

1 MERCURY AND RADIOCESIUM ACCUMULATION AND ASSOCIATIONS WITH
2 SUBLETHAL ENDPOINTS IN THE FLORIDA GREEN WATERSNAKE (*NERODIA*
3 *FLORIDANA*)

4
5 **Abstract:**

6
7 Mercury (Hg) and radiocesium (^{137}Cs) are well-known environmental contaminants with the
8 potential to impact the health of humans and wildlife. Snakes have several characteristics
9 conducive to studying environmental contamination but have rarely been included in monitoring
10 of polluted sites. We investigated the bioaccumulation of Hg and ^{137}Cs and associations with
11 sublethal effects (standard metabolic rate and hemoparasite infections) in Florida green
12 watersnakes (*Nerodia floridana*). We captured 78 snakes from 3 former nuclear cooling
13 reservoirs on the United States Department of Energy's Savannah River Site (SRS) in South
14 Carolina. For captured snakes, we (1) determined whole-body ^{137}Cs , (2) quantified total Hg
15 (THg) using snake tail clips, (3) conducted hemoparasite counts, and (4) measured standard
16 metabolic rate (SMR). We used multiple regression models to determine associations among
17 snake body size, capture location, sex, tail THg, whole-body ^{137}Cs , *Hepatozoon* spp. prevalence
18 and parasitemia, and SMR. Average whole-body ^{137}Cs (0.23 ± 0.08 Bq/g; range: 0.00-1.02 Bq/g)
19 was correlated with snake body size and differed significantly by capture site (Pond B: $0.67 \pm$
20 0.05 ; Par Pond: 0.10 ± 0.02 ; Pond 2: 0.03 ± 0.02). Tail THg (0.33 ± 0.03 mg/kg dry weight;
21 range: 0.16-2.10 mg/kg) was significantly correlated with snake body size but did not differ by
22 capture site. We found no clear relationship between SMR and contaminant burdens. However,
23 models indicated prevalence of *Hepatozoon* spp. in snakes was inversely related to increasing

24 whole-body ^{137}Cs burdens. Our results indicate the bioaccumulation of Hg and ^{137}Cs in *N.*
25 *floridana* and further demonstrate the utility of aquatic snakes as bioindicators. Our results also
26 suggest a decrease in *Hepatozoon* spp. prevalence related to increased burdens of ^{137}Cs . While
27 intriguing, further research is needed to understand the dynamics between ^{137}Cs and *Hepatozoon*
28 spp. infections in semi-aquatic snakes.

29

30 **Keywords:** radionuclide; heavy metal; reptile; pollution; standard metabolic rate; *Hepatozoon*

31

32 INTRODUCTION

33 Anthropogenic contaminants have altered ecosystems globally, leading to numerous
34 impacts on wildlife. For example, increases in environmental pollution associated with human
35 activities have been identified as a major factor contributing to the decline of vertebrate species
36 worldwide (Gibbons *et al.* 2000; Ceballos *et al.* 2017). Contaminants can have direct impacts on
37 the health of wildlife and can lead to an increased susceptibility to other stressors, such as
38 disease, predation, and parasitism (Relyea and Mills 2001; Kiesecker 2002; Martin *et al.* 2010;
39 Hanlon and Parris 2013). Thus, continued monitoring of contaminant levels across taxa and
40 ecosystems is needed to gain a better understanding of contaminant fate and associated risks to
41 wildlife. Despite possessing attributes that make them ideal candidates for environmental
42 monitoring, reptiles are understudied relative to other vertebrates regarding ecotoxicology
43 (Hopkins 2000; Haskins *et al.* 2017). Snakes are strictly carnivorous, have relatively long-life
44 spans and exhibit smaller home ranges compared to other vertebrate taxa (Burger 1992; Hopkins
45 *et al.* 1999; Campbell and Campbell 2001; Haskins *et al.* 2019). Thus, they are a suitable

46 candidate for studying local contamination, bioaccumulation (Bauerle *et al.* 1975; Beaupre and
47 Douglas 2009; Drewett *et al.* 2013) and potential impacts of chronic exposure to contaminants.

48 Radiocesium and mercury are two persistent, harmful contaminants impacting
49 environments on a global scale. Radiocesium (^{137}Cs) is a well-known environmental contaminant
50 closely associated with the production of nuclear power and weapons. Radiocesium has been
51 released into the environment due to fallout associated with nuclear weapons testing, waste from
52 nuclear power generation and weapons productions, and accidents at nuclear power plants
53 (Smith and Beresford 2005). In particular, the events of Chernobyl and Fukushima brought
54 awareness of ^{137}Cs to the general public and generated substantial interest in its fate and
55 environmental impact (Beresford and Copplestone 2011; Steinhauser *et al.* 2014). With a
56 physical half-life of roughly 30 years, ^{137}Cs is a gamma-emitter and can persist in water, air, and
57 sediment for decades after release into the environment (Kennamer *et al.* 1998). As an analog for
58 potassium, ^{137}Cs can be easily incorporated into potassium transport systems and bioaccumulate
59 in muscle tissue as organisms assimilate food (Mettler *et al.* 2007).

60 Mercury has been extensively studied as an environmental contaminant, much more so
61 than ^{137}Cs . Since the early 1800s, concentrations of Hg have reportedly tripled due to
62 anthropogenic activities, making Hg contamination a global concern (Lamborg *et al.* 2014).
63 Although Hg occurs naturally (e.g., through volcanic emission, forest fires, volatilization), human
64 activities including mining, fossil fuel combustion, gold manufacturing, and caustic soda
65 produced through chlor-alkali processes and cement production, have drastically increased Hg
66 mobilization and bioavailability to biota (Wang *et al.* 2004; Pacyna *et al.* 2006; Schneider *et al.*
67 2013). Once released into the environment, elemental Hg can be transformed into the more toxic
68 and bioavailable methylmercury (MeHg) largely through microbial methylation – especially in

69 aquatic habitats. When ingested via contaminated food items, Hg can become widely distributed
70 throughout an organism and accumulate in various tissues, such as liver and muscle, over time
71 (Green *et al.* 2010; Azevedo *et al.* 2012; Drewett *et al.* 2013).

72 Radiocesium and mercury have both been shown to bioaccumulate in wildlife (¹³⁷Cs:
73 Brisbin *et al.* 1974; Kennamer *et al.* 1998; Leaphart *et al.* 2020; Hg: Wolfe *et al.* 1998; Nilsen *et al.*
74 *et al.* 2017) and often biomagnify in food webs, especially in aquatic habitats (Sundbom *et al.*
75 2003; Chumchal *et al.* 2011). Thus, high trophic predators inhabiting aquatic habitats may be at
76 an increased risk of accumulating and experiencing subsequent harmful effects of ¹³⁷Cs and Hg.
77 Effects of acute exposure, particularly to high doses of a contaminant, have been documented for
78 both ¹³⁷Cs (e.g., radiation sickness and death; Djomina and Barilyak 2010) and Hg (e.g.,
79 neurotoxicity and death; Wren *et al.* 1987; Heinz 1996); however, chronic, low-dose exposure
80 has also been associated with sublethal effects in a broad array of taxa (¹³⁷Cs: Shugart *et al.*
81 1989; Stark *et al.* 2004; Hg: Wolfe *et al.* 1998; Evers 2018). Several studies have quantified
82 contaminant levels, including ¹³⁷Cs and Hg, in reptiles (Brisbin *et al.* 1974; Hopkins *et al.* 1999;
83 Burger *et al.* 2006; Lemaire *et al.* 2018; Haskins *et al.* 2021a). However, potential sublethal
84 effects in reptiles – particularly snakes – have received scant attention.

85 The specific objectives of the present study were to determine relationships between
86 ¹³⁷Cs and Hg body burdens and (i) body size; (ii) sex; (iii) capture location; and (iv) sublethal
87 health metrics in an aquatic snake (*Nerodia floridana*; the Florida green watersnake) inhabiting
88 three former nuclear cooling reservoirs with varying contamination histories of Hg and ¹³⁷Cs. We
89 used non-destructive indices to quantify ¹³⁷Cs body burden (whole-body counts) and total Hg
90 (tail clips). Sublethal endpoints we measured included standard metabolic rate (SMR) and
91 prevalence and parasitemia of *Hepatozoon* spp., an intraerythrocytic parasite common in snakes.

