Invasive wild pig carcass availability does not affect coyote abundance in South Carolina, USA

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2   Running header: Coyote abundance and wild pig carcasses

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24

Short summary

In the United States, control programs often leave wild pig carcasses on the landscape where

they are freely available for consumption by scavengers such as coyotes. This study tested if

coyote abundance is affected by wild pig carcasses created by control programs, and found

coyote abundance did not change in response to wild pig carcass availability. We conclude that

wild pig carcass removal will not be an effective coyote management strategy. Photograph by M.

Vukovich.

Abstract

Context: Control of invasive wild pigs (*Sus scrofa*) is a growing management concern throughout

their invaded range. In the United States, control programs often leave wild pig carcasses on the

landscape where they are freely available for consumption by scavengers such as coyotes (*Canis*

latrans). Coyotes consume wild pigs, but no studies have investigated the importance of pig

carcasses for maintaining coyote abundance.

Aims: We tested the hypothesis that coyote populations may be bolstered by wild pig carcasses

created by control programs.

Methods: From July 2014 to July 2017, we surveyed road transects for scat to monitor coyote

abundance in response to changing levels of pig carcass availability. From June 2015 to July

2017, wild pigs were removed from the eastern half of the study area and placed at one of four

carcass dump sites on the western side. We analysed the scat data using an open population

spatially-explicit capture-mark recapture model to estimate seasonal abundance and movement

of coyotes in response to the carcass treatment.

47   *Results:* Coyote density across the entire study area declined from 95 coyotes/100 km^2 in July

48   2014 to 65 coyotes/100 km^2 by July 2016, but declines were unrelated to the carcass availability

49   treatment. Additional analysis on non-genotyped scat data showed no apparent effect of carcass

50   availability on coyote density. Coyote activity centers moved fewer than 100 meters towards the

51   nearest carcass dump site in response to the carcass treatment.

52   *Conclusions:* Wild pig carcass availability is likely not a primary driver of coyote abundance or

53   territory selection at the study location.

54   *Implications:* We conclude that the availability of wild pig carcasses had little effect on coyote

55   abundance and thus wild pig carcass removal will not be an effective coyote management

56   strategy.

57

58   **Keywords:** abundance**,** *Canis latrans,* coyote, invasive wild pig, feral hog, Savanah River Site,

59   supplemental forage, *Sus scrofa*

60

61   **Introduction**

62   Wild pigs (*Sus scrofa*) are a highly abundant and destructive invasive species throughout

63   their introduced range (Barrios-Garcia and Ballari 2012; Bevins *et al.* 2014; Lewis *et al.* 2019).

64   Originally from Eurasia, wild pigs are now present on all continents except Antarctica as well as

65   several oceanic islands (Mayer *et al.* 2020). Wild pigs cause millions of dollars of damage

66   annually, negatively impacting agricultural crop production, removing native understory cover,

67   and transmitting disease (Barrios-Garcia and Ballari 2012; Lewis *et al.* 2019; Pepin *et al.* 2022).

68   Globally, wild pigs threaten over 670 taxa and have had a major contribution to at least 14

69   species extinctions (Risch *et al.* 2021). Due to their high fecundity, extensive distribution, and

70   ability to disperse in response to trapping pressure, wild pig populations present a global

71   management concern (Bevins *et al.* 2014; Risch *et al.* 2021; Garabedian and Kilgo 2024).

72   Most wild pig control programs typically involve lethal removal of pigs. Common

73   removal methods include trapping, professional sharp-shooting, hunting with dogs, sport

74   hunting, and aerial gunning (Ditchkoff and Bodenchuk 2020, Gaskamp et al. 2021, Kilgo et al.

75   2023). Due to food safety concerns and regulations, meat from removed pigs usually cannot be

76   sold or donated (West *et al.* 2009). Wild pigs are known to carry almost 40 parasites that can be

77   transmitted to humans or other wildlife as well as at least 30 viral and bacterial diseases (Miller

78   *et al.* 2017). Regulations on wild pigs vary by country and region, but donation and sale of wild

79   pig meat is banned or discouraged across most of the United States (West *et al.* 2009). As a

80   result, carcasses of removed pigs are typically buried or simply left in the woods.

81   In the Southeastern United States, where wild pigs are well established and highly abundant

82   (Barrios-Garcia and Ballari 2012, Lewis et al. 2019), pigs can be removed in all seasons,

83   potentially providing scavengers with a year-round, low effort food resource. One dominant

84   scavenger that may benefit is the coyote (*Canis latrans*), a highly adaptable and controversial

85   predator in North America. Prior to 1900, coyotes were restricted to the western two-thirds of

86   North America (Hody and Kays 2018), but have since expanded their range to encompass the

87   majority of the continent (Sillero-Zubiri *et al.* 2004). In the absence of red wolves (*Canis rufus)*,

88   coyotes are now the dominant carnivore in much of the eastern United States (Berger and Gese

89   2007), with eastern densities often exceeding those in the western portion of the range

90   (Knowlton *et al.* 1999; Schrecengost *et al.* 2009; Way and Timm 2011). The expansion and

91   increase of coyote populations has led to several management concerns including predation of

92   game and livestock (Knowlton *et al.* 1999; Kilgo *et al.* 2010)*,* interference competition with

93   other carnivores (Dyck *et al.* 2022), and negative human-wildlife interactions (Poessel *et al.*

94   2017). Though levels of predation vary throughout the eastern United States, coyotes are the

95   main predator of white-tailed deer (*Odocoileus virginianus*) fawns, and reduced recruitment has

96   been instrumental in localized declines of many deer populations in the Southeast (Kilgo *et al.*

97   2012; Chitwood *et al.* 2015; Kilgo *et al.* 2019). Consequently, considerable interest in coyote

98   populations exists among hunters and wildlife managers.

