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Breeding dynamics of gopher frog metapopulations over 10 years
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Abstract:	Populations of amphibians that breed in isolated, ephemeral wetlands may be particularly sensitive to breeding and recruitment rates, which can be influenced by dynamic and difficult-to-predict extrinsic factors. The gopher frog Rana capito is a declining species currently proposed for listing under the U.S. Endangered Species Act, as well as one of many pond-breeding amphibians of conservation concern in the southeastern United States. To represent gopher frog breeding dynamics, we applied an occupancy modeling framework that integrated multiple datasets collected across the species' range to (i) estimate the influence of climate, habitat, and other factors on wetland-specific seasonal breeding probabilities, and (ii) use those estimates to characterize seasonal, annual, and regional breeding patterns over a 10-yr period. Breeding probability at a wetland was positively influenced by seasonal precipitation (Standardized Precipitation Index) and negatively influenced by fish presence. We found some evidence that the amount of suitable habitat surrounding a wetland was positively correlated with breeding probability during drought conditions. The percentage of sampled wetlands (N = 192) predicted to have breeding varied seasonally, annually, and regionally across the study. Within-year temporal patterns of breeding differed across the range: in most locations north of Florida, peaks of breeding occurred in winter and spring months; whereas breeding was more dispersed throughout the year in Florida. Peaks of breeding across the 10-yr period often occurred during or in the season following high rainfall events (e.g., hurricanes). These results have direct applications for site-level management that aims to increase successful breeding opportunities of gopher frogs and other associated pond-breeding amphibians, including monitoring protocol and intensity, removal of fish, and improving terrestrial habitat conditions surrounding wetlands (e.g., via tree/shrub removal and prescribed fire). The results also have implications for better-informed management through the closer alignment of breeding activity monitoring with predicted seasonal peaks. Furthermore, estimates of breeding frequency can be incorporated into population viability analyses to inform forthcoming assessments of extinction risk and designation of the species' conservation status by the U.S. Fish and Wildlife Service.

1   **Breeding dynamics of gopher frog metapopulations over 10 years**

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30

31   **Abstract**

32   Populations of amphibians that breed in isolated, ephemeral wetlands may be particularly

33   sensitive to breeding and recruitment rates, which can be influenced by dynamic and difficult-to-

34   predict extrinsic factors. The gopher frog *Rana capito* is a declining species currently proposed

35   for listing under the U.S. Endangered Species Act, as well as one of many pond-breeding

36   amphibians of conservation concern in the southeastern United States. To represent gopher frog

37   breeding dynamics, we applied an occupancy modeling framework that integrated multiple

38   datasets collected across the species' range to (i) estimate the influence of climate, habitat, and

39   other factors on wetland-specific seasonal breeding probabilities, and (ii) use those estimates to

40   characterize seasonal, annual, and regional breeding patterns over a 10-yr period. Breeding

41   probability at a wetland was positively influenced by seasonal precipitation (Standardized

42   Precipitation Index) and negatively influenced by fish presence. We found some evidence that

43   the amount of suitable habitat surrounding a wetland was positively correlated with breeding

44   probability during drought conditions. The percentage of sampled wetlands (N = 192) predicted

45   to have breeding varied seasonally, annually, and regionally across the study. Within-year

46   temporal patterns of breeding differed across the range: in most locations north of Florida, peaks

47   of breeding occurred in winter and spring months; whereas breeding was more dispersed

48   throughout the year in Florida. Peaks of breeding across the 10-yr period often occurred during

49   or in the season following high rainfall events (e.g., hurricanes). These results have direct

50   applications for site-level management that aims to increase successful breeding opportunities of

51   gopher frogs and other associated pond-breeding amphibians, including monitoring protocol and

52   intensity, removal of fish, and improving terrestrial habitat conditions surrounding wetlands

53   (e.g., via tree/shrub removal and prescribed fire). The results also have implications for better-

54   informed management through the closer alignment of breeding activity monitoring with

55   predicted seasonal peaks. Furthermore, estimates of breeding frequency can be incorporated into

56   population viability analyses to inform forthcoming assessments of extinction risk and

57   designation of the species' conservation status by the U.S. Fish and Wildlife Service.

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Introduction

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76   The gopher frog *Rana capito* is a pond-breeding amphibian and one of many at-risk species

77   currently designated for reviews of current and future population trends (i.e., through Species

78   Status Assessments: U.S. Fish and Wildlife Service 2016; Smith et al. 2018) by the U.S. Fish and

79   Wildlife Service (USFWS) to determine a listing decision under the U.S. Endangered Species

80   Act (ESA 1973, as amended). Regional or range-wide population declines have been observed or

81   suspected over the past century due to extensive habitat loss, degradation, and other stressors

82   (Semlitsch et al. 1995; Enge et al. 2014; Crawford et al. 2020a). Subsequently, the species has

83   been a focus of conservation planning efforts by Federal, State, and other partners to stem

84   ongoing declines and sustain the species across its range. State wildlife agencies, Federal

85   agencies, non-government organizations, and academic researchers have increased efforts to

86   survey gopher frog populations, study its life history traits, and estimate key demographic rates

87   (e.g., Greenberg 2001; Roznik et al. 2009; Humphries and Sisson 2012; Enge et al. 2014; Richter

88   et al. 2014). These efforts have revealed an immediate need for research to characterize

89   dynamics of breeding and recruitment to estimate extinction risk for gopher frogs at local and

90   range-wide scales, which will inform forthcoming conservation status and management

91   decisions. Because gopher frog monitoring often employs various sampling techniques and

92   intensities, research estimating breeding frequency and recruitment must also account for

93   imperfect detection rates to reduce potential bias in any population parameter estimates

94   (MacKenzie et al. 2003; MacKenzie et al. 2006; Kéry et al. 2009).