92 We predicted that Hg and ¹³⁷Cs body burdens would (1) increase with body size, (2) differ
93 between sexes, (3) vary among capture sites and reflect site contamination histories, and (4) be
94 positively associated with SMR and prevalence and parasitemia of *Hepatozoon* spp. infections.

95

96 **METHODS**

97 *Study system*

98 The Savannah River Site (SRS) is a 780 km² United States Department of Energy reserve
99 located in west-central South Carolina. It was established in 1951 as a nuclear production facility
100 with five nuclear reactors operational for varying durations from the late 1950s to the early
101 1990s, although most legacy ¹³⁷Cs and Hg was introduced prior to 1964. The Par Pond reservoir
102 system was constructed in 1958 to cool thermal effluent from two of the site's five reactors (all
103 no longer operational) and consists of canals and several former cooling reservoirs. Of the
104 reservoirs sampled in the present study, Par Pond is the largest (1068 ha), followed by Pond B
105 (87 ha) and Pond 2 (23 ha; **Figure 1**).

106 Both Par Pond (1958–1964) and Pond B (1961–1964) received thermal effluent directly
107 from R-Reactor. Peak releases of ¹³⁷Cs, resulting from faulty fuel rods in R-Reactor occurred in
108 1963 and 1964, with an estimated 5.7 x 10¹² Becquerels (Bq) introduced into the Par system
109 (Carlton *et al.* 1992). Another reactor, P-Reactor, was constructed in 1961 and discharged
110 effluent into a system of canals and ponds, including Pond 2 and Par Pond, until 1988 (Halverson
111 and Noonkester 1998). While direct releases of ¹³⁷Cs from R-reactor to Pond B and Par Pond
112 were documented, there were no known ¹³⁷Cs releases from P-Reactor directly into Pond 2.
113 However, ¹³⁷Cs is present in Pond 2 as a result of recirculated water from the Par Pond system
114 and earlier releases from R-Reactor (Whicker *et al.* 1990; Halverson and Noonkester 1998).

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115 Based on the histories of each reservoir, including a gamma-detecting flyover in 1991 (Feimster
116 1993), ¹³⁷Cs levels and bioavailability are likely highest in Pond B, followed by Par Pond, and
117 lowest in Pond 2.

118 Although Hg was used or generated as part of site operations of the SRS, most was
119 recycled or disposed of in seepage basins, underground waste tanks, or solid waste disposal
120 facilities (Kvartek *et al.* 1994). The primary source of Hg generated on site was through the
121 combustion of coal used for steam energy, releasing an estimated 600 kg of Hg prior to 1974 and
122 556 kg from 1980-1993 into the atmosphere and into aquatic settling basins. The Savannah River
123 borders the western edge of the SRS and water from the river, contaminated with Hg by
124 upstream off-site sources (including a now inactive chlor-alkali facility in Augusta, GA), was
125 used to cool SRS nuclear reactors during production. This water was then circulated through the
126 cooling reservoir systems, including Par Pond, Pond B, and Pond 2. In 1991, Savannah River
127 water was used to refill Par Pond after a draw down for dam repairs, potentially introducing and
128 redistributing Hg in the reservoir. In contrast, Pond B and Pond 2 have not received water
129 originating from the Savannah River since reactors were closed and have remained relatively
130 undisturbed since 1964 (Sugg *et al.* 1995) and 1988, respectively (Halverson and Noonkester
131 1998). More recently, atmospheric deposition has been identified as the primary source of Hg in
132 the SRS area, accounting for ~99% of the Hg loading (EPA, 2000).

133

134 *Study species*

135 The Florida green watersnake (*Nerodia floridana*) is the largest watersnake in North
136 America, reaching a snout-vent length (SVL) of 760-1800 mm and a mass up to 1880 g (Gibbons
137 and Dorcas 2004). *Nerodia floridana* may be dietary generalists as juveniles, feeding on anurans,

138 salamanders, and small fish, but as adults shift to a diet consisting mostly of fish (when
139 available, Gibbons and Dorcas 2004; Vogrinc *et al.* 2013). Compared to other aquatic snakes, *N.*
140 *floridana* appear to be poor overland dispersers and are thus more commonly associated with
141 permanent freshwater wetlands with emergent vegetation such as reservoirs, where they can be
142 the dominant snake species (Durso *et al.* 2011; Vogrinc 2018). As they appear to exhibit strong
143 fidelity to these permanent wetlands, *N. floridana* are likely reliable indicators of local
144 contaminant levels.

145

146 *Snake collection*

147 We captured snakes from 10-30 June 2016 using a combination of aquatic minnow and
148 funnel traps set in the shallow areas of each reservoir. We checked traps each morning and
149 transported captured snakes to the Savannah River Ecology Laboratory for initial processing,
150 which included determining mass to the nearest 1 g and assigning a unique identification
151 number. We released any recaptured individuals immediately at their trapping location. After
152 sample collection and metabolic measurements and data collection, snakes were permanently
153 marked with a passive integrated transponder (PIT) tag (AVID, Norco, CA, USA) via ventral
154 injection into the coelomic cavity (Gibbons and Andrews 2004) and released at their capture
155 location. We collected and handled snakes under a scientific collecting permit issued by the
156 South Carolina Department of Natural Resources (#SC-02-2016) in accordance with University
157 of Georgia's IACUC Animal Use Protocol (# A-201602-006-A3).

158

159 *Whole-body ¹³⁷Cs determination*

160 Within 48 hours of capture, we obtained whole-body ^{137}Cs counts of snakes with a 10.2
161 cm x 15.2 cm NaI(Tl) gamma detector (Bicron Model 6H3Q/5; Bicron, Torrington, CT, USA)
162 coupled to a computer equipped with gamma spectroscopy software (Canberra Genie, Canberra
163 Industries, Meriden, CT, USA), which used a counting window (region of interest) of 596-728
164 kiloelectron volts (keV) to record total absorptions of ^{137}Cs at 662 keV. We calibrated the
165 machine daily using a traceable ^{137}Cs calibration chip (Gamma Reference Disc Source Set,
166 Catalogue No. NES-101S, ^{137}Cs disc; New England Nuclear, Boston, MA, USA). Before each
167 series of whole-body counts, we ran a background count by placing an empty holding container
168 into the detector for 30 minutes. We acquired whole-body counts of individual snakes by placing
169 the snake in a holding container for a counting period of 15 minutes. We counted aqueous
170 standards containing known ^{137}Cs quantities to produce background-corrected count rates
171 (counts per second) that were used to produce mass-specific yield counts. We then used mass-
172 specific yield counts to create a predictive equation of expected yields for varying sample mass
173 ($\text{yield} = 0.4449 * \text{mass}^{-0.343}$; Kennamer *et al.* 1998). We used background-adjusted whole-body
174 counts of snakes with mass-specific yields to determine whole-body ^{137}Cs (Bq). We then
175 converted whole-body ^{137}Cs to Bq/g by dividing by the mass of the snake. Minimum Detectable
176 Concentrations of ^{137}Cs counts were calculated by the equation described in Currie (1968).

177

178 *Standard metabolic rate measurements*

179 We fasted snakes for 7-10 days to ensure that they were post-absorptive. We measured
180 standard metabolic rate using a flow-through respirometry system (Field Metabolic System,
181 FMS; Sable Instruments, Las Vegas, NV). We conducted respirometry trials from 0700-1500
182 hours, the period in which *N. floridana* were predicted to be least active (Gibbons and Dorcas

183 2004), and at 27°C, a temperature shown to be preferred by closely related *Nerodia* (Lillywhite
184 1987, Mills 2002). We ran a maximum of three snakes per trial, with each snake housed in
185 individual plastic metabolic chambers and placed inside the FMS cooler, which was dark to
186 minimize visual disturbances to snakes during respirometry trials. Each chamber had an ‘in’ and
187 ‘out’ flow airline and individuals experienced constant airflow, with flow rates ranging from 30
188 to 150 mL/min depending on snake mass. With each trial, we ran an empty chamber to serve as a
189 baseline. We allowed snakes to acclimate to their chambers for 75 minutes prior to the 30 min
190 period during which O₂ consumption (VO₂; mL O₂/hr) was recorded. We monitored individual
191 snakes sequentially and collected baseline measurements every hour from the empty chamber to
192 allow for corrections to VO₂ data due to lag and drift. We calculated resting VO₂ values from
193 raw metabolic data with ExpeData-P Data Analysis Software (Sable Systems, Las Vegas, NV,
194 USA).