99   Coyotes have a high degree of dietary plasticity, altering their diets in response to seasonal

100   food availability, prey characteristics, and the availability of carrion on the landscape (Knowlton

101   *et al.* 1999; Schrecengost *et al.* 2008; Jensen *et al.* 2022). In addition to ungulates, coyotes have

102   been documented consuming a wide variety of food items, including small mammals, vegetation,

103   birds, and invertebrates (Schrecengost *et al.* 2008; Jensen *et al.* 2022). Coyotes also consume

104   invasive wild pigs, particularly in the early spring when vegetation and ungulate carcasses are

105   less readily available (Turner *et al.* 2017; Watine and Giuliano 2017; Jensen *et al.* 2022). As

106   invasive wild pig populations increase throughout the Southeast (Davis *et al.* 2020; Garabedian

107   and Kilgo 2024), coyote diets may shift to take advantage of this abundant food resource.

108   In addition to direct predation, scavenging appears to be an important foraging strategy for

109   coyotes, particularly when other food options are scarce or population density is high (Prugh

110   2005; Schrecengost *et al.* 2008; Jensen *et al.* 2023). Previous studies have noted the importance

111   of carrion in coyote diets (Mastro 2011; Ruprecht *et al.* 2021; Parsons and Young 2024), and

112   wild pig remains were detected in 24.7% of coyote stomach samples in Florida (Watine and

113   Giuliano 2017). However, it remains unclear if wild pig carcass availability directly contributes

114   to higher coyote abundance. Our objectives were to evaluate if wild pig carcasses produced by

115   wild pig control efforts are bolstering local coyote densities.

116

Methods

Study area

119   We conducted the study at the United States Department of Energy's Savannah River Site (SRS),

120   a 78,000-ha National Environmental Research Park located in the Southeastern Plain ecoregion

121   of South Carolina (Fig. 1). Upland sites were dominated by planted pine forests comprised of

122   loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*). Longleaf pine stands were managed

123   on 120-year rotations, with loblolly stands managed on 50 – 100-year rotations. River drainages

124   and floodplains were occupied by bottomland hardwoods and cypress (*Taxodium distichum*)-

125   tupelo (*Nyssa aquatic* and *N. sylvatica* var. *biflora*) forests. Terrain was generally flat to gently

126   rolling, with elevations ranging from 20 m to 130 m. The climate was humid subtropical, with a

127   mean annual temperature of 18°C and mean annual rainfall of 122.5 cm (Kilgo *et al.* 2017).

128   Dominant mammalian wildlife in the study area included white-tailed deer, coyotes,

129   bobcats (*Lynx rufus*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), and

130   wild pig. The wild pig population at the SRS descended from domestic pigs released on the

131   property prior to 1950 and pigs that colonized since that time containing Eurasian wild boar

132   ancestry. Thus, the current population consists of domestic x Eurasian wild boar hybrids (Mayer

133   *et al.* 2020). A targeted control program was implemented in 1985, and since 2010, 1,100 –

134   1,900 individuals/year have been removed through trapping, shooting, and hunting with dogs.

135   Additionally, an average of 69 individuals/year were taken incidental to recreational deer

136   hunting. Across all age classes, average body mass of removed pigs at the SRS is 39.3 kg,

137   resulting in an average 52,976 kg of carrion annually. At the time of this study, the estimated

138   wild pig density varied across the SRS from 3-20 pigs/km^2 (Kilgo *et al.* 2021; Kilgo *et al.* 2023).

139   Coyotes were first reported on site in 1986, with densities reaching an estimated 103 -192

140   coyotes/100 km^2 by 2006 (Schrecengost 2007). Prior to 2010, coyotes at the SRS were mostly

141   unexploited, with incidental harvest during white-tailed deer hunting resulting in 20-30

142   coyotes/year harvested (Kilgo *et al.* 2017). Experimental coyote trapping was conducted from

143   2010 – 2012, removing 471 coyotes from the property in addition to incidental harvest (Kilgo *et*

144   *al.* 2017).

145

146   *Carcass treatments and sampling methodology*

147   We structured our study as a BACI design (before-after controlled impact; Stewart-Oaten et al.

148   1986). Prior to May 2015, wild pig carcasses were left on the landscape at the location where

149   they died and were freely available for scavengers. Total annual culling during 2014–2017

150   averaged 1,419 pigs. Starting June 1, 2015, all wild pigs killed on the eastern side of the property

151   (hereafter, removal area) were transported to the western side and placed in one of four dump

152   locations (hereafter, carcass area; Fig. 1), while those killed on the western side remained where

153   they were died. Thus, the removal area had essentially no carcasses and the carcass area had

154   approximately double the baseline number of carcasses, both distributed across the landscape

155   and concentrated at dump locations.

156   From July 2014 to July 2017, we monitored coyote abundance using road transect

157   surveys for scat. We drove transects at approximately 10 km/hr, using the edges of the road as the

158   boundary of our sampling area and collected any scat detected. Sampling was split into nine

159   primary sampling occasions, separated by three-month intervals, to capture potential seasonal

160   changes in coyote abundance. Within each primary occasion, we sampled each transect for four

161   days (secondary occasions). Sampling days were usually three days apart to allow time for scat

162 to accumulate on the roads. On several occasions, weather or other field conditions impeded

163 sampling, in which case sampling was delayed an additional day. All detected scat samples were

164 collected using tongs and placed in Whirl-pak® bags, which were stored in a cooler with ice

165 packs until the end of the day, whereupon they were placed in a -20ºC freezer. For each sample,

166 we recorded the GPS coordinate, date, and transect name.