95   Gopher frogs are one of many amphibian species of conservation concern that breed in

96   isolated and ephemeral or semipermanent wetlands embedded within xeric pine savannas in the

97   southeastern United States, including the once extensive longleaf pine *Pinus palustris* forest

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98 (Dodd 1992; Gibbons et al. 2006; Enge et al. 2014; Erwin et al. 2016). Populations of ephemeral

99 pond-breeding amphibians may be particularly sensitive to dynamic and difficult-to-predict

100 extrinsic factors that influence rates of breeding and recruitment (i.e., of larvae into the terrestrial

101 juvenile stage class). Successful annual breeding and juvenile recruitment from ephemeral

102 wetlands requires local climate conditions that allow wetlands to fill and hydroperiods to be

103 sufficiently long for larval development (e.g., Palis 1998; Greenberg 2001; Jensen et al. 2003;

104 Chandler et al. 2016; Chandler et al. 2017). For example, Chandler et al. (2016) estimated that

105 isolated wetlands used by endangered reticulated flatwoods salamanders *Ambystoma bishopi*

106 only had sufficiently long hydroperiods to support larval development in 61% of years and that

107 frequency was declining over recent decades as a result of climate change. For gopher frogs,

108 Greenberg et al. (2015) forecasted that hydroperiods at most isolated wetlands in a central

109 Florida sandhill would be insufficient – including many multi-year periods – for juvenile gopher

110 frog recruitment. Such low probabilities of juvenile recruitment increase the risk of extirpation.

111 Hydroperiods of isolated wetlands across the Southeast can be further altered by urbanization

112 (McCauley et al. 2013), forest cover, and silvicultural practices (Chandler et al. 2017; Jones et al.

113 2018; Haggerty et al. 2019), which may interact with climate change to increase extirpation rates

114 of amphibian species such as gopher frogs (Snodgrass et al. 2000; Chandler et al. 2017). In

115 addition, other factors, including the periodic colonization or introduction of fish into isolated

116 wetlands, may increase egg and tadpole mortality and decrease recruitment rates (Gregoire and

117 Gunzburger 2008; Liner et al. 2008). Finally, studies of gopher frog breeding frequency and

118 juvenile recruitment rates are often limited in temporal and spatial extent due to logistical

119 constraints and difficulty predicting relatively brief breeding activity, and they rarely account for

120 imperfect detection when estimating demographic rates (i.e., the probability that breeding

121 occurred but was not observed via sampling methods: MacKenzie et al. 2002; Kéry et al. 2009).

122   There is clearly both a need and an opportunity to better estimate gopher frog breeding

123 dynamics across broader scales. In this study, we applied an occupancy modeling framework to

124 estimate gopher frog breeding dynamics, which integrated multiple datasets collected across the

125 species' range under different sampling intensities. Our objectives were (i) to estimate the

126 influence of terrestrial and aquatic habitat factors and weather on seasonal breeding probabilities,

127 and (ii) to use those estimates to characterize seasonal, annual, and regional breeding dynamics

128 at the metapopulation scale over a 10-yr period. This analysis builds on previous collaborative

129 research between the University of Georgia and State, Federal, and other partners to develop

130 status and decision models for at-risk amphibian and reptile species in the longleaf pine system.

131 Previous work on gopher frogs included predicting habitat suitability across the species' range

132 (Crawford et al. 2020a), a multi-partner decision-making workshop run by the National

133 Conservation Training Center (USFWS), and additional expert elicitation efforts estimating

134 persistence under current conditions and potential management scenarios.

135

136 <div align="center">**Methods**</div>

137 **Study system and extent**

138 The study extent encompassed 192 ephemeral to semi-permanent wetlands sampled across the

139 southeastern coastal plain in Alabama, Florida, Georgia, North Carolina, and South Carolina in

140 the United States (Figure 1) that were known or expected to have historical or recent gopher frog

141 breeding. Sampled wetlands were typically isolated, ephemeral, and had open canopies

142 (Greenberg 2001; Humphries and Sisson 2012; Enge et al. 2014). The surrounding uplands

143   varied across the species' range but included pine savannas, scrub, flatwoods, and sandhill

144   habitats with well-drained, sandy soil, low canopy cover, high herbaceous ground cover, and

145   adequate density of refugia such as gopher tortoise *Gopherus polyphemus* burrows or stump

146   holes (Greenberg 2001; Roznik et al. 2009; Humphries and Sisson 2012; Enge et al. 2014; Smith

147   et al. 2020).

148   Recognizing that gopher frogs can exist in metapopulations of connected wetlands and

149   uplands (Greenberg 2001; Roznik et al. 2009; Humphries and Sisson 2012), we delineated

150   metapopulation boundaries *i* by buffering all sampled wetlands *j* and additional terrestrial gopher

151   frog locations (Crawford et al. 2020a) within 3.5 km of each other corresponding to the longest

152   known movement distance (Humphries and Sisson 2012). We subdivided the polygons by

153   features believed by species experts (see Acknowledgments for list of experts and institutions

154   from which communications were obtained in 2019 and 2022) to represent significant barriers to

155   movement, such as corridors of unsuitable habitat or major roads (Figure 1 inset shows seven

156   metapopulations, where five that occur as a contiguous cluster are nevertheless assumed to be

157   demographically isolated from one another). These steps yielded 67 metapopulations (Figure 1).

158   Although some metapopulation boundaries only contained one sampled wetland (see Results),

159   we assumed other non-sampled wetlands could exist and referred to these as metapopulations.

160   Still, we believed the sampled wetlands to be the primary breeding sites within each

161   metapopulation boundary based on previous ground surveys and aerial imagery. We performed

162   all spatial analyses in ArcGIS version 10.4 (ESRI, Redlands, CA).

163

164   **Sampling design**

165 This study integrated independent detection-non-detection and covariate datasets (S2-7)

166 collected by State wildlife agencies and other researchers in all five States to estimate gopher

167 frog breeding dynamics using an occupancy modeling framework (MacKenzie et al. 2002; Royle

168 and Kéry 2007). Although some sampling design components varied between Florida and non-

169 Florida datasets (described below), some methods were consistent. All researchers collected data

170 of evidence of gopher frog breeding – defined as observing egg masses or tadpoles – obtained

171 from timed dipnet and visual surveys of focal wetlands. We structured observation data collected

172 in sampling occasion k into seasons t (an index for the combination of year and season) using the

173 following season designations: Spring (1 Mar – 31 May), Summer (1 Jun – 31 Aug), Fall (1 Sep

174 – 30 Nov), and Winter (1 Dec – 28 Feb). We defined a year as 1 September – 31 August.