195

196 *Morphometrics and sample collection*

197 After SMR trials, we determined snake sex by examining tail morphology and/or probing
198 the cloaca (Fitch 1960). We measured snout-vent length (SVL) to the nearest 1 mm by stretching
199 the snake along a meter stick. For the quantification of total Hg (THg), we used snake tail clips
200 as a proxy for whole-body Hg (see Hopkins *et al.* 2001, Drewett *et al.* 2013). We removed
201 approximately 10 mm of tail tip from each snake, unless the snake was missing a substantial
202 amount of its tail (within ~10-15 mm from vent) before capture. We weighed tail clips to the
203 nearest 0.001 g (Sartorius Research Analytical Balance R160D, Goettingen, Germany) and
204 stored them at -70°C until subsequent analysis. During the process of collecting tail clips, we
205 collected blood from the caudal vein to create blood smears, which were fixed with 100%

206 methanol and stained with modified Wright-Giemsa (Diff-Quik, PolySciences Inc., Warrington,
207 PA, USA) to facilitate *Hepatozoon* quantification.

208

209 *Mercury quantification*

210 We dried tail clips in an oven for a minimum of 24 hours at 50°C and recorded the mass
211 of each tail clip to the nearest 0.001 g (Mettler-Toledo AX504 Delta Range, Columbus, OH,
212 USA). We quantified total mercury on a DMA-80 Tri-cell Direct Mercury Analyzer (Milestone,
213 Shelton, CT, USA) using the Environmental Protection Agency method 7473 (US EPA 1998).
214 The DMA-80 uses decomposition, catalytic conversion, amalgamation, and atomic absorption
215 spectrophotometry to quantify THg. For quality assurance, we ran two blanks and two standard
216 reference materials (TORT-3 and PACS-2; National Research Council of Canada, Ottawa, ON),
217 before sampling began and after every 10 samples. The detection limit for THg in tail tissue was
218 defined as three times the standard deviation of the procedural blanks (0.0000475 mg/kg dry
219 mass). Average percent recoveries for TORT-3 and PACS-2 reference materials were 106.0%
220 (range: 102.9-109.8%, n=9) and 96.7% (range: 89.0-110.3%, n=9), respectively. We report all
221 THg values in mg/kg dry weight (see Supplemental Table 1 for wet weight values).

222

223 *Hepatozoon counts*

224 We scanned blood smears in a zig-zag manner using a standard light microscope (Zeiss
225 Axioscope 50, Jena, Germany) at 1000x magnification using oil immersion. For each slide, we
226 counted a total of 8000 erythrocytes and recorded the number of cells infected with *Hepatozoon*
227 spp.. Although several species of *Hepatozoon* may infect a single species of *Nerodia*, we did not
228 identify hepatozoa beyond the genus or by developmental stage. We calculated prevalence (the

229 proportion of individuals infected with *Hepatozoon*) and parasitemia (the proportion of infected
230 erythrocytes; Davis and Sterrett 2011, Haskins et al. 2017) for snakes sampled.

231

232 *Statistical analyses*

233 We used program R (R Core Team 2020) for statistical analyses. We tested data for
234 normality (Shapiro-Wilks) and for homogeneity of variances (Bartlett's test). We used log-
235 transformations for data not meeting the assumptions of normality prior to analysis. We used
236 preliminary Pearson's correlations to detect multicollinearity among variables. If any two
237 variables had correlations where $r \geq 0.80$, we excluded one of the variables from models. We
238 used analysis of covariance (ANCOVA) followed by Tukey's HSD post-hoc test to compare
239 differences in tail THg and whole-body ^{137}Cs among sites, while controlling for the effect of
240 snake body size (SVL).

241 We used a logistic regression to assess the importance of site- and individual-level factors
242 associated with presence of *Hepatozoon* infections in *N. floridana*. We used multiple linear
243 regression models to assess the importance of factors associated with response variables of tail
244 THg and whole-body ^{137}Cs burdens. Predictor variables we included were mass, site, sex, and
245 suspected interactions. We used multiple linear regression models to investigate associations
246 between SMR (VO_2) and potential explanatory variables, including mass, whole-body ^{137}Cs , tail
247 THg, site, sex, and suspected interactions. We used corrected Akaike's information criterion
248 (AICc) values to select the most supported among candidate models based on an information-
249 theoretic approach (Burnham and Anderson 1998, Burnham and Anderson 2004). We considered
250 variables in the candidate model with the lowest AICc and any candidate models $< 2 \Delta\text{AICc}$ to
251 have the most support for a relationship with the response variable.

252

253 **RESULTS**

254 We captured a total of 78 *N. floridana* (11 from Par Pond, 23 from Pond B, 44 from Pond
255 2; see Supplemental Table 2), of which 56% were male (n=44) and 44% (n= 34) were female.
256 However, sex ratios differed by site with more females captured at Par Pond (8F:3M) and more
257 males captured at Pond 2 (14F:30M). Sex ratios were nearly 1:1 at Pond B (12F:11M). Females
258 ranged from 18.0 – 545.0 g (Mean \pm 1 SE = 179.0 \pm 26.9 g) in mass and 290 – 820 mm (540 \pm
259 31 mm) in SVL; males ranged from 22.0 – 154.0 g (65.9 \pm 6.3 g) and 300 – 615 mm SVL (417 \pm
260 13 mm). Analysis of variance on log-transformed SVL indicated *N. floridana* captured from Par
261 Pond were significantly larger compared to snakes from Pond B, which were significantly larger
262 than snakes from Pond 2 ($F_{2,73} = 16.73, p < 0.001$).

263

264 *Radiocesium burdens*

265 Average whole-body ^{137}Cs in snakes was 0.23 \pm 0.08 Bq/g (range: 0.00-1.02 Bq/g) and
266 was higher in females (0.30 \pm 0.06 Bq/g) than in males (0.17 \pm 0.05 Bq/g), but differences were
267 not statistically significant after controlling for the effect of SVL (ANCOVA: $F_{1,74}=0.61,$
268 $p=0.43$). Snakes from Pond B had the highest average whole-body ^{137}Cs burdens, which were
269 significantly higher than those from Par Pond (Tukey's HSD: $t= 8.21, p<0.001$) and Pond 2
270 (Tukey's HSD: $t= 14.03, p<0.001$) after controlling for SVL (ANCOVA: $F_{2,74}=106.94, p<0.01$).
271 Whole-body ^{137}Cs was significantly and positively correlated with snake SVL at both Par Pond
272 (Pearson's $r=0.75, p<0.01$) and Pond B (Pearson's $r=0.53, p<0.01$), but not at Pond 2 (Figure 2)
273 where levels were lowest. The most parsimonious model for whole-body ^{137}Cs burdens in *N.*
274 *floridana* included site and mass (Table 1) – both of which were significant predictors of whole-

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275 body ^{137}Cs . The next most parsimonious model ($<2 \Delta\text{AICc}$) included site, mass, and an
276 interaction between site and mass, but site was the only significant predictor in this model.

277

278 *Mercury burdens*

279 Average tail THg for all 78 *N. floridana* was 0.33 ± 0.03 mg/kg dry weight (range: 0.16-
280 2.10 mg/kg). After controlling for the effect of body size, average tail THg in females ($0.42 \pm$
281 0.07 mg/kg) and males (0.26 ± 0.01) was not significantly different (ANCOVA: $F_{1,74}=1.16$,
282 $p=0.28$). Tail THg was highest in snakes from Par Pond but was not significantly different
283 among sites after controlling for the effect of SVL (ANCOVA: $F_{2,74}=1.84$, $p=0.16$). There was a
284 significant, positive relationship between tail THg and SVL (Figure 3, Pearson's $r=0.52$,
285 $p<0.01$). The most parsimonious model predicting tail THg included only mass as a significant
286 predictor (Table 2). Although, the next most parsimonious model ($<2 \Delta\text{AICc}$) included sex, it
287 was not a significant predictor in the model.