167

168 *Laboratory methodology*

169 Due to staffing shortages, we only performed genetic analysis on samples collected from July

170 2014 to July 2016. We extracted scat samples using Qiagen Mini Stool Kits (Qiagen, Valencia,

171 California, USA) following the manufacturer's protocol. Following the collection of an outer

172 segment of each scat sample to capture epithelial cells, we performed all extractions using two

173 QiaCube automated machines (Qiagen, Valencia, California, USA). We then genotyped each

174 sample across a 9 loci microsatellite panel to identify individuals for subsequent recapture

175 histories. We conducted polymerase chain reaction (PCR) using microsatellite primers FH2001,

176 FH2004, FH2010, FH2054, FH2161 (Francisco et al. 1996); FH2328 (Hellmann et al. 2006);

177 FH2457, FH2062, and FH2289. For every 96-well PCR plate run, we included two negatives of

178 molecular grade water to screen for cross-contamination. The PCR master mix included 1.7 µl of

179 1x Amplitaq gold PCR Buffer, 1.7 µl 1x Bovine Serum Albumin (BSA), 1.5 µl 2.2µM MgCI$_2$, 1

180 µl 0.59 mM Deoxynucleotide (dNTP) Solution Mix (Fisher Scientific #FERR1122), 0.5 µl each

181 of two microsatellite primers, 0.1 µl Tween 20 (Fisher Scientific #BP337-100), 0.06 µl 0.3-unit

182 Amplitaq gold Taq DNA Polymerase (Fisher Scientific #4311814), and 4.94 µl molecular grade

183 water. We used 5 µl of extracted DNA for a total reaction mix of 17 µl. We ran our PCR on a

184 thermocycler for an initial denaturation step of 95°C for 5 minutes and then 20 annealing cycles

185 at 95°C for 30 seconds, followed by 65°C for 30 seconds with a decrease of 0.5°C every cycle to

186 55°C and then 72°C for 30 seconds. We ran 20 extension cycles of 95°C for 30 seconds, 55°C for

187 30 seconds, and 7°2C for 30s. We finished PCR at 72°C for 5 minutes.

188   We genotyped samples on a 3130x capillary machine and used GeneMapper 4.1 (Applied

189 Biosystems) to visualize and score alleles. We required that all homozygous loci be observed in

190 two separate replicates to confirm consensus. Additionally, we selected 500 samples and ran

191 three separate replicates to calculate allelic dropout and false allele rates using RELIOTYPE

192 (Miller et al. 2002). To further test for null alleles and large allele dropout, we selected 304

193 samples to use MICROCHECKER (Van Oosterhout et al. 2004). Finally, we used DROPOUT

194 (McElvey and Schwartz 2005) to check our genotype dataset for errors caused by low quality

195 DNA. We required that seven loci be confirmed per individual to identify recaptures and built

196 capture histories for downstream analysis from consensus genotypes.

197

198 *Statistical analysis*

199 We fit the genotyped scat data (scats collected from July 2014 to July 2016) to an open

200 population spatially-explicit capture-mark recapture (SCR) model in a Bayesian framework

201 (Gardner et al. 2009; Gardner et al. 2010). Due to uncertainty associated with the unmarked data,

202 we then fit unmarked spatial capture-recapture models for each primary sampling period to all

203 the scat data collected (July 2014 to July 2017) as an index of population abundance across time.

204 We begin by describing the model for the marked scat data.

205

206 *Marked spatial capture recapture*

207   We discretized all transects into 'traps' spaced 500 m apart and associated each coyote

208   scat sample to the closest point. To reduce bias in SCR analysis, the probability of detecting

209   animals outside the study area needs to be negligible (Borchers and Efford 2008). In previous

210   work on coyotes at the SRS, coyote home ranges averaged $30 - 31$ km^2 (Schrecengost *et al.*

211   2009); We therefore buffered the boundary of the SRS by 10 km, approximately half the width

212   of a circular coyote home range.

213   We calculated abundance for each of the 9 primary periods (4 pre-treatment and 5 post-

214   treatment periods). We assumed the population of coyotes was closed during secondary

215   occasions, but open between primary periods. Since we could not separate coyotes by age, we

216   did not distinguish between immigration and reproduction. Instead, we modeled the probability

217   of a coyote entering the population, either by reproduction or immigration, as a single 'entrance

218   probability' parameter that varied by occasion. We assumed constant apparent survival

219   throughout the study period.

220   Individual level data presents a problem when working with Markov chain Monte Carlo

221   because the dimension of the parameter space depends on abundance, *N*, which changes with

222   each Monte Carlo iteration. To resolve this, we use a data augmentation framework (Royle *et al.*

223   2007; Royle *et al.* 2013) where we propose a value *M,* which is some integer value much larger

224   than *N.* Let $z_{i,t}$ be a binary variable that indicates if an individual is real and present in the

225   population. The probability that individual *i* is real ($z_{i,t} = 1$) is just $\psi = N/M$. As long as *M* is

226   much larger than *N,* the posterior for *N* is unaffected by the value of *M*. However, extremely

227   large values of *M* will greatly increase computation time. Thus, under data augmentation the

228   model for abundance is simply:

229
$$N_t = \sum_{i=1}^{M} z_{i,t}$$

230
$$z_{i,t} \sim \text{Bernoulli}(\psi)$$

231   Although carcasses were widely distributed throughout the carcass area, to assess the

232   possibility of coyote territories moving in response to carcass availability at carcass dump

233   locations specifically, we fit a biased, correlated random walk model to the activity centers of all

234   coyotes in the study area. Let $\mathbf{X_{i,t}}$ represent the inverse distance weighted average direction of the

235   nearest carcass dump location with respect to each individual's location in primary period t -1. If

236   in each time period, individuals were attracted with strength δ towards the carcass dump

237   locations, then the location of individual i's activity center at primary period t is given by:

238
$$s_{i,t} \sim \text{Normal}\big(s_{i,t-1} + \delta \mathbf{X_{i,t}}, \ \kappa^2\big)$$

239   with random error κ^2. This formulation allows for a strong movement response from coyotes

240   located close to carcass piles, while accounting for the (likely negligible) effect of carcass

241   placement on coyotes with territories hundreds of kilometers away. If carcass dump location had

242   no impact on individual locations ($\delta = 0$), the movement process reverted to a Gaussian random

243   walk.