175 Although breeding can occur year-round, especially in lower latitude or more coastal locations

176 (Enge et al. 2014), summer through early fall generally represents the period of driest conditions

177 and lowest breeding activity that can serve as a reasonable division between one annual term and

178 the next in our model. Season designations aligned with how researchers often structured their

179 monitoring efforts, such that wetlands were targeted for sampling at least once per season. The

180 pooled dataset constituted sampling between Fall 2009 and Summer 2019 (40 seasons, across 10

181 years in total), but each wetland was not sampled every season or year. Researchers noted if

182 wetlands were dry during any visit.

183   We obtained more detailed detection-non-detection data from the Florida Fish and

184 Wildlife Conservation Commission (FWC: Data S1). Researchers from FWC sampled 96

185 wetlands (grouped into 48 metapopulations) between Fall 2015 and Fall 2018, and they recorded

186 detection-non-detection data from repeat samples of wetlands within a given season. Sampling

187 was sometimes conducted with multiple observers simultaneously dipnetting random areas of a

188   wetland that we treated as separate samples within the same season for this study. Samples taken

189   by different observers on the same day or on different days within a season were treated equally

190   as secondary sampling events. Many wetlands were large (between 1 and 47 ha) and remote,

191   posing logistical constraints for field surveys, so researchers often used spatial replication (as

192   opposed to temporal replication) of sampling random locations within a wetland during one visit

193   to obtain information on detection probability.

194   We also obtained detection-non-detection data from State agencies and additional

195   researchers in Alabama, Georgia, North Carolina, and South Carolina (Data S2). These groups

196   performed opportunistic sampling of 96 wetlands (grouped into 19 metapopulations) between

197   Fall 2009 and Summer 2019. Non-Florida datasets included season- and wetland-specific

198   observations (i.e., whether evidence of breeding was observed), but researchers did not record

199   how many times they visited each wetland each season (see below).

200

201   **Environmental covariates**

202   We collected several spatial and temporal covariates during field sampling and previous work

203   that could influence breeding dynamics. We assigned each metapopulation to one of seven

204   regions (Figure 1), which were used when summarizing breeding patterns. In Florida, we

205   assigned sites to one of four regions representing NOAA Climate Divisions

206   (https://www.ncdc.noaa.gov/monitoring-references/maps/us-climate-divisions.php [April 2022]).

207   Climate Divisions represent areas of similar patterns of temperature, precipitation, drought, and

208   other climatic factors, based on long-term data. Using Climate Divisions as regions outside of

209   Florida would have resulted in some regions containing only one or two wetlands. Therefore, we

210   assigned sites outside of Florida into one of three larger regions representing grouped EPA IV

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211   ecoregions (https://www.epa.gov/eco-research/ecoregions [April 2022]) that had similar

212   ecological and climatic characteristics. We captured site quality, which may influence breeding

213   rates, by calculating the mean habitat suitability index (HSI: 0 – least suitable; 1 – most suitable

214   habitat) within a 1-km buffer of a wetland using predictions from a habitat suitability model

215   (Crawford et al. 2020a). We chose this buffer size to capture habitat quality in the wetland and

216   adjacent uplands while minimizing overlap between buffers of nearby wetlands. HSI for gopher

217   frog habitat was positively influenced by mean soil drainage, compatible land cover (evergreen

218   forest, mixed forest, shrub/scrub, grassland/herbaceous, and barren land), and fire frequency in

219   the surrounding neighborhood, which ranged from 500 to 2,000 m, depending on the predictor

220   (Crawford et al. 2020a).

221   We collected additional covariates at each wetland that could vary across seasons and

222   sampling occasions that may influence breeding dynamics. At each sampling occasion, FWC

223   researchers recorded the presence of fish, which can increase tadpole predation risk and decrease

224   the probability of tadpoles surviving to metamorphosis. Fish were originally identified to species,

225   but we pooled data to indicate detection of any species, which included predatory fish (e.g.,

226   warmouth *Lepomis gulosus*) as well as gape-limited fish that may only deprecate eggs and small

227   larva (e.g., eastern mosquitofish *Gambusia holbrooki*). Data indicated high detection probability

228   for fish (i.e., fish were often detected in all or no samples within a season), so we fixed fish

229   presence across all sampling occasions within a season as 0 when fish were not detected and 1

230   otherwise. For non-Florida sites that did not collect fish presence data, we imputed fish presence

231   each season using a Bernoulli trial with a probability of 0.5. We used the Climate Engine Portal

232   (https://clim-engine.appspot.com/climateEngine [April 2022]) to download raster datasets

233   summarizing remotely-sensed climatic conditions for each season within the study period for all

234   wetlands. We obtained raster data for mean Standardized Precipitation Index (SPI), which

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235   measures the deviation of amount of rainfall in a specific period of a year (e.g., March – May

236   2010) relative to the distribution of rainfall in that same period across many years (McKee et al.

237   1993). We obtained rasters that calculated SPI for each season relative to long-term climate data

238   from 1980 to 2019. Gopher frogs have a relatively long larval period of approximately 90 to 120

239   days (Semlitsch et al. 1995). Because climatic conditions favorable for breeding in the months

240   preceding and during the season when sampling was conducted may influence the probability of

241   breeding and presence of egg masses and tadpoles, we developed a final covariate dataset where

242   the seasonal SPI represented climate conditions in the sampling season and the one prior (i.e., a

243   6-mo window). Climate rasters were available at a 4-km resolution, and we extracted seasonal

244   climate values for each wetland.