288

289 *Hepatozoon prevalence and parasitemia*

290 We were not able to collect blood smears from all snakes from Par Pond and excluded
291 them from analyses for *Hepatozoon* prevalence and parasitemia. Overall mean prevalence of
292 *Hepatozoon* spp. in snakes sampled from Pond 2 and Pond B was 58.7% (37/63) but prevalence
293 was higher in Pond 2 (73.8%) than in Pond B (28.6%) snakes. Likewise, mean parasitemia was
294 higher in snakes from Pond 2 (0.13 ± 0.04) than Pond B snakes (0.03 ± 0.02) but the difference
295 was not significant after controlling for snake body size (SVL; ANCOVA: $F_{1,60}=1.36$, $p=0.24$).
296 The most parsimonious model predicting *Hepatozoon* spp. infection in *N. floridana* from Pond 2
297 and Pond B included only ^{137}Cs (Table 3). However, ^{137}Cs and the interaction of ^{137}Cs and mass

298 were significant predictors in the next most supported model ($<2 \Delta\text{AICc}$). Based on the best
299 supported model, the probability of *Hepatozoon* spp. infection decreased as ^{137}Cs whole body
300 burdens increased (Figure 4).

301

302 *Standard metabolic rates*

303 Overall, VO_2 for all 78 *N. floridana* ranged from 0.04-56.75 mL O_2/hr (mean: $12.57 \pm$
304 1.16 mL O_2/hr). There was a significant, positive relationship between VO_2 and mass (Figure 5,
305 Pearson's $r=0.80$, $p < 0.01$). Snakes from Par Pond exhibited the highest average VO_2 compared
306 to those from Pond B or Pond 2. However, an ANCOVA of log-transformed VO_2 indicated no
307 significant difference among sites (ANCOVA: $F_{2,74} = 2.18$, $p=0.12$), but mass was a significant
308 covariate ($F_{2,74} = 37.67$, $p < 0.01$), with VO_2 increasing with increasing mass. Preliminary
309 investigations into the relationship between *Hepatozoon* spp. infection and SMR were evaluated
310 but were excluded from final models (lack of samples from Par Pond). Of the models we
311 investigated, the most parsimonious model predicting VO_2 in *N. floridana* included mass, sex,
312 and the interaction of mass and sex as predictors; mass and the interaction of mass and sex were
313 both significant (Table 4). However, the next best model included mass as the only factor and
314 was within $<2 \Delta\text{AICc}$. A third model within $<2 \Delta\text{AICc}$ included mass and site.

315

316 **DISCUSSION**

317 The present study evaluated ^{137}Cs and Hg bioaccumulation in a watersnake species (*N.*
318 *floridana*) inhabiting three former nuclear cooling reservoirs in South Carolina. To our
319 knowledge, this is the first study to evaluate burdens of ^{137}Cs and Hg in association with
320 sublethal health metrics—in this case, standard metabolic rate and hemoparasite infections. As

321 expected, body burdens of both Hg and ^{137}Cs increased with SVL; however, after accounting for
322 size effects, contaminant levels did not differ between sexes. Average whole-body ^{137}Cs in
323 snakes varied among reservoirs and followed the trend expected based on their relative
324 contamination histories, but tail THg was similar at all three study sites. We found no clear
325 relationship between body burdens of contaminants and SMR. However, *Hepatozoon* spp.
326 prevalence and parasitemia appeared to be negatively associated with whole-body ^{137}Cs .

327

328 *Patterns of ^{137}Cs bioaccumulation*

329 The observed among-reservoir variation in ^{137}Cs body burdens in *N. floridana* from Pond
330 B, Par Pond and Pond 2 was consistent with the known contamination histories of the three
331 former nuclear cooling reservoirs, demonstrating that *N. floridana* can serve as a useful
332 bioindicator of local contaminant levels. This finding is consistent with previous works where
333 watersnakes have been used to document spatial trends of contamination (Burger *et al.* 2006;
334 Drewett *et al.* 2013; Haskins *et al.* 2021b). Our results were also similar to prior studies which
335 found higher concentrations of ^{137}Cs in Pond B biota compared to Par Pond and elsewhere on the
336 SRS (Kennamer *et al.* 1993; Paller *et al.* 1999; Oldenkamp *et al.* 2017). Prior studies of biota
337 inhabiting SRS reservoirs have also shown longer ecological half-lives of ^{137}Cs in sunfish (Paller
338 *et al.* 1999), largemouth bass (Paller *et al.* 1999), and American coots (Kennamer *et al.* 2017)
339 inhabiting Pond B compared to Par Pond. More recently, Fulghum *et al.* (2019) found higher
340 concentrations of ^{137}Cs in fish from Pond B compared to other components of the Par Pond
341 system. Similarly, the higher body burdens of ^{137}Cs documented in *N. floridana* from Pond B
342 compared to other SRS reservoirs in our study seem to reflect an increased bioavailability and
343 persistence of the contaminant in the reservoir. Our work has shown that *N. floridana* still

344 accumulate ^{137}Cs more than 50 years after contaminated effluent was released into the reservoir
345 system; however, snakes living in SRS reservoirs are exposed to much lower levels of the
346 radionuclide compared to those in environments with a more recent history of contamination.
347 Arboreal snakes living within an area of contamination resulting from the 2011 Fukushima
348 Daiichi Power Plant disaster were documented to have average ^{137}Cs whole-body concentrations
349 of 6600 ± 5900 Bq/kg (Gerke *et al.* 2020), approximately 10 times the average body burdens
350 documented in snakes from Pond B in our study. As expected, body burdens of ^{137}Cs in snakes
351 sampled in our 2016 study from Par Pond have declined when compared to snakes captured at
352 the same site during a 1974 study (Brisbin *et al.* 1974), with average body burdens decreasing
353 from 1.02 Bq/g to 0.10 Bq/g, confirming the species' utility as a bioindicator of temporal
354 contaminant trends.

355 Not surprisingly, capture site and body size were important predictors of whole-body
356 ^{137}Cs in *N. floridana*. Body burdens increased with SVL for snakes captured from Pond B and
357 Par Pond but not Pond 2, likely reflecting the lower bioavailability of ^{137}Cs in Pond 2. Increasing
358 ^{137}Cs with increasing body size has also been observed in fish (Rowan *et al.* 1998), and slider
359 turtles in Pond B (Peters and Brisbin 1996). Interestingly, a previous study detected no
360 relationship between body size and ^{137}Cs in cottonmouths (*Agkistrodon piscivorus*) captured
361 from R Canal, which is in the immediate vicinity of Pond B (Leaphart *et al.* 2020). The
362 conflicting results between studies may be related to differences in feeding ecology between the
363 two species and their relative propensity to access or forage in the surrounding terrestrial
364 habitats. While *N. floridana* are primarily piscivorous (i.e., consume mostly fish), *A. piscivorus*
365 are more generalist in nature (Ditmars 1912) and may forage more terrestrially where potential
366 prey items (e.g., snakes, amphibians, birds) may have lower exposure to ^{137}Cs . Furthermore,

367 investigation into the overland dispersal of aquatic snake species at the SRS has shown that *N.*
368 *floridana* are less likely than *A. piscivorus* to migrate from wetlands even under extreme
369 conditions such as drought (Willson *et al.* 2006). This suggests that *N. floridana* are likely to
370 reside within the ^{137}Cs -contaminated reservoirs throughout their lives while other co-occurring
371 species may be less restricted to the aquatic habitat where ^{137}Cs levels are highest.

372

373 *Patterns of Hg bioaccumulation*

374 In contrast to our finding that whole-body ^{137}Cs in *N. floridana* varied among reservoirs,
375 snake tail THg patterns were similar across sites. Although differences were not statistically
376 significant, the highest tail THg was observed in *N. floridana* from Par Pond, which may be
377 related to a more recent influx of water from the Savannah River (Kennamer *et al.* 1998).
378 However, since we only captured 11 snakes from Par Pond, our ability to detect THg differences
379 in *N. floridana* among reservoirs may have been hindered. In addition, snakes captured at Par
380 Pond were significantly larger and had a female-biased sex ratio when compared to snakes
381 captured from the other two reservoirs, further impeding efforts to disentangle site and size
382 effects. Thus, further sampling is warranted to elucidate any potential differences in THg in *N.*
383 *floridana* among SRS reservoirs.

