Use of Site-Specific Data for Modeling Selenium Bioaccumulation by Terrestrial Animals

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Abstract
We developed a bioaccumulation model from an extensive set of monitoring data to predict selenium (Se) concentrations in biota within a terrestrial system (Kesterson Reservoir, CA). The model uses water-extractable Se and total Se concentrations in soil to estimate the expected mean and ranges of Se concentrations in biota at Kesterson for future scenarios. Biological monitoring data collected at Kesterson from 1989 to 1994 were used to parameterize the initial model. The model was tested and updated with additional sample results from 1995 through 2001 biological monitoring and validated and calibrated using Se concentrations from sampling conducted in 2004 and 2006. Minor adjustments were made to the model based on each additional year’s results, and the model was used in 2014 to assess whether there were continuing threats to wildlife at Kesterson. The model predicts Se concentrations in small mammals, bird blood, and bird eggs in common species found at Kesterson. This model was used for the final assessment of Kesterson in 2014 and performed well, but there was variability in results, probably due to differences in individual diets and feeding ranges of animals. The model has been further refined since 2014, as we describe here. The model performs well for predicting central tendency and is conservative as the predicted upper limits of the biotic exposure distributions were mostly similar or higher than the measured. The trophic and tissue transfer factors and regression equations should be applicable to other Se-contaminated sites; adjusting weighting factors based on diet and range allows the model to be adapted and used at other sites.

Kesterson Reservoir (hereafter, “Kesterson”) received subsurface agricultural drainwater contaminated with selenium (Se) in the late 1970s and early 1980s (Ohlendorf and Santolo 1994). Kesterson is in western Merced County, California, within the San Joaquin Valley (37°15’N, 120°53’W). Severe adverse effects in aquatic birds led to remediation efforts by the US Bureau of Reclamation in 1988 (Ohlendorf 2011; Ohlendorf et al. 2020). Kesterson, formerly a reservoir composed of 12 adjoining shallow ponds intended primarily for storage and evaporation of drainwater, was dewatered and low-lying areas were filled with clean soil. Post-filling, Kesterson is a mosaic of filled areas, areas of preexisting grassland, and dewatered former cattail (Typha sp.) areas. Plant species at Kesterson are predominantly non-native annual forbs and grasses. Those species occur most abundantly in the more disturbed filled areas. In contrast, the less disturbed areas support dominant native plant species such as saltgrass (Distichlis spicata), which continues to dominate many of the grassland areas. Most of the former cattail-dominated wetlands that were drained had a thick thatch layer that persisted over many years due to the lack of moisture for decomposition, partly because of the drought conditions through 1993. Those areas showed the greatest habitat change as the cattail thatch decomposed.

The filling transformed Kesterson into grassland and alkali scrub habitat used by terrestrial birds and other upland wildlife species (Ohlendorf and Santolo 1994). Risk assessments were conducted for Kesterson (CH2M HILL and Lawrence Berkeley National Laboratory 2000; Ohlendorf and Santolo 1994; Santolo 1994) using a bioaccumulation model developed from Kesterson sampling results in 1989 through 1994 (Santolo 1994). The model was tested and updated with additional sample results from 1995 through 2001 biological monitoring (USBR, 1989–2001 Kesterson Annual Biological Monitoring Reports). Measured Se concentrations from sampling conducted in 2004 and 2006 were used to validate and calibrate the terrestrial Se bioaccumulation model.
model. The model was used in 2014 to assess whether there were continuing threats to wildlife at Kesterson; the conclusion was that no further management actions were needed to mitigate or control exposures and recommended that no further scheduled monitoring should occur (Ohlendorf et al. 2020; USBR 2015). In this paper, we describe the model and how it was modified over time as more information became available.

The original model was used to predict dietary Se concentrations for species such as red-tailed hawks (Buteo jamaicensis) and northern harriers (Circus cyaneus) 20 years into the future under varying assumptions of Se bioavailability (Ohlendorf and Santolo 1994) and was modified to assess the risk to waterbirds using ephemeral pools at Kesterson (Byron et al. 2003). Although field-sampling data indicated that model-predicted values were conservative (i.e., over-predicted), we concluded that long-term monitoring and management planning for Kesterson (Ohlendorf et al. 2020), and other sites with elevated Se, would benefit from an improved bioaccumulation model that uses the large database of site-specific and experimental information now available. Furthermore, the original model predicted dietary concentrations for receptors of interest, but a more refined model would provide estimates of accumulation in receptor tissues, particularly bird eggs, so that potential effects could be more directly and accurately evaluated.

In a wide variety of species, if one expresses Se concentrations in both the diet and eggs on a dry-weight (dw) basis, concentrations in bird eggs range from roughly equal to about three or four times those in the diet of the female at the time of egg-laying (Ohlendorf 2003). However, Se transfer from diet to eggs varies by bird species and likely by the chemical form, toxicokinetics, concentration, and metabolic pathways of the different Se forms in the diet (see: Davis et al. 2013, 2017; Heinz and Hoffman 1996; Tiwary et al. 2006). For example, when mallards (Anas platyrhynchos) were fed a diet containing 10 µg Se/g as selenomethionine (SeMet), eggs from the treated birds contained a mean of about 15 µg Se/g dw (4.6 µg Se/g wet weight [ww]), whereas eggs from those fed a diet containing 10 µg Se/g as sodium selenite had only about 1.7 µg Se/g dw (0.53 µg Se/g ww; Heinz et al. 1987). In a study where quail were dosed with selenite (SeO₄²⁻) or the L and DL isomeric mixture of SeMet in their diet (Santolo and Yamamoto, unpublished data), Se concentrations in the SeMet groups were higher in the protein fraction of the blood than the non-protein fraction (Se-L-Met, F₁,₄₀ = 43.1, P < 0.001; Se-DL-Met, F₁,₄₀ = 10.4, P = 0.003). However, there was no difference in Se concentration between protein and non-protein fractions of blood in the SeO₄²⁻ group.