245

246   **Integrated occupancy model for breeding dynamics**

247   We developed an integrated model using an occupancy framework to estimate seasonal, annual,

248   and regional responses in gopher frog breeding as a function of wetland- and season-specific

249   covariates. We used a hierarchical state-space formulation fitted in a Bayesian framework (Royle

250   and Kéry 2007; Kéry and Schaub 2012) that separately accounted for the ecological processes of

251   breeding and the observation process of detection, thereby reducing bias and increasing precision

252   of estimates (MacKenzie et al. 2003; Clark and Bjørnstad 2004; Kéry et al. 2009). Specifically,

253   we estimated the breeding probability for wetland j during season t ($\theta_{j,t}$), and detection

254   probability $p_{j,t,k}$ during sampling occasion k, given that breeding occurred at a wetland in season

255   t. We assumed closure (i.e., the breeding state of each wetland did not change) within seasons

256   but not between seasons following the "robust design" (Pollock 1982; Kendall et al. 1995)

257   implementation of state-space dynamic occupancy models (Royle and Kéry 2007).

258   We modeled the breeding state history ($z_{j,t}$) of each wetland j for each season t using a

259   Bernoulli trial with a seasonal wetland-specific breeding probability $\theta_{j,t}$, where a wetland could

260   have breeding ($z_{j,t} = 1$) or not ($z_{j,t} = 0$). We estimated breeding probability from a logit-linear

261   model of wetland- and season-specific covariates using the relationship

262    $\text{logit}(\theta_{j,t}) = \mu_{breed} + \beta_{fish}FISH_{j,t} + \beta_{HSI}HSI_j + \beta_{SPI}SPI_{j,t} + \beta_{HSI.SPI}HSI_j \cdot SPI_{j,t} +$

263    $$\beta_{lag}z_{j,t-1} + \varepsilon_i \qquad (1)$$

264   where estimated parameters were μ_{breed} (intercept), β_{HSI} (fixed effect for HSI, multiplied by

265   wetland-specific mean HSI), β_{fish} (fixed effect for fish presence, multiplied by fish presence [0

266   or 1] in each wetland and season), β_{SPI} (fixed effect for SPI, multiplied by SPI [mean SPI across

267   the season and season prior] in each wetland and season), $\beta_{HSI.SPI}$ (fixed effect for the interaction

268   between HSI and SPI), β_{lag} (fixed effect for breeding state in the season prior to represent

269   temporal autocorrelation across seasons, multiplied by the breeding state in the season prior in

270   each wetland [$z_{j,t-1}$]), and ε_i (random metapopulation effect). We included the interaction term to

271   test the hypothesis that suitable habitat surrounding a wetland may influence hydroperiod and

272   breeding opportunities, especially in drier seasons. The random metapopulation effect was drawn

273   from a zero-centered normal distribution with variance parameter σ_i^2, where all wetlands within

274   a metapopulation shared the same value. We assumed breeding did not occur ($z_{j,t} = 0$) when we

275   observed wetlands were dry during a season and supplied this information as known states within

276   the model. We intended to include a fixed effect for region, but preliminary models with this

277   effect showed poor convergence and produced unreliable estimates. This outcome may have

278   been due to the relatively small number of sampled wetlands, metapopulations, and occasions

279   from some regions, as well as modest collinearity between region and SPI. Therefore, we

280   removed the fixed region effect from the final model structure.

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281   We modeled the observation state histories ($y_{j,t,k}$) of each wetland for each sampling

282   occasion k as a Bernoulli random variable with probability of detecting at least one gopher frog

283   egg mass or larva during a dipnet survey $p_{j,t}$. We modeled the observation process as conditional

284   on the breeding state of a given wetland and season. Gopher frogs could be observed ($y_{j,t,k} = 1$) or

285   not observed ($y_{j,t,k} = 0$) if breeding had occurred in the wetland that season. If breeding did not

286   occur in the wetland that season, frogs would not be observed ($y_{j,t,k} = 0$) for all sampling

287   occasions that season. Because data were too sparse to support estimation of all $p_{j,t}$ separately

288   and since non-Florida datasets did not include information on number of occasions wetlands

289   were sampled during a season, we modeled detection differently for Florida and non-Florida

290   wetlands where

291
$$p_{j,t} = \begin{cases} p & \text{for Florida wetlands} \\ 1 - (1-p)^{K_{j,t}} & \text{for non-Florida wetlands} \end{cases} \qquad (2)$$

292   We constrained detection probability (p) to be constant across all Florida wetlands and sampling

293   occasions, and we used p in a cumulative seasonal detection probability for non-Florida

294   wetlands, where $K_{j,t}$ is a random variable representing the number of sampling occasions (1, 2, 3,

295   or 4) within a season at a wetland modeled as a categorical distribution with probabilities 0.4,

296   0.3, 0.2, and 0.1, respectively. We chose these probabilities in consultation with data collectors to

297   approximately represent sampling effort.

298   The model framework required a few key assumptions. Although gopher frogs typically

299   exist in metapopulations with multiple, connected wetlands, we estimated breeding dynamics at

300   the wetland level without explicitly capturing processes in metapopulation models (e.g., patch-

301   specific movement probabilities: Royle and Dorazio 2008). Most metapopulations in our study

302   only included one sampled wetland (see Results), so we included a random metapopulation

303   effect to implicitly account for variation in dynamics that may influence the overall probability

13

304   of breeding at wetlands within a metapopulation. Our model also assumed metapopulations were

305   persisting across the study period (i.e., breeding was possible each season, when wetlands were

306   not dry) and lacked mechanisms for site survival (1 − extinction) and recolonization typical of

307   dynamic occupancy models (MacKenzie et al. 2003; Bailey et al. 2004; Royle and Kéry 2007;

308   Kéry et al. 2010). Preliminary models that included site survival and recolonization parameters

309   showed poor convergence and produced unreliable estimates that predicted entire

310   metapopulations were becoming extirpated and recolonized multiple times within the 10-yr study

311   period. We know that a failure to observe breeding at focal wetlands could be the result of

312   wetlands not filling sufficiently, individuals migrating to proximate alternate breeding sites

313   (Petranka et al. 2004), or most individuals skipping breeding (Bailey et al. 2004; Church et al.