384 As expected, concentrations of THg in tail tips increased with increasing SVL in *N.*
385 *floridana* from the three SRS reservoirs sampled. Similar trends of a strong positive relationship
386 between body size and THg have been observed for northern watersnakes (*N. sipedon*) in
387 Virginia (Drewett *et al.* 2013), cottonmouths (*A. piscivorus*) in Texas (Rainwater *et al.* 2005),
388 Burmese pythons (*Python bivittatus*) in Florida (Rumbold and Bartoszek 2019), viperine snakes
389 (*Natrix maura*) in Europe (Lemaire *et al.* 2018), and brown watersnakes (*N. taxipilota*) in the

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390 Savannah River adjacent to the SRS (Haskins *et al.* 2021a, b). A pattern of increasing THg
391 burdens with increasing body size does provide support for bioaccumulation (Wolfe *et al.* 1998).
392 However, the positive relationship could also be influenced by ontogenetic shifts in diet and
393 metabolic differences between juvenile and adult snakes (Peters and Brisbin 1996; Drewett *et al.*
394 2013). Generally, body size is correlated with age in snakes (Halliday and Verrell 1988); thus,
395 age may also be a factor determining THg as older individuals have had more time to accumulate
396 Hg (Hopkins *et al.* 2013). Overall, tail THg burdens in *N. floridana* from former nuclear cooling
397 reservoirs of the SRS are relatively low compared to concentrations reported from other Hg
398 contaminated locations around the globe (see Drewett *et al.* 2013; Haskins *et al.* 2019), and
399 similar to those documented in brown watersnakes (*N. taxispilota*) inhabiting the Savannah River
400 just outside the SRS (Haskins *et al.* 2021b). However, due to the scarcity of information on
401 sublethal effects of Hg in reptiles, specifically snakes, more research is warranted to determine
402 thresholds at which chronic, low-dose THg could pose problems for snakes at the individual and
403 population level.

404

405 *Patterns of hemoparasite infections*

406 We expected to find an increase in hemoparasite prevalence and parasitemia in
407 association with increasing body burdens of contaminants but this was not supported by our
408 results. Although greater endoparasite abundance has been documented with higher levels of Hg
409 or other contaminants in other taxa captured on the SRS (Borchert *et al.* 2019), we found no
410 evidence of an association between *Hepatozoon* spp. infections and tail THg in *N. floridana*. In
411 contrast to our hypotheses, we found that *Hepatozoon* spp. infections may actually decrease with
412 increasing ¹³⁷Cs body burdens in *N. floridana*. Infections were much more common for snakes

413 captured from Pond 2 compared to Pond B and the probability of *Hepatozoon* spp. infection
414 decreased with increasing ^{137}Cs body burdens. Our results suggest that ^{137}Cs could be related to
415 *Hepatozoon* spp. infections in *N. floridana* either by directly harming the parasite, or indirectly
416 by affecting the parasite's vectors or initial vertebrate hosts (e.g., anurans). Field studies
417 investigating the relationship between radionuclides and parasite infections in wildlife are
418 limited. Krivolutsky and Pokarzhevsky (1992) documented an increase in caterpillar survival
419 with increasing radioactive contamination and a decrease in parasitic infections. Similarly, in two
420 separate studies, prevalence of protozoan parasites was lower in rodents collected from
421 radionuclide-contaminated habitats compared to reference sites (Childs and Cosgrove 1966;
422 Wilber *et al.* 1994). Thus, low-level radionuclides could provide an indirect, positive effect on
423 the health of wildlife. Because many protozoan parasites have complex life cycles with multiple
424 vectors and several potential intermediate hosts (Smith 1996; Telford *et al.* 2001), a more holistic
425 approach would be needed to determine if decreases in *Hepatozoon* spp. infections in *N.*
426 *floridana* are the result of negative impacts on the parasites, vectors, or initial hosts.

427 Mass and site were included along with ^{137}Cs in models within 2 ΔAICc of the top model
428 predicting *Hepatozoon* spp. infection probability. It is possible that shifts in diet of *N. floridana*
429 and differences in prey base among the three reservoirs impacted *Hepatozoon* spp. infection
430 probability. Ontogenetic diet shifts are not well understood in *N. floridana*, but anuran tadpoles
431 are a readily available food source that can be consumed by smaller juvenile *N. floridana*.
432 Anurans are more likely to harbor *Hepatozoon* spp. compared to fish (Smith 1996), which are
433 more commonly consumed by adult *N. floridana* (Durso *et al.* 2013). Furthermore, Pond 2 is a
434 smaller body of water with fewer species of fish (Bennett and McFarlane 1983), and resident *N.*
435 *floridana* may rely on amphibians to a greater extent compared to snakes residing in the larger

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436 Pond B. Previous research into factors that influence parasitism in snakes has found that diet can
437 play a major role in prevalence (Lettoof *et al.* 2020). Thus, irrespective of the higher ¹³⁷Cs levels
438 at Pond B reservoir, *N. floridana* living there may be less likely to become infected with
439 *Hepatozoon* spp. through their diet compared to snakes living in Pond 2.

440

441 *Standard metabolic rate*

442 Metabolic rate in *N. floridana* increased with mass, a common phenomenon in snakes
443 (Hopkins *et al.* 1999; McCue and Lillywhite 2002; Dorcas *et al.* 2004) and other taxa (Sims
444 1996; Homyack *et al.* 2010). Although we expected to see a relationship between contaminant
445 burdens and SMR, we observed no strong positive or negative relationship between SMR and
446 THg or ¹³⁷Cs. Metabolic rate perturbations in biota exposed to contaminants has been observed
447 in a wide range of taxa (Hopkins *et al.* 1999; Rowe *et al.* 2001; Du *et al.* 2018). For example,
448 Hopkins *et al.* (1999) found that *N. fasciata* from habitats with coal combustion waste exhibited
449 higher SMR compared to snakes from reference sites. In contrast, a depressed SMR was
450 observed in turtles living in similar coal combustion impacted habitats (Nagle *et al.* 2001;
451 Cochran *et al.* 2018). However, as previously noted, the body burdens of contaminants in *N.*
452 *floridana* in the present study are relatively low compared to those documented elsewhere (Chin
453 *et al.* 2013a & b; Gerke *et al.* 2020). Thus, snakes at our study sites may not be exposed to
454 thresholds of contaminants that would induce perturbations to metabolic rate.

455 Our most supported model included sex in addition to mass, with a significant interaction
456 between mass and sex. This is not surprising as *N. floridana* exhibit sexual dimorphism often
457 observed in the genus of *Nerodia*, with females growing significantly larger than males. It is also
458 worth noting that we did not exclude gravid female *N. floridana* from our models evaluating

459 SMR. Of our respirometry trials, the 13 highest measurements came from females, of which
460 eight were believed to be gravid based on abdomen palpation. Prior investigations into the
461 physiological costs of reproductive effort in snakes have reported elevated metabolic rates
462 (Birchard *et al.* 1984; Schultz *et al.* 2008; Dupoué and Lourdais 2014) in gravid females
463 compared to non-gravid and male snakes. Gravid female snakes are generally larger in mass and
464 deal with additional metabolic demands such as providing nutrients and dealing with nitrogenous
465 wastes from developing embryos (Birchard *et al.* 1984). The stage of reproductive effort and
466 subsequent effects on metabolic rate were beyond the scope of this project; however, it is
467 possible that our results are reflective of the influence of gravidity on SMR.

468

469 CONCLUSIONS

470 Our results indicate that *N. floridana* residing in former nuclear cooling reservoirs of the
471 SRS bioaccumulate Hg and ¹³⁷Cs despite most documented contamination occurring more than
472 50 years ago. Whole-body ¹³⁷Cs and tail THg in *N. floridana* in the present study increased with
473 body size. Body burdens of ¹³⁷Cs in *N. floridana* followed the expected spatial gradient based on
474 contamination histories of the three reservoirs sampled; however, we were unable to detect any
475 significant differences in THg among reservoirs. We found no support for strong, positive
476 associations between sublethal effects measured and body burdens of ¹³⁷Cs or THg. In fact, we
477 found that snakes with higher whole-body burdens of ¹³⁷Cs were less likely to be infected with
478 *Hepatozoon* sp. While intriguing, this finding requires further investigation to determine the
479 importance of other factors involved with hemoparasite infection in semi-aquatic snakes.

