, cadmium, mercury, and lead in birds: A review. Environ Pollut 46:263–295

Sjoberg K (1988) Food selection, food-seeking patterns and hunting success of captive Goosanders *Mergus merganser* and Red-breasted Mergansers *M. serrator* in relation to the behaviour of their prey. Ibis 130:79–93

Skorupa JP, Ohlendorf HM (1991) Contaminants in drainage water and avian risk thresholds. In: Dinar A, Zilberman D (eds) The economics and management of water and drainage in agriculture. Kluwer Academic Publishers, Boston, pp 345–368

Smith VE, Spurr JM, Filkins JC, Jones JJ (1985) Organochlorine contaminants of wintering ducks foraging on Detroit River sediments. J Great Lakes Res 11:231–246

Stickel LF, Stickel WH, McLane MAR, Bruns M (1977) Prolonged retention of methyl mercury by Mallard drakes. Bull Environ Contam Toxicol 18:393–400

Swartzman GL, Kaluzny SP (1987) Ecological simulation primer. Macmillan Publishers, NY

Szefer P, Falandysz J (1987) Trace metals in the soft tissues of scaup ducks (*Aythya marila* L.) wintering in Gdansk Bay, Baltic Sea. Sci Tot Environ 65:203–213

Takekawa JY (1987) Energetics of Canvasbacks staging on an upper Mississippi River pool during fall migration. PhD thesis, Iowa State Univ, Ames, IA

Thompson WA, Vertinsky I, Krebs JR (1974) The survival value of flocking in birds: A simulation model. J Anim Ecol 43:785–820

Tome MW (1988) Optimal foraging: Food patch depletion by Ruddy Ducks. Oecologia 76:27–36

USEPA (U.S. Environmental Protection Agency) (1993) Wildlife exposure factors handbook, Vol. 1. EPA/600/R-93/187a, Washington, DC

Vermeer K, Cretney WJ, Elliott JE, Norstrom RJ, Whitehead PE (1993) Elevated polychlorinated dibenzodioxin and dibenzofuran concentrations in grebes, ducks, and their prey near Port Alberni, British Columbia, Canada. Mar Pollut Bull 26:431–435

Vermeer K, Peakall DB (1979) Trace metals in seaducks of the Fraser River Delta intertidal area, British Columbia, Mar Pollut Bull 10:189–193

White DH, Finley MT (1978) Uptake and retention of dietary cadmium in Mallard ducks. Environ Res 17:53–59

White DH, Finley MT, Ferrell JF (1978) Histopathologic effects of dietary cadmium on kidneys and testes of Mallard ducks. J Toxicol Environ Health 4:551–558

White DH, Mitchell CA, Kaiser TE (1983) Temporal accumulation of organochlorine pesticides in shorebirds wintering on the south Texas coast, 1979-80. Arch Environ Contam Toxicol 12:241–245

White DH, Stendell RC, Mulhern BM (1979) Relations of wintering Canvasbacks to environmental pollutants—Chesapeake Bay, Maryland. Wilson Bull 91:279–287

Woakes AJ, Butler PJ (1983) Swimming and diving in Tufted Ducks, *Aythya fuligula,* with particular reference to heart rate and gas exchange. J Exp Biol 107:311–329