244   We modeled detection at each discretized trap location using a half-normal function for

245   detection probability. To allow for seasonal changes in coyote home range size, we modeled σ,

246   the decay of detection probability with increasing distance (d) between the trap and an

247   individual's activity center, as varying by season. We assumed the baseline detection probability,

248   g_0, was constant across time. The expected number of detections ($\lambda_{i,j,k,t}$) of individual i ($i = 1$,

249   … , M) at trap j during survey k in primary period t was:

250
$$\lambda_{i,j,k,t} = g_0 e^{-d_{ijt}^2/2\sigma_t^2}$$

251   where d_{ijt}^2 is the distance between individual i's activity center and trap j. Following standard

252   SCR assumptions, home ranges of all individuals were assumed to follow a bivariate normal

253   distribution, as implied by the capture probability function (Royle *et al.* 2013). The code and

254   data needed to run this analysis can be found in the data archive associated with this manuscript.

255   We used MCMC to draw posterior samples in NIMBLE 1.0.1 with the 'nimble' package

256   in R 3.6.3 (de Valpine *et al.* 2017; R Core Team 2022; NIMBLE Development Team 2023). We

257   ran three chains for 20,000 iterations each with 15,000 burnin iterations and a thinning rate of

258   two. At each iteration, we calculated abundance in each half of the study area by summing the

259   number of individual activity centers that fell within each region of the study area. We assessed

260   convergence using the Gelman-Rubin statistic (Gelman and Rubin 1992) and visual inspection of

261   the chains.

262

263   *Unmarked spatial capture recapture*

264   Without genetic analysis, we could not confirm that scats collected after July 2016 were

265   deposited by coyotes. To address this challenge, we analyzed all scats collected (July 2014 to

266   July 2017) using closed-population unmarked spatial capture-recapture models for each primary

267   period to obtain an index of abundance over time. We assumed the proportion of scats incorrectly

268   identified as coyote were constant overtime and did not model movement of coyotes between

269   primary periods. Using the same trap discretization and boundary buffering protocol as in our

270   marked SCR analysis, we calculated abundance for each of the 13 primary periods (4 pre-

271   treatment and 9 post-treatment periods). As demonstrated by (Chandler and Royle 2013), SCR

272   analysis on small datasets of completely unmarked populations may produce biased inference;

273   We therefore only consider the results of these models as an index of population trends, rather

274   than a true estimate of population abundance.

275   We modeled detection of scats using a binary value to indicate if at least one scat was

276   detected at each discretized trap location j on each secondary occasion k ($k = 1, \dots , K$).

277   Following the binary formulation used in (Margenau *et al.* 2022), the total number of scats

278   collected at each trap in each primary occasion becomes:

279    $$n_{j,t} \sim Binomial(K, 1 - e^{-\Lambda_{j,k,t}})$$

280   where $\Lambda_{j,k,t} = \sum_{i=1}^{M} \lambda_{i,j,k,t} \, z_{i,t}$.

281   We used MCMC to draw posterior samples in NIMBLE 1.0.1 with the 'nimble' package

282   in R 3.6.3 (de Valpine *et al.* 2017; R Core Team 2022; NIMBLE Development Team 2023). We

283   ran three chains for 4,000 iterations each with 3,000 burnin iterations and a thinning rate of one.

284   We assessed convergence using the Gelman-Rubin statistic (Gelman and Rubin 1992) and visual

285   inspection of the chains.

286

287   **Results**

288   Across 123 km of transect, we collected 1404 animal scats (Fig. S1), 1086 of which were

289   analyzed for species and individual identity. We collected an average of 108 scats per primary

290   period (range: 34 – 216). We successfully obtained individual coyote identification on 509

291   samples (46.9% genotype success), corresponding to 398 individual coyotes. For our genotyped

292   scats, we detected an average of 56.5 coyote scats per survey (range: 6 – 131) and 1.3 scats per

293   coyote (range: 1 – 6). The majority of coyotes (83%) were only detected in a single primary

294   period.

295   Median estimates of coyote density from our marked SCR model were consistently

296   higher in the carcass removal area (Fig. 2). The difference in coyote density between carcass

297   treatment areas was more pronounced prior to carcass removal, though there was considerable

298   overlap in the 95% credible interval estimates between the areas. Across the SRS, coyote density

299   declined from 95 (95% CI: 87 to 105) coyotes/100 km^2 in July 2014 to 65 (95% CI: 56 to 76)

300   coyotes/100 km^2 in July 2016.

301   Median seasonal estimates of σ ranged from 1248.39 in Winter to 457.56 in Fall,

302   suggesting ad-hoc home range sizes (Efford *et al.* 2015) of approximately 4 – 29 km^2 throughout

303   the annual cycle (Table 1). The estimate of the movement parameter δ was 0.0075 (95% CI:

304   0.0052 to 0.012), suggesting coyote activity centers shifted on average fewer than 100 meters

305   towards the nearest carcass dump site in response to the carcass treatment. Similarly, κ was

306   estimated at 34.73 (95% CI: 22.77 to 44.25), implying coyote activity centers moved less than

307   150 meters between primary occasions. Throughout the study period, coyote density was highest

308   in the southwestern region of the study area (Fig. 3).

309   Density indices from our unmarked spatial capture recapture model suggested that coyote

310   density declined between July 2014 and July 2017, though estimates were much more variable

311   between seasons than the marked SCR estimates. Unmarked estimates were similar between the

312   treatment and control areas, with no obvious differences between the two halves of the study area

313   (Fig. 4). There was also no apparent difference in the average distance between estimated

314   activity centers and pig carcass locations before and after treatment (Fig. S2).

315

316   **Discussion**
317
318   Understanding the consequences of leaving wild pig carcasses on the landscape remains

319   an ongoing effort. We used spatially-explicit capture recapture to estimate changes in the

320   abundance and spatial distribution of coyotes in response to the removal of a potential food

321   resource - wild pig carcasses. Though coyote abundance decreased during the study period,

322   declines began prior to the treatment application and did not substantially change in response to

323   carcass removal. The overall impact on both coyote abundance and spatial distribution was

324   negligible, suggesting the current strategy of leaving wild pig carcasses in the woods has

325   minimal impacts on local coyote populations.