Trophic transfer factors (TrTFs) from diet to bird eggs in laboratory studies tend to be higher than expected based on field data. In the laboratory studies, birds usually are exposed to a constant concentration and a single form of highly digestible Se in their diets, whereas free-living animals are exposed to varied concentrations and different biologically incorporated dietary forms of Se with lower digestibility they encounter in their foraging. As noted by Skorupa and Ohlendorf (1991), in comparing the results from Kesterson Reservoir (where some species [especially ducks] could fly to surrounding wetlands to feed) with those from the Tulare Basin (where the evaporation ponds were isolated from other wetlands), exposure of birds such as ducks (in particular) could be “diluted” by their feeding outside the sampled habitats. Conover et al. (2008) noted that although 75% of California gulls (Larus californicus) they analyzed from Great Salt Lake, UT, were found to have eaten only brine shrimp from the lake, the diet of others varied and included items such as carp, earthworms, and hot dogs. TrTFs calculated from California gull egg and brine shrimp Se concentrations reported by Conover et al. ranged from 0.56 to 0.82, with a mean of 0.71.

One possible explanation for the differences in rates of Se uptake and transfer to eggs between laboratory feeding studies and wild birds is that Se bioaccumulation is greater under lower Se conditions than when concentrations are elevated (Stewart et al. 2010). In general, Se uptake by micro-organisms and multicellular organisms is governed by specific transport pathways that facilitate its movement from the environment and across cell membranes or epithelia into the organism. These transport pathways, which consist of transmembrane proteins, may differ with respect to specificity, but typically display high affinity for the element and a limited maximal capacity for uptake. An important consequence of such high-affinity, limited-capacity uptake pathways is that Se uptake from low ambient concentrations is highly efficient but becomes less efficient at higher concentrations due to saturation of the uptake pathway. This nonlinear relationship between ambient concentration and uptake rates is not well described by a single constant or TrTF because TrTF values are known to be inversely related to exposure concentration not only for diet to bird egg but also for diet to fish tissue concentrations (Cardwell et al. 2013). This same phenomenon is also true for bioconcentration and bioaccumulation factors (McGeer et al. 2003).

Few comprehensive studies of the effects of excessive Se on free-living terrestrial wildlife have been conducted (see Albers et al. 2000; Eisler 2000; Ohlendorf 2003; Ohlendorf and Santolo 1994). Monitoring of terrestrial wildlife species (for example, USBR 1999), and studies of Se bioaccumulation and effects on free-living wildlife such as frogs and snakes (Ohlendorf et al. 1988), predatory birds (Santolo and Yamamoto 1999, 2009), nesting songbirds (Santolo 2007), and small mammals (Clark 1987; Clark et al. 1989; Santolo 2009) have been conducted at Kesterson. There also have been very few laboratory studies investigating the
effects of excessive Se on terrestrial avian predators (eastern screech-owls \textit{Otus asio}, Wiemeyer and Hoffman 1996; and American kestrels \textit{Falco sparverius}, Yamamoto et al. 1998, Santolo et al. 1999, Yamamoto and Santolo 2000). A diet-to-whole-body TrTF of about 0.8 was identified in reptiles (\textit{Sceloporus occidentalis}) fed Se-enriched (~ 15 µg/g) crickets (\textit{Acheta domesticus}) by Hopkins et al. (2005), and no deleterious effects were observed. Those studies provide most of the available information on effects of Se to terrestrial wildlife species, and no guidelines have been established specifically for evaluating Se effects in terrestrial wildlife. Because of the limited data on effects of excess Se in free-living terrestrial animals, evaluation of effects in terrestrial systems is primarily extrapolated from effects on aquatic and semi-aquatic species (birds) or domestic animals (poultry and mammals).

Bioaccumulation models have been extensively developed for Se in aquatic systems (e.g., Chapman et al. 2010; Presser and Luoma 2010; Toll et al. 2005; USEPA 2016), but comparable models have not been well developed for terrestrial systems. Alsop et al. (1996) used measured soil metal concentrations to model plant concentrations for use as intake concentrations to estimate tissue concentrations in mammals and, because the kinetics of uptake and depuration of at least some metals in terrestrial plants and mice are not linear at high concentrations, they tended to overestimate exposure.

Here we describe a model developed from site-specific data for prediction of dietary Se exposure and consequent accumulation in terrestrial animals (i.e., invertebrates, herptiles, birds, and mammals) at Kesterson. For this model, empirical data are used to estimate uptake of Se from soils and co-located plants to diet and to animals. Verification studies to assess the model’s performance are also described. American kestrels, barn owls (\textit{Tyto alba}), and loggerhead shrikes (\textit{Lanius ludovicianus}) are predatory birds occurring year-round at Kesterson, while California voles (\textit{Microtus californicus}), deer mice (\textit{Peromyscus maniculatus}), and common small mammals as a group (i.e., deer mice, western harvest mice [\textit{Reithrodontomys megalotis}], and house mice [\textit{Mus musculus}] combined) at the site were selected as model species for this effort.

**Methods**

**Selenium Monitoring of Soil and Biota**

Soil, plant, and invertebrate samples were collected from 54 (soil samples were collected at 0–0.3 m and 0.3–1 m depths for a combined total of 107 samples) permanent sampling sites and bird, bird egg, and small mammal samples were collected from throughout Kesterson for Se analysis during 1989–2006 and in 2013/14 (USBR 2015). Se concentrations were determined for soil, above-ground plant parts, invertebrates, reptile livers and carcasses, bird livers, entire contents of bird eggs, and small mammal whole carcasses or livers. For mouse Se, three species were combined, and a regression equation based on 1989–1998 liver:carcass Se concentrations in deer mice, western harvest mice, and house mice was developed to estimate whole-body Se concentrations when only livers were analyzed (Santolo 2009). Passerine Se concentrations were based on liver Se concentrations of 22 western meadowlarks (\textit{Sturnella neglecta}) and two sparrows (\textit{Zonotrichia leucophrys gambelii}) collected during 1989 and 1990. After 1994, additional Se determinations were conducted for bird blood samples collected at Kesterson.