314   2007; Muths et al. 2010; Muths et al. 2013; Cayuela et al. 2014). Gopher frogs can likely live 6-

315   10 years, similar to longevity estimates of congeners (Richter and Seigel 2002). For these

316   reasons and because metapopulations were separated by long distance (> 7 km) or physical

317   barriers, it was more reasonable to assume gopher frogs were persisting within a metapopulation

318   boundary throughout the study period but exhibiting high year-to-year variation in breeding

319   rather than experiencing multiple extirpation and recolonization events within a 10-yr period.

320   We fit the integrated model using a Bayesian framework with Markov chain Monte Carlo

321   (MCMC) methods in JAGS (Plummer 2003) called from R (R Core Team 2019) via the R2jags

322   package (Su and Yajima 2012). We assigned vague prior distributions for all parameters and

323   hyperparameters governing random effects: breeding probability intercept (expressed on the

324   probability scale) and detection probability – Uniform(0,1); breeding probability covariate

325   parameters (logit scale) – Normal(mean=0, precision=0.37); hyperparameter (standard deviation)

326   governing the random metapopulation effect − Uniform(0,5) (see model code in Data S7 for

14

327   details). We generated three MCMC chains using 150,000 iterations where we retained the last

328   10,000 iterations, yielding a final set of 30,000 samples from posterior distributions of the

329   parameters. We assessed convergence for all models by visually inspecting chain mixing in

330   MCMC trace plots, confirming unimodality in posterior distribution plots, and verifying Brooks-

331   Gelman-Rubin statistics < 1.1 for all parameters. We based parameter inferences on posterior

332   means and 95% Bayesian credible intervals (BCIs; 2.5th − 97.5th percentile of the distribution).

333   We used model outputs to (i) estimate the breeding frequency (the proportion of years

334   with breeding over the 10-yr study period) for each metapopulation, (ii) characterize seasonal,

335   annual, and regional patterns in breeding, and (iii) inform sampling design for potential future

336   monitoring. In each MCMC iteration of the model, we recorded whether breeding occurred at

337   any wetland within a metapopulation within each year (Fall through Summer) and calculated the

338   proportion of years out of 10 with breeding. We used all retained iterations to calculate the mean

339   and 95% BCIs for the predicted breeding frequency of each metapopulation. Next, we calculated

340   the mean and 95% BCIs for the proportion of wetlands in each region predicted to have had

341   breeding during each season. Lastly, we used model outputs to inform future monitoring by

342   estimating the probability of committing a type II error (failing to detect breeding when it

343   occurred), given varying sampling effort and prior breeding probabilities. We calculated the

344   probability of detecting gopher frogs at a theoretical wetland where breeding had occurred at

345   each of one to five samples (K) as $p^* = 1 - (1 - p)^K$, where p is the estimated mean detection

346   probability in our study (MacKenzie et al. 2006). We then calculated conditional probabilities

347   (θ_{cond}) that a wetland had gopher frog breeding that went undetected after one to five samples

348   using Bayes theorem:

$$\theta_{cond} = \Pr(breeding|undetected) = \frac{\theta(1-p^*)}{\theta(1-p^*)+(1-\theta)} \qquad (3)$$

15

350   where θ represented prior breeding probability (either 0.2, 0.5, or 0.8). We calculated conditional

351   breeding probabilities using the mean and 95% BCIs estimates for detection probability, and we

352   used the conditional breeding probabilities to evaluate the minimum number of samples needed

353   to minimize the chance of breeding going undetected at a wetland. See Data S1-7 for our R and

354   JAGS code and associated datasets for the analysis.

355

356   **Results**

357   Of 67 metapopulations, 35 contained one sampled wetland and 32 contained multiple sampled

358   wetlands (range = 2 to 28). The number of wetlands and metapopulations, respectively, in each

359   region was 26 and 14 (Northwest Florida), 27 and 14 (North Florida), 26 and 12 (North Central

360   Florida), 17 and 8 (South Central Florida), 18 and 3 (Upper Coastal Plain [Carolinas]), 59 and 11

361   (Atlantic Coastal Plain [Carolinas]), and 19 and 5 (Upper Coastal Plain [Alabama/Georgia]).

362   Researchers of FWC sampled the 96 Florida wetlands between 0 and 11 times within a season

363   between Fall 2015 and Summer 2018, and the mean total number of samples per wetland over

364   the four-yr period was 21.9 (range = 9 to 37). For the 96 non-Florida wetlands, the mean number

365   of seasons sampled was 10.5 (range = 1 to 33, out of 40). Over all of the metapopulations

366   studied, gopher frogs were detected on average during 4.16 samples (range = 0 to 25) at a

367   wetland within the study period. Mean HSI of wetlands was 0.67 (range = 0.02 to 1.00). Mean

368   seasonal SPI of wetlands was 0.16 (range = -3.07 to 3.10).

369   Estimated breeding probability varied considerably by wetland and season and was

370   negatively correlated with fish presence and positively correlated with SPI and prior season

371   breeding state (Table 1). The effect of HSI on breeding was not as strong as other predictors, but

372   we saw some support for an interaction between HSI and SPI (Table 1, Figure 2), indicating that

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373   strength of relationship with SPI depended on HSI. The direction of the interaction effect

374   resulted in wetlands with high HSI predicted to have higher breeding probabilities, relative to

375   wetlands with low HSI, during drought conditions (i.e., lower SPI), but this difference became

376   negligible as SPI increased. The estimated mean detection rate from a sample was relatively high

377   (0.69).

378   Estimated breeding dynamics varied seasonally, annually, and regionally (Figure 3).

379   Mean estimated breeding frequency within the 10-yr study period of sampled wetlands was 0.49

380   (range = 0.11 to 0.93); mean estimated breeding frequency of metapopulations was 0.68 (range =

381   0.00 to 1.00). Mean predicted breeding frequencies within the 10-yr study period were within the

382   ranges 0-0.19, 0.2-0.49, 0.5-0.79, and 0.8-1.0 for 6, 13, 16, and 32 metapopulations, respectively.