326   If coyotes were dependent on wild pig carcasses as a primary food source, we would have

327   expected to see the highest coyote densities closest to the carcass dump sites. Ecological theory

328   suggests clumped high quality food resources will result, on average, in smaller territories with

329   increased space use near the food resource (Young *et al.* 2008; Sells and Mitchell 2020). Yet,

330   despite the abundant carrion available at carcass dump sites, we found little evidence to suggest

331   coyotes were attracted to these locations. Conversely, if removal of carrion reduced the carrying

332   capacity of coyotes on the landscape, we would have expected coyote densities to decline in the

333   treatment areas. Resident coyotes can rapidly transition to transient behavior irrespective of age

334   and social status in response to ecological demands (Hinton *et al.* 2015). However, the spatial

335   distribution of coyotes remained stable throughout the study period, even as overall abundance

336   declined. Though previous studies at the SRS have found evidence of pig consumption in coyote

337   scat (Schrecengost et al. 2008, Ward et al. 2018, Youngmann et al. 2023), wild pig does not

338   appear to be a primary driver of population dynamics for this species.

339   The importance of scavenging for maintaining coyote populations remains an open

340   question. Ward et al. (2018) argued that scavenging was not an important foraging strategy for

341   coyotes in the Southeast, noting the infrequency of both roadkill species and wild pig in coyote

342   scat, despite their widespread distribution within the study area. Previous research on western

343   coyotes found that carrion represented the most commonly used prey when primary prey species

344   were in decline, but only comprised a small proportion of the diet when primary prey species

345   were abundant (Prugh 2005). These findings suggest that scavenging is most important when

346   food resources are limited and may mostly be employed by coyotes experiencing food scarcity.

347   Given the observed decline in coyote abundance within our study area and previous research

348   suggesting eastern coyote populations are often below carrying capacity (Morin *et al.* 2016),

349   food scarcity may be uncommon for coyotes in this region. Thus, while coyotes on the SRS may

350   opportunistically consume wild pigs, the availability of white-tailed deer and other preferred

351   food resources may negate the need for reliance on scavenging.

352   Few of the individual coyotes detected by our scat surveys were detected in more than

353   one primary period, suggesting a high proportion of transient individuals. Both transience and

354   dispersal are common in coyote populations (Harrison 1992; Windberg *et al.* 1997; Morin and

355   Kelly 2017), and individual coyotes can disperse distances upwards of 390 km (Harrison 1992;

356   Hinton *et al.* 2012). Transient coyotes are less reliant on local food sources and may exhibit

357   different patterns of prey selection compared to resident coyotes (Mills and Knowlton 1991;

358   Gese *et al.* 1996). While resident coyotes may be more directly impacted by removal of pig

359   carrion on the landscape, there is little evidence to suggest wild pigs are a primary food resource

360   for Southeastern coyotes (Ward et al. 2018, Jensen et al. 2022, but see Watine and Giuliano

361   2017). Moreover, the high proportion of transient individuals in many eastern coyote populations

362   (Hinton *et al.* 2015; Webster *et al.* 2022) implies that local removal of a non-primary food

363   resource is unlikely to result in meaningful reductions in coyote abundance.

364   One difficulty with assessing coyote response to environmental change is the large study

365   area required to accurately capture local coyote dynamics. Coyote home range sizes vary

366   seasonally and depend in part on the abundance of food resources within a pack's territory

367   (Schrecengost *et al.* 2009; Ward *et al.* 2018; Youngmann *et al.* 2022). Previous work at the SRS

368   found home range size ranged from 5.4 – 39.2 km^2 across the annual cycle with a core area size

369   of 1 – 6.1 km^2 (Ward *et al.* 2018). These estimates suggest the size of our study area was

370   sufficient to detect changes between treatment blocks, but would not have been large enough to

371   allow for spatial replication of the carcass removal treatment. Thus, while our results suggest

372   current pig management efforts are not subsidizing coyote populations on the SRS, we

373   acknowledge these findings may be limited to this geographic region.

374   One limitation to our study is the lack of direct diet information from the coyotes in our

375   study area. Previous research has demonstrated that coyote populations can respond rapidly to

376   changes in food availability or habitat conditions, often in the form of prey switching (Andelt

377   and Andelt 1984; Prugh 2005). Without additional information on the diets of the coyote

378   population during our study period, we cannot rule out the possibility that the apparent lack of

379   response to the carcass treatment was simply the product of coyotes shifting their diets to include

380   alternative food sources. However, if coyotes on the SRS can shift their diets to alternative food

381   sources without suffering noticeable declines in abundance, the pig carcasses produced by

382   current pig management efforts are unlikely to represent a meaningful subsidy for the coyote

383   population.

384   Though we found no effect of wild pig carcass availability on coyote abundance, our

385   findings suggest a decline in the coyote population at the SRS between 2014 and 2016.

386   Schrecengost (2007) estimated the 2006 coyote density at the SRS as 103 -192 coyotes/100 km^2,

387   compared to our July 2014 estimate of 95 (87 - 105) coyotes/100 km^2. Recent research by

388   Youngmann (2023) reported densities of 15 – 36 coyotes/100 km^2 in 2019, much lower than our

389   July 2016 estimate of 65 (56 - 76) coyotes/100 km^2. Similarly, estimates of the numbers of

390   coyotes shot by deer hunters statewide in South Carolina declined between 2014 and 2021

391   (South Carolina Department of Natural Resources 2022). Yet to our knowledge, little evidence

392   exists to suggest coyotes are declining elsewhere in the Southeast. On the contrary, most coyote

393   studies report increasing populations, even in areas with substantial hunting or trapping pressure

394   (Conner and Morris 2015; Morin *et al.* 2016). Although we did not investigate the drivers of the

395   decline we observed, as this was beyond the scope of our study, we suggest additional

396   monitoring is warranted to determine whether coyote abundance may be moderating in the state

397   after initially increasing post-colonization.