Most samples were stored frozen until they were shipped to a commercial laboratory (Environmental Trace Substances Research Center, Columbia, Missouri from 1989 to 1991 or Laboratory and Environmental Testing, Columbia, Missouri after 1991) on dry ice for total Se analysis. Some bird blood samples were frozen and then analyzed by California Animal Health and Food Safety (formerly California Veterinary Diagnostic Laboratory Service; University of California, Davis). Sample preparation consisted of lyophilization, followed by homogenization and sequential acid digestions (nitric acid followed by hydrochloric acid). Total Se concentrations were determined using hydride generation atomic absorption spectrometry. Blood was analyzed by hydride vapor generation inductively coupled argon plasma spectrometry (Tracy and Möller 1990). Lyophilization data were used to calculate percent moisture in all samples. Water-extractable soil Se (WxSe) was analyzed by treating 5.0 mL supernatant sample with 0.2 mL of 2% ammonium persulfate and 5.0 mL of concentrated HCL before it was fed into the instrument. After being placed on a reciprocating shaker table and agitated for 60 min, the mixture was centrifuged at 7800 revolutions per minute for 15 min and the supernatant solution was filtered through a 0.45-micron membrane filter before analysis. WxSe includes selenite and selenate, and minor amounts of organically associated Se (Wahl et al. 1994).

Total soil Se concentrations (TSe) and WxSe concentrations are expressed as mg Se/kg dw; all other Se concentrations are expressed as µg/g on a dw basis.

**Model Development**

This terrestrial bioaccumulation model was based on an earlier model developed by Santolo (1994) and Ohlendorf and Santolo (1994) using data collected from 1989 to 1994 for predicting Se concentrations in bird and mammal food chain items using measured WxSe and enhanced by incorporation of subsequently collected data as described in the next
section (Wahl et al. 1994). About 93% of the Se inventory at Kesterson is immobile but slowly oxidizing into bioavailable forms and only a limited fraction of the total Se inventory, the WxSe fraction, is mobile and available for plant uptake (Wahl et al. 1994). Thus, the primary driving parameter for Se in the food chain is Se concentrations in soil water. This terrestrial bioaccumulation model uses measured WxSe concentrations in all years when samples were collected to predict Se concentrations in food-chain items. Se uptake by plants was then modeled using a regression equation based on paired soil and plant samples collected during biological monitoring at Kesterson. Although there is a general increase in plant Se with increasing WxSe, this is not a constant ratio, and the relation between these two matrices is highly variable (Ohlendorf and Santolo 1994); this is also true of the soil-to-plant ratio. Wahl et al. (1994) demonstrated the gradual temporal increase of the water-extractable soil component at Kesterson, which represents an increase in the more mobile and bioavailable fraction of the Se inventory. However, the data reflect that the soil-to-plant and WxSe-to-plant relations are similar, and about 40% of the variability is accounted for by either method. Data from monitoring of plants, invertebrates, and vertebrates at Kesterson were used to develop Se TrTFs through the food chain.

We assumed that offsite diet item Se concentration was 1.9 µg/g based on small mammal offsite Se concentrations (2.0 µg/g; Santolo 2009), background concentrations reported by NIWQP (<2.0 µg/g in mammals and <1.5 µg/g in invertebrates; 1998), and the mean Se concentration of 1.7 µg/g found in invertebrates collected from a nearby uncontaminated site, the Volta Wildlife Area, near Kesterson (Hothem and Ohlendorf 1989). For insects and other consumers, a fractional weighting factor (≤ 1) was assigned to each compartment of their diet and a TrTF (concentration in the consumer divided by concentration in the food item) was determined. Weighting factors (WFs) were based on food habits and home range studies conducted at Kesterson whenever possible (Santolo 2007; Santolo and Yamamoto 2009). When site-specific data did not exist for Kesterson, data from other published sources were used (e.g., Marti et al. 2020; Vickerman and Trumble 2003; Yosef 1996). The home ranges were used to estimate the proportion of onsite foraging for various species. Se concentrations in dietary items from offsite were assumed to average 1.9 µg Se/g, as described above. In addition, more recent results were used to adjust equations.

Regression analysis was used to develop TrTFs, based on available measured Se concentrations from Kesterson biological monitoring, to simulate Se accumulation through the food-chain (e.g., from plant to herbivorous invertebrate or plant to herbivorous mammal). Detailed dietary, home range (Santolo and Yamamoto 2009), and experimental Se accumulation data for kestrels (Santolo et al. 1999; Yamamoto et al. 1998) were used to develop TrTFs and WFs based on the percent of various dietary items and the extent of onsite foraging for the Kesterson food-chain. Ohlendorf and Santolo (1994) previously described the equations used to develop those factors.

These regression models and weighting factors, along with species-specific diet data, were used to model Se accumulation in other species (such as barn owl and killdeer [Charadrius vociferus]). The percentage of onsite foraging by other species was estimated using published foraging ranges and site-specific information such as where on Kesterson they tended to nest (Kesterson Biological Monitoring Reports 1989–2001; Santolo 2007; Santolo and Yamamoto 2009).