480 Similar to prior research (Brisbin *et al.* 1974; Burger *et al.* 2006; Haskins *et al.* 2021a, b),
481 our results lend further credence to the use of aquatic snakes, such as *N. floridana*, as effective

482 bioindicators for monitoring spatial and temporal trends of contamination in aquatic habitats.
483 *Nerodia floridana* readily accumulate Hg and ¹³⁷Cs that can be measured through non-lethal
484 techniques. Our trapping efforts indicate that *N. floridana* is the dominant snake species found in
485 former nuclear cooling reservoirs on the SRS and can be captured with relative ease. Thus, *N.*
486 *floridana* and other watersnakes should be considered as viable ecological receptors for future
487 monitoring efforts at the SRS and other locations where legacy contamination exists.

488

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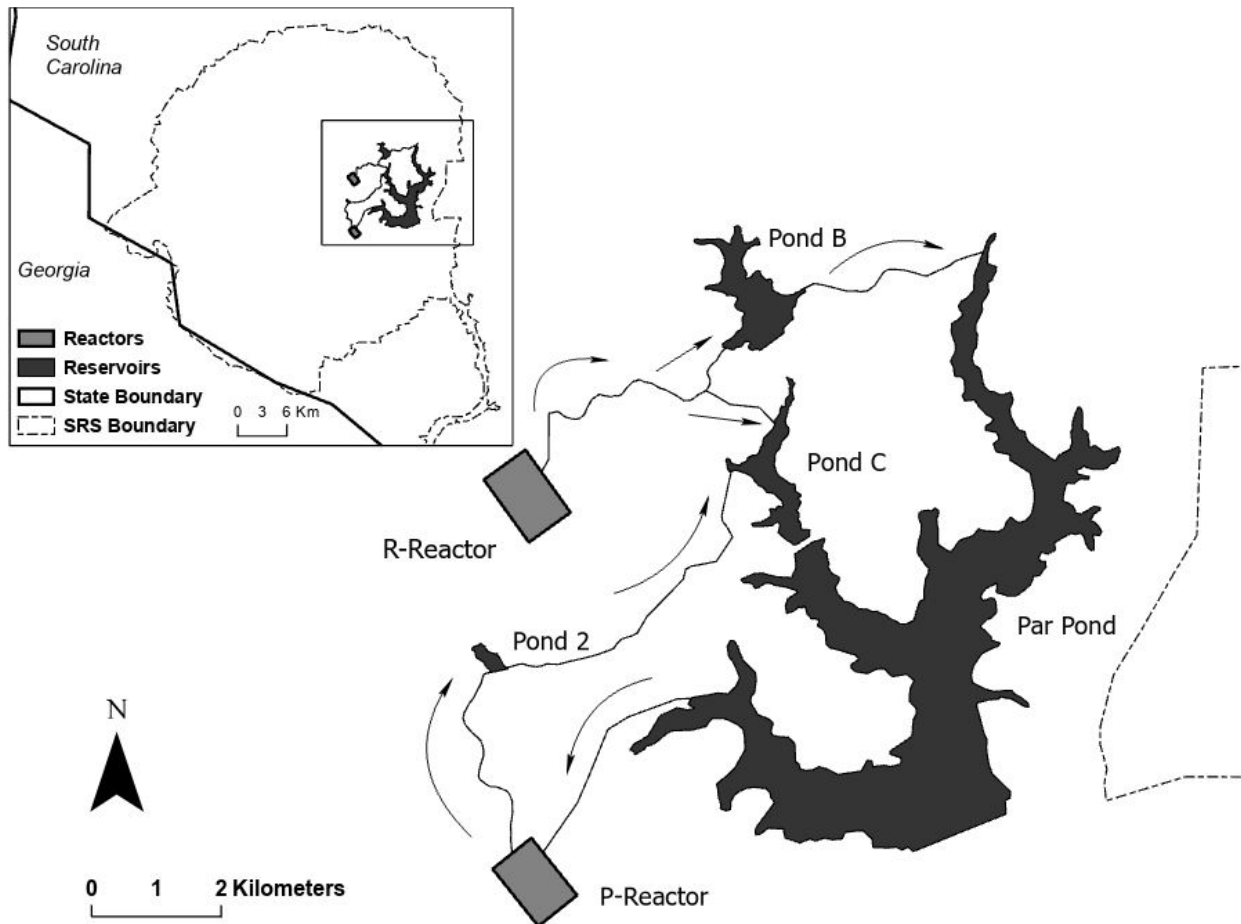


Figure 1.

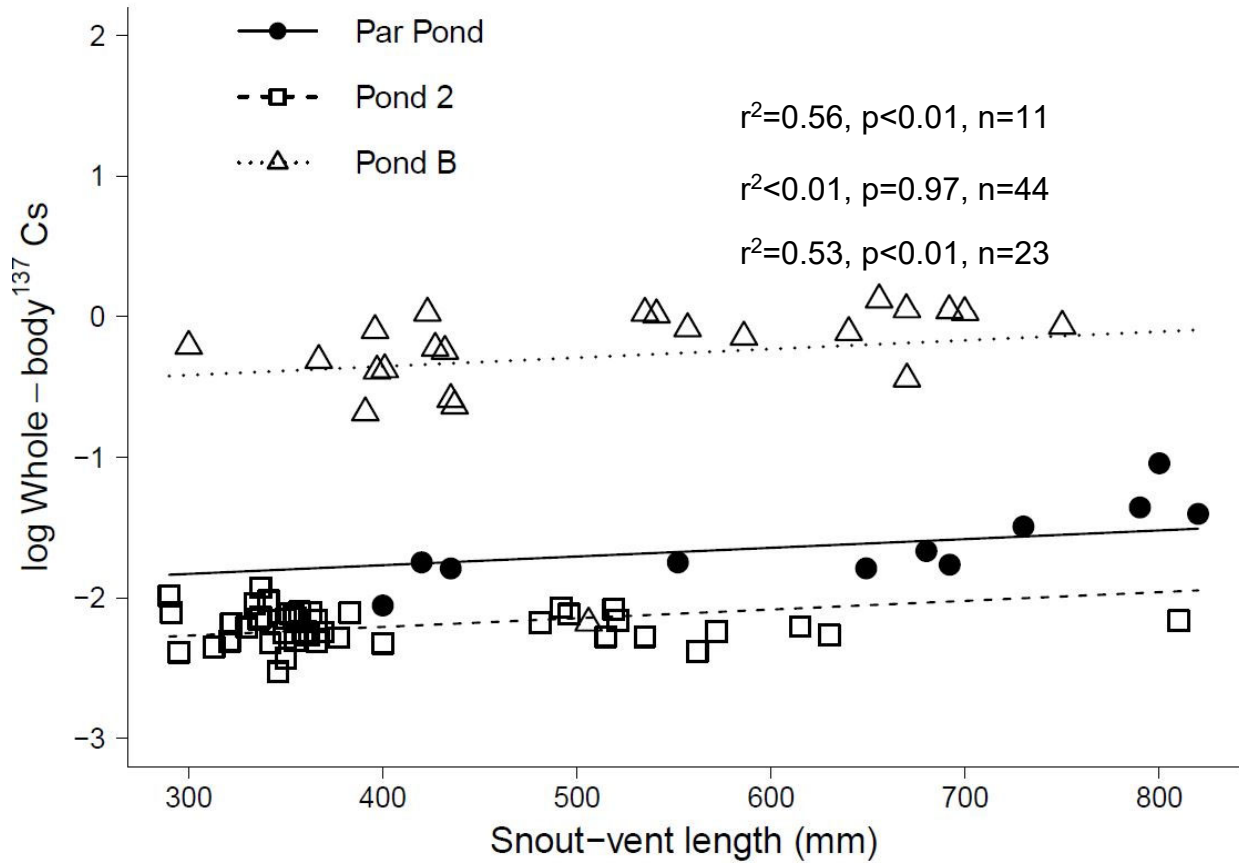


Figure 2.