398   Invasive wild pigs are numerous and pig management efforts create a large volume of

399   carrion on the landscape. Carrion produced by human activities can increase scavenger presence

400   and alter predator dynamics on the landscape (Newsome *et al.* 2015; Turner *et al.* 2017; Spencer

401   *et al.* 2021). Additional food resources for apex predators can decouple interactions between

402   predators and prey populations (Letnic and Dickman 2010), potentially leading to surges in

403   mesoscavenger populations (O'Bryan *et al.* 2019). Though the consequences of increased pig

404   carcasses for other scavengers remains unclear, our results suggest that pig carcasses produced

405   by current pig management efforts are not subsidizing coyote populations in the southeastern

406   United States. Our work highlights the need to study how invasive animal carcasses are

407   impacting other scavenger populations, both within the southeastern United States and globally.

408

409   **Data Availability Statement**

410   All data and code are publicly available at: https://zenodo.org/records/13912786

411

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416   **Conflict of interest statement**

417   The authors declare no conflict of interest.

418

419   **Declaration of funding**

426

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627

628   Figure captions:

629   Figure 1. Location of 123 km of scat transects at the Savannah River Site, South Carolina, USA.
630   Transects were located on existing roads with surveys repeated over 9 periods from 2015 to 2016
631   to estimate density and spatial distribution of coyotes. Pigs hunted on the eastern half of the
632   property (blue polygon) were placed at carcass dump sites (pig icons) on the western side (beige
633   polygon) starting June 1, 2015.

634

635   Figure 2 Density of coyotes per 100 km^2 at the Savannah River Site, South Carolina, USA from
636   July 2014 to July 2016 before and after pig carcass removal treatment. Error bars show the
637   median and 95% credible intervals for the eastern (blue) and western (brown) halves of the study
638   area. The vertical dotted line signifies when pig carcasses were first removed from the eastern
639   half of the study area.

640

641   Figure 1. Heat map of coyote activity centers at the Savannah River Site, South Carolina, USA
642   from July 2014 to July 2016. Points represent individual coyote activity centers within each 500
643   meter hex. Areas in white represent hexes with an estimated density lower than 5 coyotes per 100
644   km^2. Only coyote territory centers located within the study area boundary are shown.
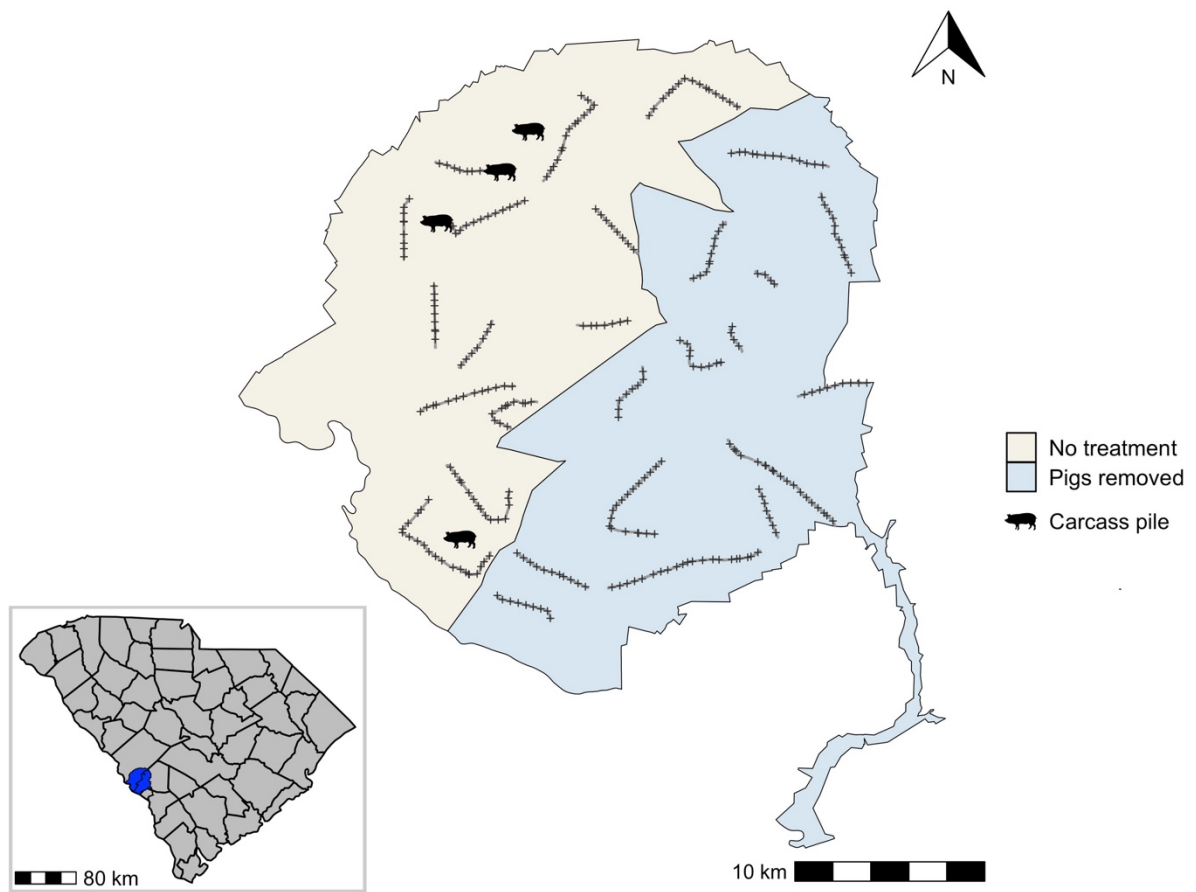
645