Model Testing, Validation, and Calibration

Kesterson Se monitoring data collected from 1995 to 2001 (sampling methodology was similar from year-to-year, although not all sample types were collected in each year) were used to test and update the model. Results from sampling conducted in 2004 and 2006 were used to validate model assumptions and to calibrate the model. For each year, WxSe data were used as model input, and model predictions of Se concentrations in food-web species, birds, and mammals were compared to Se concentrations measured in biota for that year. These comparisons of modeled and measured Se concentrations provided a basis for evaluating the model’s predictive value and improving the model’s predictions. The final calibrated model was used to assess risk at Kesterson under conditions found in 2014 (Ohlendorf et al. 2020; USBR 2015).

Statistics

We used simple and second-order polynomial regression analysis to develop equations based on measured parameters for predicting Se concentrations and nonparametric Mann–Whitney test to measure the quality of the models. The assumption of normality was not met for most of the data results (Shapiro–Wilk test) and geometric means (GMs), geometric confidence intervals (GCIs), and nonparametric Mann–Whitney tests were used (GraphPad Software 2020) to compare between values such as measured and predicted Se results ($\alpha = 0.05$). The 95% GCI is used to describe the uncertainty around the means, and the CI of the slope (CIS) was used to describe the uncertainty around the slope of regressions, and the estimated TrTFs and tissue transfer factors (TrTTFs).
Results
Regression Model Components and Updates

The various components of the model were updated, and the model was applied in 2014 to compare measured and predicted concentrations.

When WxSe data were not available (as in 2014), WxSe (mg/kg) in soils was estimated from the regression equation described in Fig. 1 ($0.747 \times (\log \ TSe) - 1.17$; 95% CIS = 0.702–0.792) for paired TSe and WxSe. In 2014, WxSe was estimated using a regression equation based on 621 paired TSe and WxSe samples analyzed from 1989 to 2001 ($r^2 = 0.63; P < 0.001$). Estimated WxSe for 107 soil samples in 2014 was from 0.018 to 0.74 mg/kg (GM = 0.13 µg/g; 95% GCI = 0.11–0.15), with WxSe about 5.7% of TSe. The predicted ranges, GMs, and GCIs are shown in Table 1. Equations developed for the predictive model are provided below and listed by equation number in Table 2.

Paired samples were also used to describe the relation between detritus (i.e., organic matter produced by the decomposition of organisms; primarily dead plants) and WxSe concentrations ($r^2 = 0.27, n = 156, P < 0.001$, 95% CIS = 0.648–0.956). Detritus Se concentrations (GM = 3.1, 95% GCI = 2.2–4.4) were estimated using the following regression equation:

\[
\text{Detritus [Se]} = 10^{(0.802 \times \log \ WxSe + 1.773)}
\]  

The log–log relations between paired plant and WxSe ($r^2 = 0.398, n = 90, P < 0.001$, 95% CIS = 0.248–0.423; Fig. 2A) or TSe (Fig. 2B) concentrations ($r^2 = 0.399, n = 90, P < 0.001$, 95% CIS = 0.208–0.353) were examined and there was no difference between the two calculations ($P = 0.528$). The GM plant Se was 8.7 (95% GCI = 8.1–9.4) and the following equations describe WxSe and TSe to plant Se:

\[
\text{Plant [Se]} = 10^{(0.335 \times \log \ WxSe + 0.808)}
\]  

\[
\text{Plant [Se]} = 10^{(0.280 \times \log \ TSe + 0.405)}
\]  

We used the GMs of Se by trisection (Ohlendorf and Santolo 1994) for samples from 1989 to 2001 to relate TSe, WxSe, and plant Se to Se in herbivorous insects (GM = 8.3 µg/g; $n = 939$, 95% GCI = 7.9–8.7). Because Se concentrations in carnivorous invertebrates were significantly higher than concentrations in herbivorous insects (non-carnivores; $P < 0.001$), terrestrial invertebrates were separated into categories of herbivorous insects (38% were herbivorous beetles [Coleoptera], 12% were crickets, and 49% were grasshoppers [Orthoptera]) and carnivorous invertebrates (381 samples of which 6% were mantids [Orthoptera], 12% were scarab beetles [Scarabaeidae], and 82% were spiders [Arachnida]). We assumed that terrestrial non-carnivorous insects are only plants. The TrTF was based on 667 spatially and temporally paired plant and insect samples collected from 1989 to 1994. The plant-to-herbivorous-insect regression ($r^2 = 0.335, n = 84, P < 0.001$, 95% CIS = 0.374–0.723) was not as strong as (i.e., more variable than) the relation between TSe ($r^2 = 0.397, n = 81, P < 0.001$, 95% CIS = 0.164–0.290) or WxSe and herbivorous insect Se ($r^2 = 0.492, n = 81, P < 0.001$, 95% CIS = 0.222–0.353). This result may be an anomaly related to a taxonomic breadth of plant data that may not match up very well with the species of plants or plant parts that herbivorous insects might be limited to feeding on:

\[
\text{Herbivorous Insect [Se]} = 10^{(0.227 \times \log \ TSe + 0.780)}
\]  

\[
\text{Herbivorous Insect [Se]} = 10^{(0.288 \times \log \ WxSe + 1.12)}
\]  

We assumed that carnivorous invertebrates (GM = 13 µg/g; $n = 78$, 95% GCI = 11–14) were eating only insects. Carnivorous invertebrate Se then was related to herbivorous insect Se ($r^2 = 0.335, n = 78, P < 0.001$, 95% CIS = 0.374–0.730) and a calibration factor (CF) was developed using the GM carnivorous invertebrate Se divided by herbivorous insect GM Se (1989–2001):

\[
\text{Carnivorous Invertebrate [Se]} = (10^{(0.552 \times \log \ HerbInse + 0.605)}) \times 1.58
\]  