383   The skewed distribution of metapopulations in the highest breeding frequency category occurred

384   because we calculated breeding frequency as the number of years when breeding was predicted

385   at any wetland within a metapopulation, and 32 of 67 metapopulations contained multiple

386   sampled wetlands. The percentage of wetlands predicted to have breeding varied by year and

387   season but was often highest in Winter and Spring across the species' range (Figure 3). Within a

388   single year cycle (Fall to Summer), mean predicted breeding was highest most often in Winter or

389   Spring in northern (non-Florida) regions. Conversely, some Florida regions had noticeable

390   predicted peaks of breeding in Fall in some years, while breeding was more dispersed across all

391   seasons in other years for North, North Central, and South Central Florida regions (e.g., breeding

392   was highest in Summer, relative to other seasons in a year cycle, for 4 out of 10 years in the

393   study period for these regions: Figure 3). Peaks in predicted breeding often occurred during or in

394   the season following high rainfall events when SPI was high. For example, the increased

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395   percentage of wetlands with breeding between Fall 2017 and Spring 2018 in multiple Florida

396   regions corresponded with Hurricane Irma impacting that area in Fall 2017.

397   Using the estimated detection probability when conducting a sample (timed dipnet

398   sampling and visual surveying), we found that the minimum number of samples needed to

399   achieve a < 5% probability of breeding going undetected at a wetland depended on prior

400   breeding probability of a site (Figure 4). Two samples were necessary to achieve a <5%

401   probability of failing to detect breeding when prior breeding probability was 0.2; three samples

402   were needed when prior breeding probability was 0.5; and four samples were needed when prior

403   breeding probability was 0.8. In other words, these findings reflect the number of samples

404   needed to be 95% confident that breeding has not occurred when gopher frogs are not observed.

405

406   **Discussion**

407   Our work contributes an approach for leveraging multiple available datasets collected by

408   different partners across a species' range – even when sampling timing and frequency vary – to

409   improve estimation of population parameters of interest. It is our experience that State and

410   Federal agencies and other partners often collect datasets for pond-breeding amphibians and

411   other species of concern within their separate jurisdictions that may be compatible for unified

412   analyses similar to those undertaken in this study. Recent efforts have successfully coordinated

413   partners and developed appropriate modeling frameworks for these contexts (e.g., Ahrestani et

414   al. 2017; Crawford et al. 2020b; McGowan et al. 2020). Our study also advanced previous work

415   on gopher frogs by estimating the influence of climatic and wetland-specific factors on breeding

416   dynamics over a 10-yr period and across the species' range, which can directly inform site-level

417   management and future models predicting persistence of gopher frog metapopulations. We found

418   that (i) breeding probability at a wetland was positively influenced by seasonal precipitation and

419   negatively influenced by fish presence, (ii) there was some evidence that wetlands surrounded by

420   higher quality terrestrial habitat may have increased breeding probability during drought

421   conditions, (iii) the percentage of sampled wetlands predicted to have breeding varied seasonally,

422   annually, and regionally across the study, but peaks of breeding in most regions occurred in

423   Winter and Spring and often following high rainfall events (e.g., hurricanes) – with more

424   dispersed breeding across seasons in regions in the Florida Peninsula, and (iv) sampling wetlands

425   two to four times within a short period where closure can be assumed (e.g., a few days),

426   depending on prior probability of breeding at a site, can sufficiently reduce the probability of

427   failing to detect breeding events.

428   Our results offer insights into the effects of climate, habitat, and other wetland-specific

429   factors on gopher frog breeding dynamics that support previous findings of several studies

430   conducted at smaller temporal or spatial scales. Estimated positive relationships between

431   seasonal precipitation (captured with Standardized Precipitation Index in this study) and

432   breeding success agree with previous findings for gopher frogs (Palis 1998; Jensen et al. 2003)

433   and other ephemeral pond-breeding amphibians (e.g., yellow-bellied toad *Bombina variegata*:

434   Cayuela et al. 2014). Future precipitation patterns will likely influence or restrict successful

435   breeding opportunities for gopher frogs and other pond-breeding amphibians, but these patterns

436   are uncertain in the Southeast. Greenberg et al. (2015) predicted future precipitation and other

437   climatic factors would shorten hydroperiods for ephemeral wetlands in Florida, whereas

438   Keellings and Engström (2019) predicted increased rainfall and decreased number of consecutive

439   dry days throughout most of the gopher frog's range, but we note the latter study did not include

440   other climatic factors (e.g., temperature) that may influence hydroperiod. Additionally, increased

441   rainfall and flooding events could increase the frequency that isolated wetlands become

442   temporarily connected to other waterbodies and colonized by fish. Invasive (e.g., African

443   jewelfish *Hemichromis letourneuxi*) and other predatory fish have already been detected in

444   gopher frog wetlands following floods in southern Florida (AHG, pers. observation.).

445   We found some evidence that the effects of seasonal droughts could be mitigated by

446   increasing habitat suitability within and around wetlands. Specifically, high HSI of the

447   surrounding landscape – characterized by well-drained sandy soils, open-canopied land cover

448   types (evergreen or mixed forest, shrub/scrub, grasslands), and frequent fires (Crawford et al.

449   2020a) – tended to increase the breeding probability during drier periods (when SPI was

450   negative: Figure 2). Burrow and Maerz (2021) demonstrated experimentally that shading and

451   hardwood leaf litter – which occur with succession within wetland basins when fire is excluded

452   and/or suppressed – interact to extend the larval period of gopher frogs, making them more

453   susceptible to wetland drying. Greenberg (2001) observed that metamorph recruitment was

454   significantly lower in wetlands where hardwoods had invaded wetland basins. We also expect

455   that upland habitat suitability, including the maintenance of high densities of refugia (e.g.,

456   tortoise burrows, mammal burrows, and stump holes) and ground cover, has a strong effect on

457   gopher frog survival in terrestrial stages (Roznik and Johnson 2009; Roznik et al. 2009;

458   Humphries and Sisson 2012; Burrow 2021; Burrow et al. 2021). The terrestrial stages of many

459   pond-breeding amphibians are key "storage" phases for populations to withstand episodic

460   droughts that limit breeding success (Taylor et al. 2006); therefore, habitat conditions that

461   increase terrestrial fitness of gopher frogs may be more likely to sustain some breeding success

462   during drier years and lead to resilient populations. Future field research measuring habitat

463   effects on demographic rates could complement future models that separate population

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464   persistence and breeding dynamics to better characterize the effects of climate and terrestrial and

465   aquatic habitat conditions on those dynamics.