646   Figure 4. Index of coyote density per 100 km^2 based on unmarked coyote scat data collected at
647   the Savannah River Site, South Carolina, USA from July 2014 to July 2017. Dotted lines show
648   the 95% credible intervals for index estimates. The vertical dotted line signifies when pig
649   carcasses were first removed from the eastern half of the study area.
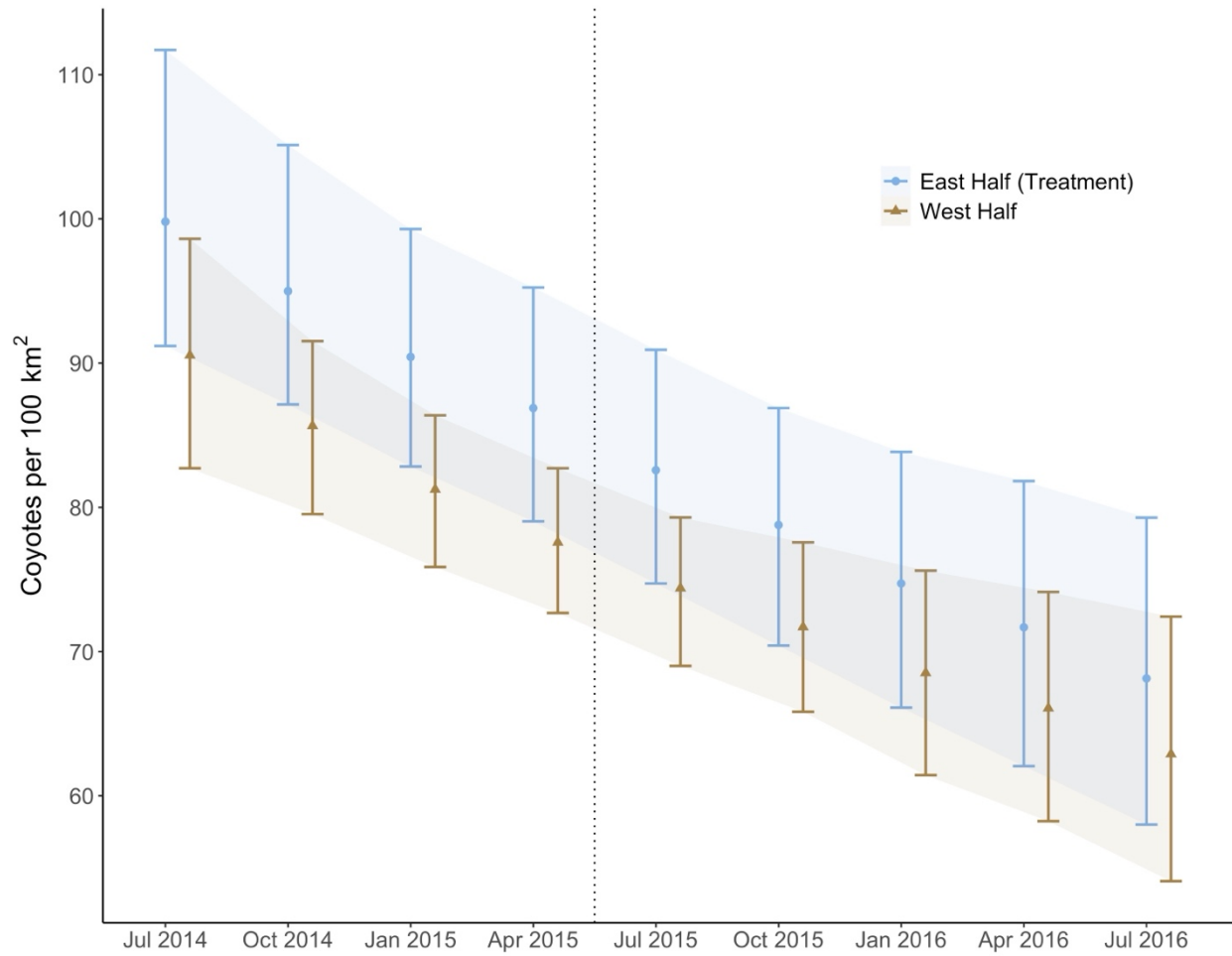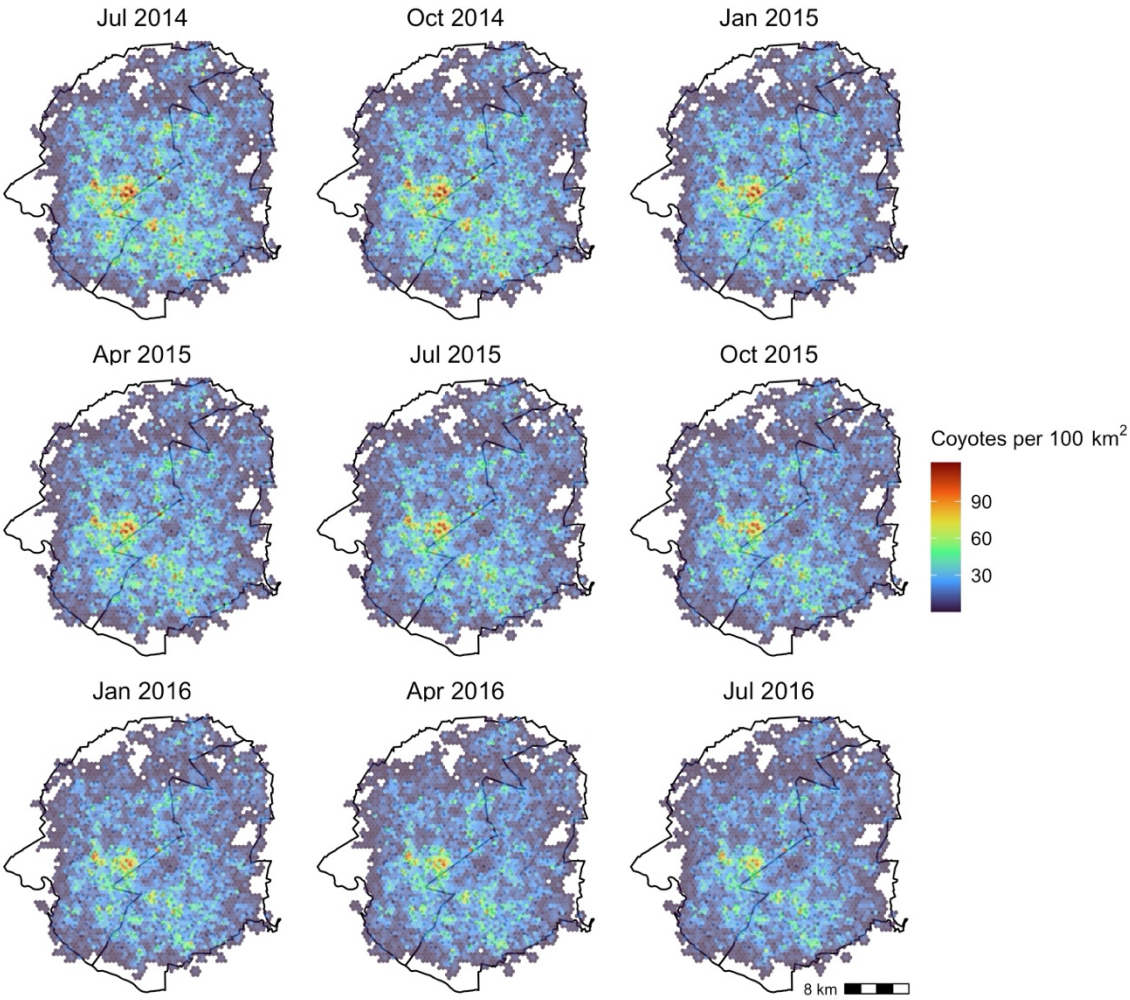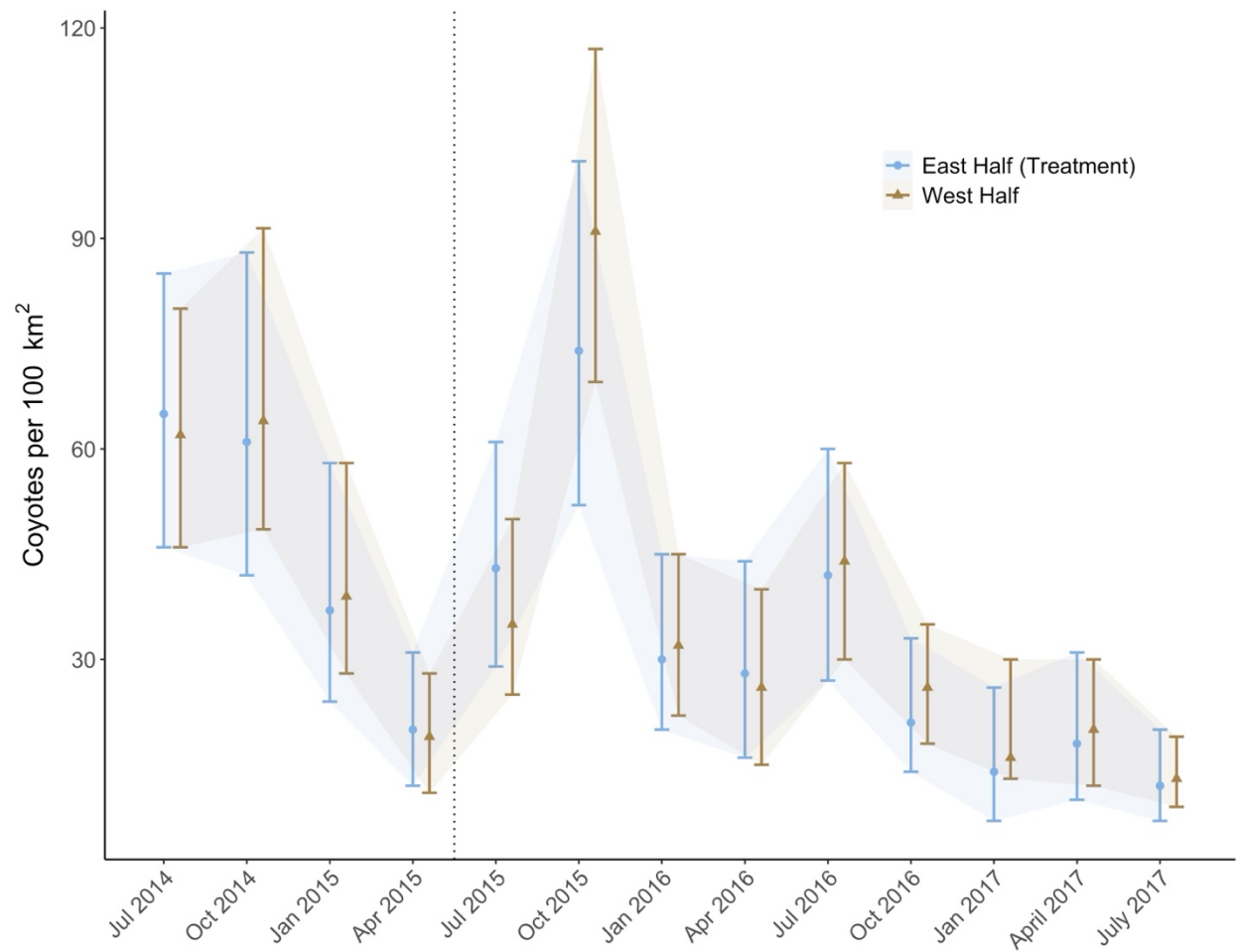650

651

652

653   Table 1. Parameter median estimates and 95% credible intervals for an open population spatial
654   capture recapture model of coyote abundance at the Savannah River Site, South Carolina, USA
655   from July 2014 to July 2016.

656

Parameter	Description	Estimate	95% CI
g_0	Baseline detection	0.01	0.005, 0.02
σ_{Winter}	Detection decay parameter - Winter	1248.39	1116.12, 1310.77
σ_{Spring}	Detection decay parameter - Spring	1197.23	1124.58, 1270.1
σ_{Summer}	Detection decay parameter - Summer	575.56	469.98, 663.74
σ_{Fall}	Detection decay parameter - Fall	457.56	363.37, 575.02
δ	Attraction to carcasses	0.0075	0.0052, 0.012
κ	Movement parameter – sd	34.73	22.77, 44.25

657

658

659

Jul 2014   Oct 2014   Jan 2015

Apr 2015   Jul 2015   Oct 2015

Coyotes per 100 km²

90

60

30

Jan 2016   Apr 2016   Jul 2016

660

8 km

661

662