Previous studies using kestrels fed seleno-L-methionine (SeMet) mixed into a commercial meat-based diet (Yamamoto et al. 1998) described the relation between diet and blood Se ($r^2 = 0.91, n = 157, P < 0.001$). In that study, two groups of American kestrels were fed a prepared diet (i.e., either 5.1 µg/g or 9 µg/g as SeMet) and another group were fed animals collected at Kesterson with a mean concentration of 8 µg Se/g. Blood samples were taken during the time...
they were being fed these diets on Days 14, 35 and 56; then they were put on the control diet and blood samples were taken on Days 77 and 91. The average TrTFs from diet to blood for the 5.1 and 9 µg/g SeMet birds were 0.82 and 0.85, respectively, and a regression equation (blood Se = 1.132 (log diet Se + 0.801) was developed (relation shown in Fig. 2 of Yamamoto et al. (1998). The ratio of GM blood Se of kestrels and diet items sampled at Kesterson from 1989 to 2001 provided a TrTF of 0.83 and was in agreement with the laboratory-derived TrTFs. This was used as the CF for diet-to-blood Se. Thus, the relation of Se in kestrel blood to their SeMet laboratory diets ($r^2 = 0.919$, $n = 152$, $P < 0.001$).
95% CIS = 0.527–0.580) was re-analyzed as described by the regression equation:

\[
\text{Kestrel blood } [\text{Se}] = 10^{(0.554 \times \text{Log kestrel diet } [\text{Se}]) + 0.379}
\]  

(7)

The GM for kestrel blood without calibration was 8.2 µg Se/g whereas using the CF of 0.83 described above, the GM was 6.8 µg Se/g, lower than the kestrel blood measured in 2014 (GM = 7.6 µg/g).

For estimating barn owl blood Se, we used the kestrel blood Se equation and estimated barn owl diet samples from Kesterson, and adjusted the diet from Kesterson and offsite based on published foraging ranges (Séchaud et al. 2021):

\[
\text{Barn owl blood } [\text{Se}] = 10^{(0.554 \times \text{Log barn owl diet } [\text{Se}]) + 0.379}
\]  

(8)

The calculated GM for barn owls was 5.5 µg Se/g applying an estimated CF of 0.58 based on the ratio of calculated barn owl diet to GM blood concentrations from Kesterson (1995–2000), the GM was 3.5 µg Se/g, closer to the samples collected in 2014 (i.e., 2.4 and 2.5 µg Se/g).

Paired samples of starling (Sturnus vulgaris) diet Se and their blood Se (Santolo 2007) were used to describe the relation between passerine diet and blood Se concentrations ($r^2 = 0.59$, $n = 10$, $P = 0.009$, 95% CIS = 0.174–0.928) and estimated diet samples from Kesterson. Passerine blood Se concentrations were estimated using the following regression equation:

\[
\text{Passerine blood } [\text{Se}] = 10^{(0.551 \times \text{Log Diet } [\text{Se}]) + 0.519}
\]  

(9)

The passerine blood Se equation was used to calculate shrike blood Se using estimated diet samples from Kesterson (2000–2010). The GM was 2.4 µg Se/g, closer to the samples collected in 2014 (i.e., 2.4 and 2.5 µg Se/g).

Paired samples of starling (Sturnus vulgaris) diet Se and their blood Se (Santolo 2007) were used to describe the relation between passerine diet and blood Se concentrations ($r^2 = 0.59$, $n = 10$, $P = 0.009$, 95% CIS = 0.174–0.928) and estimated diet samples from Kesterson. Passerine blood Se concentrations were estimated using the following regression equation:

\[
\text{Passerine blood } [\text{Se}] = 10^{(0.551 \times \text{Log Diet } [\text{Se}]) + 0.519}
\]  

(9)

The calculated blood Se for passerines (GM = 9.7 µg/g) was similar to the 2014 measured Se in passerines (GM = 9.8 µg/g). A CF (1.09) using the ratio of GM of passerine blood sampled from 1989 to 2006 (5.0 µg/g) and estimated diet slightly overestimated blood Se (GM = 11 µg/g).
Kesterson. Shrike blood Se was estimated using the following regression equation:

\[
\text{Shrike blood [Se]} = 10^{0.551 \times \log \text{Diet [Se]} + 0.519}
\]

A CF (0.92) using the ratio of GM of shrike blood sampled from 1994 to 2013 (7.0 µg/g) and estimated diet slightly overestimated blood Se (GM = 9.4 µg/g).

We did not have paired diet: blood samples for killdeer. However, at Hailstone National Wildlife Refuge (HNWR), MT, generally co-located brine shrimp (76 µg Se/g) and American avocet (Recurvirostra americana) blood (64 µg Se/g) samples (Personal communication, J. Skorupa, USFWS) gave a TrTF of about 0.84. Comparing the kestrel blood Se equation for diet-to-blood and the passerine diet-to-blood equations and the avocet diet Se suggests that both equations perform poorly for killdeer. Inputting the brine shrimp Se concentration for the diet, the kestrel equation predicts blood Se concentration of 7.1 µg/g, and the passerine equation performs somewhat better predicting blood Se concentration of 36 µg/g. Thus, we used the passerine equation and an estimated killdeer diet for killdeer and the GM for blood was 5.6 µg Se/g:

\[
\text{Killdeer blood [Se]} = 10^{0.551 \times \log \text{killdeer diet [Se]} + 0.519}
\]

A CF of 0.71 was observed in gulls (Conover et al. 2008), which was lower than the CF for avocets of 1.19, and the calculated CF using diet and blood results from the model of 1.36. Using this CF, the GM of killdeer blood was calculated (GM = 7.2 µg/Se/g).