466   Similar to our study, Cayuela et al. (2014) found breeding success in one season was

467   positively influenced by the breeding state in the previous season. This may be – in part – an

468   artifact of the length of gopher frog larval periods (approximately 90 to 120 days: Semlitsch et

469   al. 1995) relative to the typical length of a "season" in our model (89 to 91 days). It is reasonable

470   that successful breeding in one season would provide tadpoles to be detected in the subsequent

471   season. This does not preclude the possibility that breeding rates in consecutive seasons and

472   years are not independent due to natural cycles of adult abundance, density-dependent mortality

473   of tadpoles (Greenberg 2001), high mortality of first-time breeding adult cohorts (V. Terrell,

474   University of Georgia, unpublished data, 2022), and the propensity for adults to skip breeding

475   seasons, which has been observed among many other amphibians (Bailey et al. 2004; Church et

476   al. 2007; Muths et al. 2010; Muths et al. 2013; Cayuela et al. 2014). Future work could estimate

477   factors that determine the effects of past breeding (e.g., during any season in the previous year)

478   on subsequent breeding while also estimating other demographic processes to better capture

479   longer-term population cycles.

480   The percentage of sampled wetlands predicted to have breeding varied seasonally,

481   annually, and regionally across the study. Peaks of breeding in most regions occurred in Winter

482   and Spring corresponding with high seasonal rainfall, which is consistent with previous studies

483   of gopher frog breeding activity (Palis 1998; Enge et al. 2014). The 10-yr period of our study

484   also highlighted the association between peak gopher frog breeding events to peak rainfall events

485   in certain years and regions, such as the peak of breeding in multiple regions in Florida in Fall

486   2017 to Spring 2018 that corresponded with Hurricane Irma (Figure 3). Breeding tended to be

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487   more evenly dispersed across seasons for North, North Central, and South Central Florida

488   regions: these regions had noticeable predicted peaks of breeding in Fall in some years, and

489   breeding was highest in Summer, relative to other seasons in a year cycle, for 4 out of 10 years in

490   the study period for these regions (Figure 3). These breeding patterns in the Florida Peninsula

491   corroborate previous findings documenting frequent breeding across all seasons in this area

492   (Enge et al. 2014). We also note that no distinct peaks of breeding were predicted for the Atlantic

493   Coastal Plains (Carolinas) region. This region had substantially more wetlands than any other

494   region, so the trend of lower season-to-season variation may reflect a degree of population and

495   regional resilience where breeding is likely to occur in at least some wetlands each season.

496   Across the study period, mean predicted annual breeding frequency of metapopulations

497   was high, on average (0.68), and greater than 0.8 for 32 of 67 metapopulations. We note that

498   surveyed metapopulations tended to be "strongholds" for the species where semi-consistent

499   breeding activity had been observed previously on sites located on public or private lands

500   managed for wildlife conservation. Other multi-year studies of gopher frogs have observed lower

501   breeding frequencies (0.06-0.67) among years at wetlands, but they did not account for detection

502   probability. Regardless, they have suggested that, although metapopulations could be stable over

503   long periods with infrequent breeding and recruitment, these conditions likely increase the risk of

504   local extirpation (Semlitsch et al. 1995; Greenberg 2001).

505   Recent work has demonstrated the value of developing integrated models that leverage

506   multiple available datasets for data-limited species (Crawford et al. 2018; Robinson et al. 2018;

507   Zipkin and Saunders 2018; Crawford et al. 2020b). Integrating multiple datasets in unified

508   analyses can increase precision of estimates, reduce effects of potential bias of individual

509   datasets, and allow for estimation of additional parameters of interest (Schaub and Abadi 2011;

510 Zipkin and Saunders 2018). However, developing integrated analyses requires that the

511 underlying demographic processes and observation protocols are shared across datasets, or that

512 ancillary information is available to analytically resolve differences among datasets. A key

513 assumption of our model was that sampling protocols (and the probability of detecting egg

514 masses and tadpoles with a sample) were equivalent across sites that were sampled by different

515 partners. We confirmed that partners used standard dipnet and visual surveys at all sampled sites,

516 but we were not able to incorporate additional details related to sampling (e.g., sampling time)

517 into the analysis. We also had to include uncertainty around the number of samples per season at

518 all wetlands outside of Florida because partners did not record this information systematically.

519 Our analysis overcame these data gaps in non-Florida samples by leveraging information from

520 Florida samples that aided in estimation of detection probability. However, more accurate

521 estimates of breeding dynamics and other population parameters can be achieved if partners

522 conducting sampling, including Federal and State agencies, systematically document and store

523 detection-non-detection data and additional information related to sampling each time a wetland

524 is visited. We hope this study illustrates the importance of keeping records of sampling efforts

525 and findings for future needs.

526   Larger-scale monitoring programs often collect detection-non-detection data of species of

527 interest using spatial replication (i.e., observers sample multiple areas at one time within a site)

528 rather than temporal replication (i.e., observers repeatedly sample one or more areas within a

529 site) in cases where limited monitoring resources prevent repeated visits to large, remote sites.

530 Estimates of detection and occupancy are prone to bias when spatial replication is used in place

531 of temporal replication; however, bias is negligible under certain sampling and ecological

532 contexts (MacKenzie et al. 2006; Kendall and White 2009; Hines et al. 2010). MacKenzie et al.