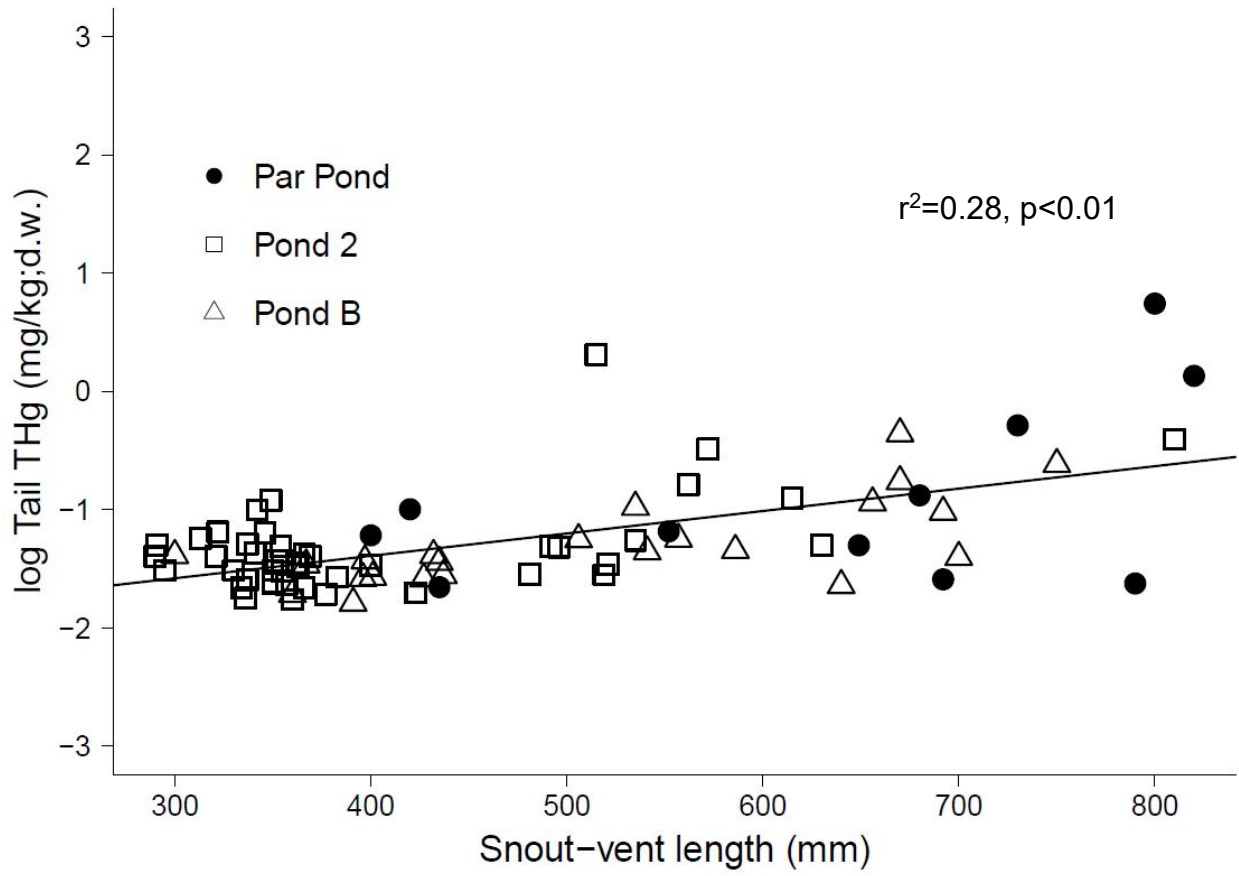


Figure 3.

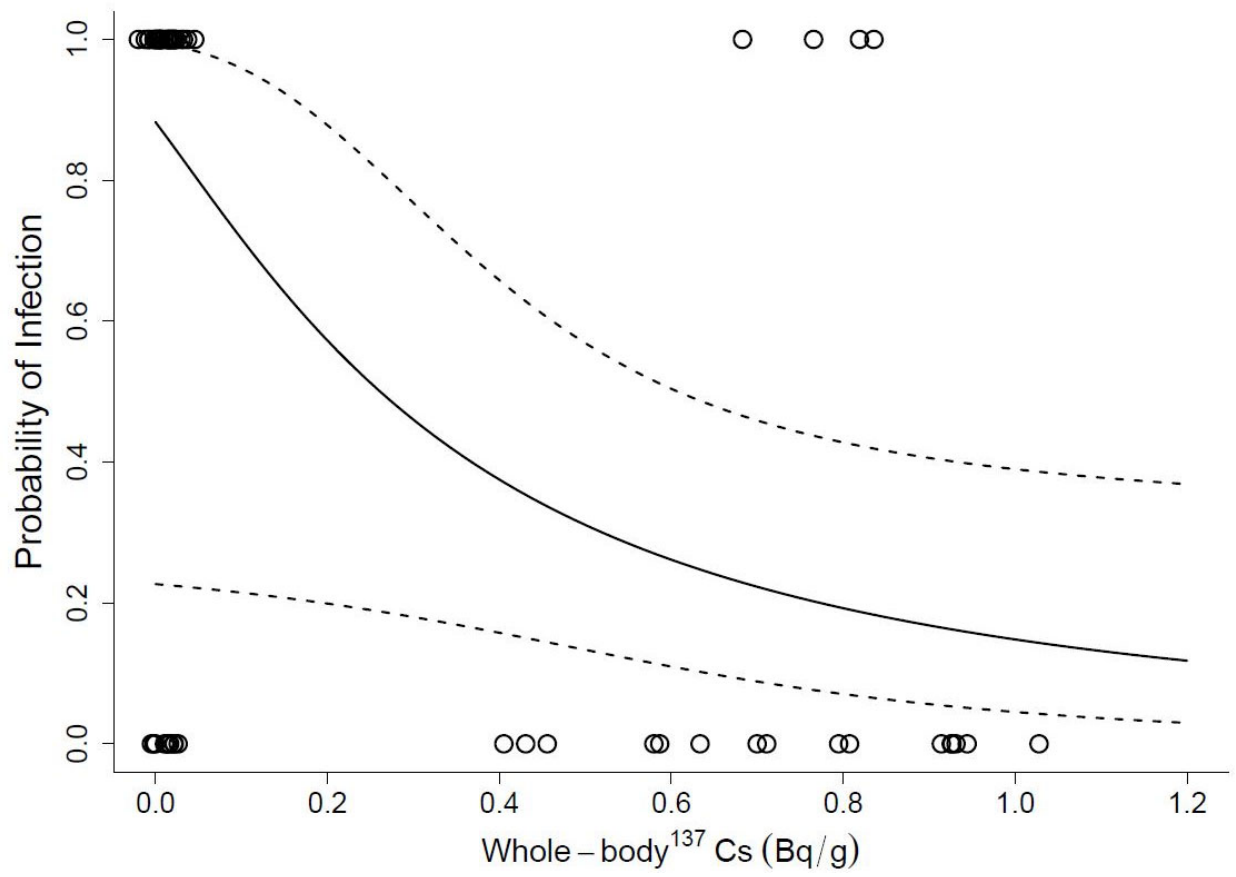


Figure 4.