Santolo and Yamamoto (1999) estimated egg Se concentrations for free-living birds using a blood-to-egg Se concentration relation established in captive American kestrel studies (Santolo et al. 1999) with a TiTF of 1.7–2.8 and assumed the relation to be similar for other predatory birds. However, it is unlikely that the relationship observed in the laboratory studies would be observed in the field (Santolo and Yamamoto 2009) because it was developed from birds fed a constant elevated concentration of SeMet. This over-estimated egg Se in birds because free-living birds would be exposed to various concentrations likely due to the differences in digestibility of the laboratory and field diets. For example, at Kesterson invertebrate Se ranged from 0.6 to 48 µg Se/g in 1994 and 1995 (Santolo and Yamamoto 1999), and small mammal Se concentrations ranged from 2.4 to 37 µg Se/g in 1999 (Santolo 2009). The TiTF of kestrels found by Santolo and Yamamoto (2009) was about 0.47, and the TiTF of 0.52 calculated for kestrel blood-to-egg Se was based on the relation of the TrTF (diet-to-blood Se) from samples collected at Kesterson between 1989 and 2006, using the equation described in previous studies (Santolo and Yamamoto 1999; Santolo et al. 1999):

\[
\text{Kestrel Egg Se} = (0.136 \times \text{parent blood Se} + 2.272) \times 0.52
\]

Paired samples of Se in starling blood and egg Se (Santolo 2007) were used to describe the relation between passerine blood and egg Se concentrations (i.e., the TiTF) \( r^2 = 0.74, n = 5, P = 0.002 \). Passerine egg Se concentrations were estimated by adjusting the diet for passerines (GM = 7.2 µg Se/g) to calculate blood Se (GM = 9.8 µg Se/g) using Eq. 9 and then the calculated passerine egg GM (5.0 µg Se/g) using the following regression equation (relation shown in Fig. 2 of Santolo 2007):

\[
\text{Passerine Egg [Se]} = 10^{0.42 \times \log \text{Pass Blood [Se]} + 0.28}
\]

We adjusted the diet for shrikes (GM = 7.3 µg Se/g) to calculate blood Se (GM = 9.4 µg Se/g) and used the passerine egg equation for loggerhead shrike eggs:

\[
\text{Loggerhead Shrike Egg [Se]} = 10^{0.42 \times \log \text{Shrike Blood [Se]} + 0.28}
\]

Blood samples of female adult California gulls and eggs \( r^2 = 0.45, n = 12, P = 0.012 \) from the Great Salt Lake, UT (Conover and Vest 2009) were used to describe the relation between killdeer blood and egg Se concentrations. Killdeer egg Se concentrations were estimated using the following regression equation:
Killdeer Egg \([\text{Se}]\) = \((1.72 \times (\log(\text{Killdeer Blood [Se]}))) + 2.32\)

(15)

Using blood data from HNWR (J. Skorupa, USFWS, Personal Communication) for generally co-located avocet blood Se (\(\text{GM} = 64 \mu g/g\)) and egg Se (\(\text{GM} = 23 \mu g/g\)) in the killdeer egg Se equation resulted in a predicted egg Se (5.4 \mu g/g) less than one-fourth the measured egg Se at HNWR. However, using it with calculated killdeer blood (\(\text{GM} = 5.6 \mu g/g, \text{GM} = 7.6 \mu g/g\) with CF) resulted in egg Se of 3.6 \mu g/g and 3.8 \mu g/g using the CF-corrected blood results, which was similar to Se in killdeer eggs collected in 2014 (3.8 \mu g/g).

Mean TrTFs were used in the initial model when there were not individually paired samples of consumers and their diet, or no strong relationship was found. However, TrTFs tend to decline as the Se concentration in the diet increases due to kinetic hindrances and saturation of metal transporters (Presser and Luoma 2010; Stewart et al. 2010) introducing error into the model because the model focuses on means. As more samples were collected, it became clear that there was a significant concentration-associated relation, and a regression equation was developed and added to the model.

We assumed that small reptiles (lizards and small snakes [i.e., \(< 15 \text{ cm}\) ), that are eaten by American kestrels and loggerhead shrikes, because of their small size would likely be eating only arthropods and that there is a higher abundance of herbivorous insects than carnivorous invertebrates in most years (e.g., of the 1430 herbivorous, detrivorous \([\text{Oniscus}\) spp.], and carnivorous invertebrates collected from 1989 to 2001, about 65% were herbivorous insects). We assumed that reptiles did not discriminate among those invertebrates and chose dietary WFs to be 50% herbivorous insects and 50% carnivorous invertebrates (to include higher-Se detrivors). Few lizards had been observed at Kesterson since the 1990s and they were not caught in pitfall traps or found in kestrel pellets during sampling at Kesterson. Common kingsnakes \([\text{Lampropeltis getulus}\) ], common garter snakes \([\text{Thamnophis sirtalis}\) ], and gopher snakes \([\text{Pituophis catenifer catenifer}\) ] had been observed during monitoring at Kesterson, and six gopher snakes \(< 15 \text{ cm} \) in length were captured and analyzed for whole-body Se concentrations in 1989 and three in 1990 (Santolo, unpublished data). A TrTF of 0.54 was developed by dividing the GM of reptiles (5.9 \mu g/g) by the GM of invertebrates (1989–2001; 11 \mu g/g). Thus, the reptile Se was calculated (GM = 4.6 \mu g/g) based on these spatially and temporally paired gopher snake and insect samples:

\[
\text{Small reptile [Se]} = (\text{Herbivorous insect [Se]} \times 0.5 + \text{Carnivorous invertebrate [Se]} \times 0.5) \times 0.54
\]

Diets, WFs, and a TrTF for voles were determined from stomach content analysis of 55 California voles captured at Kesterson (Santolo, unpublished data). We estimated that plants were over 98% of the diet and only trace amounts of invertebrates were observed, which they likely consumed incidentally during feeding. The GM of whole-body Se, plants, and invertebrates (i.e., herbaceous insects and carnivorous invertebrates combined) from Kesterson were used to calculate a TrTF (1.72) using spatially and temporally paired plant, invertebrate, and vole samples collected from 1989 to 1994 were used to derive the equation as follows:

\[
\text{California vole (whole – body) [Se]} = (\text{Plant [Se]} \times 0.98 + \text{Invertebrate [Se]} \times 0.02) \times 1.72
\]

(17)

A GM of 9.4 \mu g/g was calculated for voles at Kesterson in 2014.

We assumed that predatory birds at Kesterson did not discriminate among deer mice, western harvest mice, and house mice and fed on them based on availability. Therefore, we combined these species (termed “mice”) for predator diets. Deer mice were also modeled separately. Diets, WFs, and a TrTF (1.13) for mice and (0.929) for deer mice were determined from stomach content analysis of 158 deer mice, 47 western harvest mice, and 84 house mice captured at Kesterson (Santolo, unpublished data). The TrTF was based on 390 paired plant, invertebrate, and mouse samples collected from 1989 to 1994, as follows:

\[
\text{Mice (whole – body) [Se]} = (\text{Plant [Se]} \times 0.756 + \text{Mushroom [Se]} \times 0.003 + \text{Herbivorous insect [Se]} \times 0.232 + \text{Carnivorous invertebrate [Se]} \times 0.009) \times 1.13
\]

(18)

A GM of 4.7 \mu g/g was calculated for mice at Kesterson in 2014.

\[
\text{Deer Mouse (whole – body) [Se]} = (\text{Plant [Se]} \times 0.794 + \text{Mushroom [Se]} \times 0.004 + \text{Herbivorous insect [Se]} \times 0.101 + \text{Carnivorous invertebrate [Se]} \times 0.101) \times 0.929
\]

(19)

A GM of 4.6 \mu g/g was calculated for deer mice at Kesterson in 2014.

Diets and WFs for American kestrels at Kesterson were determined from examination of 31 pellets collected from kestrel nest boxes at Kesterson (Santolo and Yamamoto 2009). The fraction of onsite and offsite foraging is the estimated area and time that is spent foraging on Kesterson and on offsite food items. It is expressed as a fraction in the
following equation and a GM of 9.3 µg Se/g was calculated for kestrels at Kesterson in 2014:

American kestrel diet [Se] = (Herbivorous Insect × 0.30 + Carnivorous Insect × 0.24 + Reptile × 0.20 + Passerine × 0.15 + (Mice + Vole)/2 × 0.31) × ((On-site 0.90) + (Off-site 1.0 × 1.9))

(20)

Diets and WFs for shrikes were determined from the literature (Yosef and Lohrer 1995) and site observations. Because most shrike blood was collected during the fall and winter, the diet was adjusted to be dominated by vertebrate species that would be available as prey during that time and a GM of 7.3 µg Se/g was calculated for shrikes at Kesterson in 2014:

Loggerhead shrike diet [Se] = (Herbivorous Insect Se × 0.10 + Carnivorous Insect × 0.24 + Reptile × 0.20 + Passerine × 0.15 + (Mice + Vole)/2 × 0.31) × ((On-site 0.90) + (Off-site 1.0 × 1.9))

(21)

Diets and WFs for barn owls were determined from the literature (Marti et al. 2020) and site observations. Barn owls have a large foraging range of about 2–3 km² (Séchaud et al. 2021) and the nest boxes were all within 0.5 km of the Kesterson border, so we assumed that barn owls foraged about 20% onsite and a GM of 4.5 µg Se/g was calculated for barn owls at Kesterson in 2014:

Barn owl diet [Se] = (Passerine × 0.018 + Mice × 0.082 + Vole × 0.99) × ((On-site 0.20) + (Off-site 1.0 × 1.9))

(22)

Diets and WFs for passerines were determined from stomach content analysis of nine western meadowlarks collected at Kesterson and food items fed to 20 starling nestlings at Kesterson (Santolo 2007). Passerines were assumed to forage only within Kesterson. Diets and WFs were based on 22 spatially and temporally paired plant and invertebrate samples collected from 1989 to 1994 and a GM of 7.2 µg Se/g was calculated for passerines at Kesterson in 2014:

Passerine diet [Se] = (WxSe × 0.03 + Annual Plants × 0.12 + Carnivorous Invertebrate × 0.27) × (On-site 0.20 + (Off-site 1.0 × 1.9))

(23)

Diets and WFs for killdeer were determined from the literature (Jackson and Jackson 2000) and site observations. Except for 1990, aquatic invertebrates were not collected from Kesterson during sampling after 1988, when aquatic habitats were removed for mitigation (Ohlendorf and Santolo 1994; Ohlendorf et al. 2020). Terrestrial invertebrates were assumed to have similar concentrations of Se and were used in the diet calculations for killdeer. Also, because killdeer foraging was increased from 50 to 100%. Also, based on the results from 2001, the killdeer CF was changed from 0.85 to 1.36 before running the model. Mice, deer mouse, kestrel egg, and barn owl blood predicted GM Se concentrations were significantly higher than measured Se. The model results were higher in most cases but reasonably predicted central tendency in all media and similarly predicted higher maximum concentrations in most cases (Table 1).
Discussion

Se concentrations at Kesterson were highly variable both temporally and spatially (Clark 1987; Hothen and Ohlendorf 1989; Ohlendorf and Santolo 1994; Saiki and Lowe 1987; Schuler et al. 1990; Wahl et al. 1994). However, long-term terrestrial monitoring data provided relatively accurate model predictions for birds (the ecological receptors of primary concern at the site), based on verification and calibration exercises carried out with data for various biological media in several post-remediation years (1995, 1996, 1998, 2001, 2004, 2006, and 2014). The analytical techniques used in the terrestrial habitat models are based on a series of linear and log-linear relations and TTFs and TITFs among environmental variables. In each case, assumptions are made about the underlying distribution of the data and the appropriateness of the relation in explaining covariance of the variables. As is to be expected from environmental monitoring data, there remains unexplained variation in the predictions, even in cases of statistically significant relations. However, the basic assumption of the model is that the predictive relations are all descriptive of underlying causal relations.