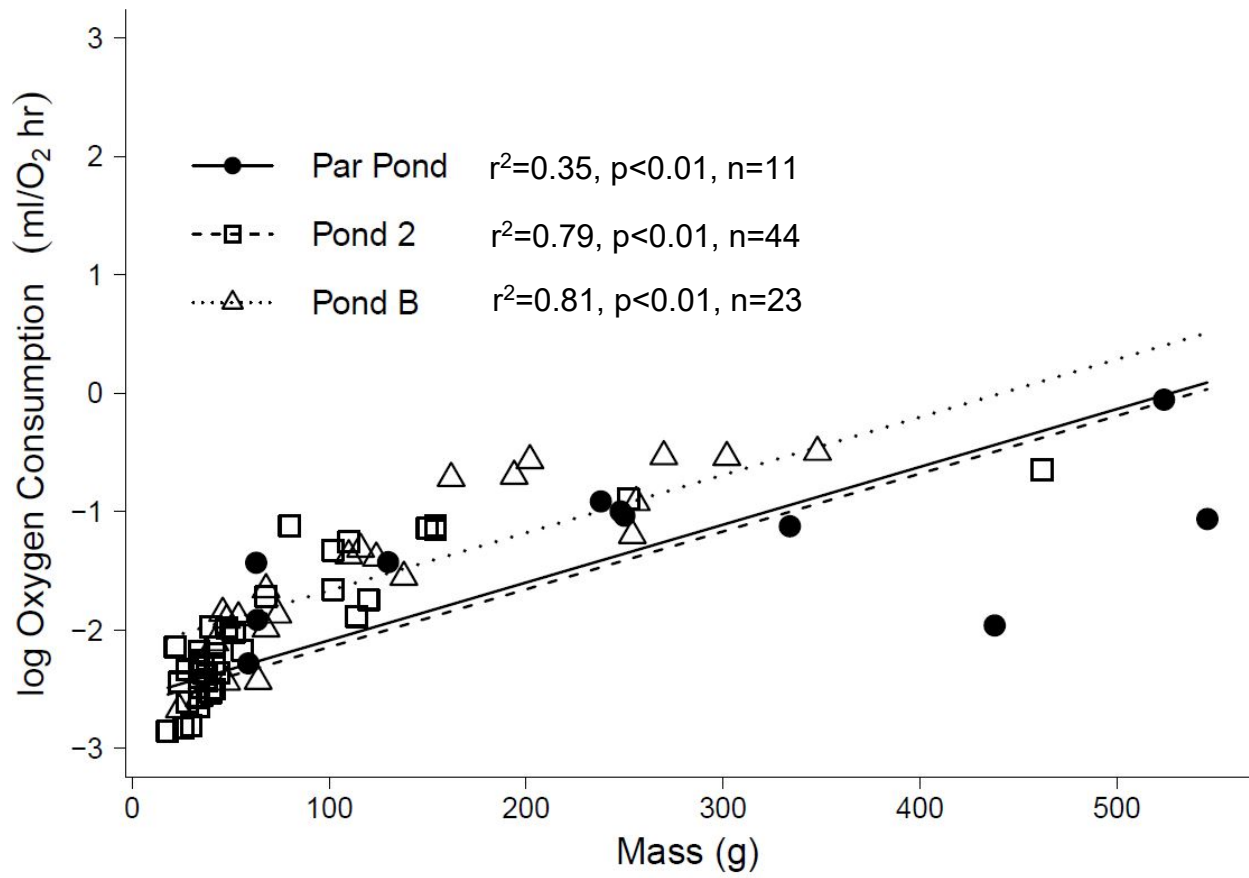


Figure 5.

Table 1. Eight candidate models to explain variation in log-transformed whole-body (^{137}Cs) in Florida green watersnakes (*Nerodia floridana*) captured from three former nuclear cooling reservoirs on the Savannah River Site, South Carolina

Model	Log-likelihood	K	AICc	ΔAICc	AICc_{wt}
Site* + Mass*	-42.99	5	96.82	0	0.36
Site* + Mass + (Site x Mass)	-40.72	7	97.04	0.22	0.32
Sex + Site + Mass + (Site x Mass)	-40.41	8	98.91	2.09	0.13
Site	-45.66	4	99.86	3.04	0.08
Site + Mass + Sex + (Mass x Sex)	-42.34	7	100.28	3.46	0.06
Site + Mass + Sex + (Mass x Sex) + (Site x Mass)	-40.24	9	101.12	4.30	0.04
Mass	-98.36	3	203.05	106.23	0.00
Sex	-99.87	3	206.06	109.23	0.00

^a Significance evaluated for all models $\ll 2\Delta\text{AICc}$

* $p < 0.05$

Table 2. Nine candidate models to explain variation in log-transformed tail THg in Florida green watersnakes (*Nerodia floridana*) captured from three former nuclear cooling reservoirs on the Savannah River Site, South Carolina

Model ^a	Log-likelihood	K	AICc	ΔAICc	AICc _{w_t}
Mass*	-34.23	3	74.79	0	0.44
Mass* + Sex	-33.34	4	75.23	0.44	0.35
Mass + Site	-33.42	5	77.67	2.88	0.10
Site + Mass + Sex + (Mass x Sex)	-31.42	7	78.44	3.65	0.07
Site + Mass + (Site x Mass)	-33.20	7	82.01	7.22	0.01
Sex + Site + Mass + (Site x Mass)	-32.48	8	83.04	8.25	0.01
Site + Mass + Sex + (Mass x Sex) + (Site x Mass)	-31.22	9	83.08	8.29	0.00
Site	-47.67	4	103.89	29.10	0.00
Sex	-50.46	3	107.24	32.45	0.00

^a Significance evaluated for all models $\ll 2\Delta AICc$

* $p < 0.05$

Table 3. Fourteen candidate logistic regression models to predict the probability of *Hepatozoon* spp. infection in Florida green watersnakes (*Nerodia floridana*) captured from three former nuclear cooling reservoirs on the Savannah River Site, South Carolina

Model ^a	Log-likelihood	K	AIC	ΔAIC	AIC _{Wt}
$\log(^{137}\text{Cs})^*$	-33.82	2	71.85	0.00	0.37
Mass + $\log(^{137}\text{Cs})^*$ + (Mass x $\log(^{137}\text{Cs})$)	-31.96	4	72.61	0.76	0.25
$\log(^{137}\text{Cs})^*$ + Site	-33.70	3	73.82	1.97	0.14
Mass + $\log(^{137}\text{Cs})$ + Site + Mass x $\log(^{137}\text{Cs})$	-31.74	5	74.54	2.69	0.10
Mass x $\log(^{137}\text{Cs})$ + logTHg	-31.88	5	74.81	2.96	0.08
Mass x $\log(^{137}\text{Cs})$ + logTHg + Site	-31.62	6	76.74	4.90	0.03
Site	-36.72	2	77.63	5.78	0.02
Mass + Site	-36.53	3	79.47	7.63	0.01
Mass + $\log(\text{THg})$ + Site	-36.37	4	81.42	9.57	0.00
Mass + Site + Sex	-36.43	4	81.54	9.70	0.00
Mass	-41.35	2	86.89	15.05	0.00
Mass + $\log(\text{THg})$	-40.39	3	87.20	15.35	0.00
Sex	-41.82	2	87.84	15.99	0.00
$\log(\text{THg})$	-42.70	2	89.61	17.76	0.00

^a Significance evaluated for all models $\ll 2\Delta\text{AICc}$

* $p < 0.05$

THg = Total mercury; ¹³⁷Cs = Radiocesium

Table 4. Fourteen candidate models to explain variation in log-transformed VO₂ (ml O₂/hr) in Florida green watersnakes (*Nerodia floridana*) captured from three former nuclear cooling reservoirs on the Savannah River Site, South Carolina

Model ^a	Log-likelihood	K	AIC	ΔAIC	AIC _{wt}
Mass* + Sex + (Mass x Sex)*	-98.24	5	208.71	0.00	0.36
Mass*	-101.78	3	209.89	1.18	0.20
Mass* + Site	-99.54	5	209.92	1.21	0.19
logTHg + Mass + Site + (logTHg x Mass)	-98.05	7	211.69	2.98	0.08
Mass + log ¹³⁷ Cs	-100.49	5	211.82	3.11	0.08
Mass + logTHg + (Mass x logTHg)	-101.67	4	211.88	3.17	0.07
Mass + logTHg + log ¹³⁷ Cs + Site + Sex + (Mass x logTHg)	-97.94	8	213.96	5.25	0.03
logTHg + log ¹³⁷ Cs	-109.61	4	227.78	19.07	0.00
logTHg + log ¹³⁷ Cs + Site	-107.65	6	228.48	19.77	0.00
Site	-110.38	4	229.30	20.59	0.00
logTHg + log ¹³⁷ Cs + Site + Sex	-107.59	7	230.78	22.07	0.00
logTHg	-113.26	3	232.84	24.13	0.00
log ¹³⁷ Cs	-113.30	3	232.93	24.22	0.00
Sex	-115.66	3	237.64	28.93	0.00

^a Significance evaluated for all models <<2ΔAICc

* $p < 0.05$

VO₂ = Oxygen Consumption; THg = Total mercury; ¹³⁷Cs = Radiocesium