Unlike aquatic models for fish in enclosed water bodies, terrestrial species can be in or out of the contaminated area, and therefore exposed to a greater range of Se concentrations. The model shows that predicting Se concentrations in species with greater foraging ranges, and therefore a greater range of dietary Se concentrations, becomes less accurate, as would be expected. However, the model produces a range of concentrations that represent the range of potential tissue concentrations. Familiarity with the species being evaluated and how the species use the site and the habitat present on the site are important for making professional judgments on such things as species diet and percent of foraging onsite and offsite that help to reduce variability in the model. The model’s predicted results do not encompass the entire range of Se concentrations observed in measured samples but instead, the predicted results have less variability and cluster around the mean (Fig. 3). However, the model reasonably predicted the range of concentrations that would be expected, especially the maximum concentrations (Fig. 4).

This Se food chain model allows for adjustments to individual species based on dietary items, which can change by season or habitat, and by estimated onsite and offsite foraging. This allows the model to be adjusted for different seasons and for different size sites where a species’ foraging range may be all or only part of the contaminated area.

Comparison of model outputs to monitoring data produced several significant discrepancies. In 1998, unusual Se dynamics in the food chain probably occurred because of a higher-than-normal rainfall (El Niño storm events) that

![Fig. 3. 2014 Modeled and measured (M-) selenium (geometric means [GMs] and 95% confidence limits of the GM [GCI]) of total Soil Se (TSe), plant Se predicted from TSe (TSe Plants), plant Se predicted from WxSe (WxSe Plants), measured Se in plants (M-Plants), predicted Se in Herbivorous Insects, predicted Se in Carnivorous Invertebrates, predicted Se in whole-body mice (deer mice, western harvest mice, and house mice; M-Mice), measured Se in whole-body mice (M-Mice), predicted Se in deer mice (M-PEMA), measured Se in deer mice (M-PEMA), predicted Se in American kestrel blood (AMKE), measured Se in American kestrel eggs (AMKE Eggs), measured Se in American kestrel eggs (AMKE Egg), predicted Se in Passerine blood (Passerine), measured Se in Passerine blood (M-Passerine), predicted Se in barn owl blood (BNOW), measured Se in barn owl blood (M-BNOW), predicted Se in loggerhead shrike blood (LOSH), measured Se in loggerhead shrike blood (M-LOSH), predicted Se in loggerhead shrike eggs (LOSH Egg), measured Se in loggerhead shrike eggs (M-LOSH Egg), predicted Se in killdeer eggs (KILL Egg), measured Se in killdeer eggs (KILL Egg), predicted Se in killdeer eggs (KILL Egg) from Kesterson Reservoir]
year that also likely affected species’ foraging ranges and availability of some dietary items. For example, in 1998, Se concentrations were higher in terrestrial invertebrates than during most other years (USBR 1999). In addition, terrestrial birds, such as loggerhead shrikes and kestrels, were observed foraging offsite to a greater degree during the breeding season, while aquatic-associated species, such as killdeer, may have had the opportunity to forage onsite more because much of Kesterson was flooded in spring. Many animals are opportunistic feeders and some individuals at other locations or in other years may have very different diet compositions than we found. For example, kestrels nesting in the Southern High Plains in 2017 fed their young diets consisting of almost 75% reptiles (Boal et al. 2021), which would have resulted in a lower predicted GM (5.4 μg Se/g, 95% GCI = 5.2–5.6) than was predicted based on the kestrel diet observed at Kesterson (Santolo and Yamamoto 2009).

This model assumes that animals use all the habitats at Kesterson and may not predict Se concentrations accurately for animals that use any single habitat type exclusively or for those that forage primarily offsite, which has been shown to mitigate Se in such birds (Santolo 2007; Skorupa and Ohlendorf 1991). Also, this model is based on Kesterson-specific data but Se uptake from the diet would likely be similar at other sites. Although the regression models and TrTFs and TiTFs are likely not site-specific, adaptation by incorporation of site-specific data for other sites would improve the predictions at those sites. Nevertheless, our model shows the possibility of modeling for terrestrial environments at a level comparable to the much greater effort that has focused on the aquatic environment (e.g., Chapman et al. 2010; Presser and Luoma 2010; USEPA 2016).

Predicted Se concentrations provided a realistic range of Se in biota based on WxSe concentrations and, in many cases, TSe. Therefore, this model can be used, with limited sampling for verification for future ecological risk assessment at Kesterson and potentially at other high-Se sites. In situations where water-extractable or total soil Se concentrations are unavailable, the model can provide predictions using available data from points within the food-chain (e.g., plant or invertebrate Se concentrations) to exposed consumers. If applied with appropriate consideration of site-specific factors and caveats discussed above, and with supporting site data, this is an adaptable tool for evaluation and management of wildlife reproductive risks in terrestrial habitats contaminated by Se.

In summary, one of the primary goals of monitoring and the development of this model was to enable managers’ ability to assess risks of adverse reproductive effects in birds nesting at the site. Results from the most recent monitoring (2013–2014) of biota were compared to those from previous years and used to verify the bioaccumulation model output (USBR 2015). Se concentrations were relatively stable over time, and animals foraging on plants at Kesterson were primarily exposed to Se concentrations below 4 μg/g. Measured and modeled bird egg GM Se concentrations in
2013–2014 were like those in previous years in all species sampled and were in the range where there is low probability of reduced egg hatchability, including effects in sensitive species (Ohlendorf et al. 2020; USBR 2015).

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Availability of Data and Material The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code Availability Not applicable.

Declarations

Conflicts of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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