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533   (2006) discussed that the use of spatial replication at a single time (e.g., on a single day) leads to

534   negligible bias in model estimates if multiple sample locations within a site are selected at

535   random with replacement (i.e., during selection of random sample locations at a site of interest,

536   any location may be selected by chance for sampling multiple times at the same visit). The FWC

537   dataset satisfies these criteria, as it represents a combination of (i) spatial replication when

538   multiple observers randomly surveyed different areas of a wetland on a single day and (ii) for a

539   subset of wetlands, temporal replication when one or more observers returned to survey a

540   wetland (including resampling the same areas) later within the closed season. Bias from

541   substituting spatial for temporal replication is also minimal when the modeled species is highly

542   mobile or distributed randomly across sampling locations within a site, which allows some

543   probability of observing all detection histories within a season (Kendall and White 2009; Hines

544   et al. 2010). Although localized patchiness of gopher frog egg masses and tadpoles can occur

545   during breeding events with a low number of breeders, our partnering species experts indicated

546   that egg masses can be distributed widely across a wetland (see Acknowledgments for list of

547   experts). Given the contexts of data collection and species' ecology in our study, we expect bias

548   of model estimates to be inconsequential. For monitoring data from other contexts that used

549   spatial replication without replacement or surveyed less mobile species, our model would likely

550   overestimate occupancy (i.e., breeding) probability. Other model structures could be used in

551   these contexts to account for potential biases (see Hines et al. 2010). For example, estimating

552   occupancy with time-to-detection methods – where detection probability is estimated using the

553   time between the start of a survey and first observation of the species – provides an efficient

554   alternative with similar performance to methods using temporal replication for a variety of

555   ecological contexts, although these methods performed best for widespread species with high

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556 detection probabilities similar to our study (Halstead et al. 2021). Future monitoring efforts could

557 collect data using spatial replication with replacement, which (i) efficiently uses resources even

558 under logistical challenges of field surveys and (ii) minimizes bias of population parameters that

559 can inform conservation decisions (Kendall and White 2009).

560   Our analysis had limitations that should be considered when interpreting the results. Our

561 data were insufficient to construct a model that could reliably separate breeding dynamics from

562 metapopulation persistence or other mechanisms typical of metapopulation models (e.g.,

563 wetland-specific immigration and extinction rates). We assumed that populations were persisting

564 over the 10-yr period and breeding could potentially occur. Gopher frogs have an expected

565 lifespan of 6-10 years and were detected at least once during the study in 56 of 67

566 metapopulations, which supported the assumption of persistence at most sites. The 11

567 metapopulations where gopher frogs were not detected had only one or two sampled wetlands,

568 no other known breeding sites, and estimated breeding frequencies of < 0.3 (i.e., < 3 out of 10

569 years with breeding). Although it is possible that gopher frogs used non-sampled, nearby

570 wetlands for breeding during this period, it is likely that some of these metapopulations are

571 extirpated, given that partners have observed degraded wetland and upland habitat conditions

572 and no detections of gopher frogs during additional surveys at some of these sites. Including

573 extirpated metapopulations in our analysis could have potentially underestimated detection and

574 overestimated breeding probabilities; however, we believe any bias introduced by their inclusion

575 was limited since only 166 of 2,910 surveys (5.7%) came from wetlands in the 11 potentially

576 extirpated metapopulations.

577   Although sampled wetlands represented what partners believed were the primary

578 breeding sites within metapopulation boundaries based on previous monitoring and habitat

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579 characteristics, the true number of potential breeding wetlands was unknown. Therefore, we

580 included a random effect in the model to account for metapopulation-to-metapopulation variation

581 in number of breeding wetlands and other factors that may influence breeding dynamics but were

582 not explicitly captured. We also note that egg and tadpole observation data used in this study is

583 informative about breeding dynamics and adult occupancy, but additional information about

584 direct rates of recruitment into terrestrial life stages would help determine if individual breeding

585 wetlands are serving as population sources or sinks, which could better inform management

586 decisions. Otherwise, the presence of declines might be masked by unsuccessful breeding

587 attempts of long-lived adults. Future efforts could use an integrated modeling framework that

588 operates over multiple scales of effort to estimate persistence and other metapopulation

589 dynamics; for example, detection-non-detection data from dipnet sampling of many wetlands and

590 metapopulations could be leveraged with capture-mark-recapture data from a subset of

591 metapopulations (Schaub and Abadi 2011; Zipkin and Saunders 2018).

592   Our results have direct applications for site-level monitoring and management aimed at

593 increasing successful breeding opportunities of gopher frogs and other associated pond-breeding

594 amphibians. First, partners could tailor monitoring of breeding activity to align with predicted

595 seasonal peaks and conduct two to four samples within a season (ideally within a few days when

596 population closure can be assumed), depending on prior knowledge or estimates of breeding

597 frequency at a site, to minimize the probability of missing breeding events. Because gopher frog

598 wetlands are often dispersed across a state or region making it logistically difficult to monitor

599 with repeated visits, conducting two to four samples could be accomplished using multiple

600 observers during a single visit, if sample locations can be selected randomly with replacement.

601   Second, partners can consider efforts to monitor and prevent fish colonization or remove

602   fish when detected in known gopher frog breeding wetlands. Limiting fish presence in ephemeral

603   breeding wetlands has become an interest of amphibian conservation efforts by our partnering

604   species experts and their management partners (see Acknowledgments for list of experts), as

605   predatory and invasive fish are commonly detected in wetlands (Enge et al. 2014) and predation

606   can decrease egg and larval survival (Gregoire and Gunzburger 2008). In some cases, this may

607   require hydrological restoration of uplands or wetlands, if ditching or other alterations have

608   increased fish colonization or lengthened the wetland hydroperiod. Removal of invasive and

609   predator fish with piscicides (e.g., rotenone), applied carefully when rare amphibians are absent

610   from the wetland to avoid non-target mortality of amphibians (e.g., Shulse and Semlitsch 2014),

611   is a strategy under consideration in some conservation efforts.

612   Third, our analysis suggests that improving upland habitat conditions surrounding

613   breeding wetlands by providing a relatively open canopy and midstory with mechanical removal

614   or prescribed fire may increase wetland hydroperiods in periods of drought and provide more

615   opportunities for successful breeding (Chandler et al. 2017; Simpson et al. 2021). This may be

616   particularly important for gopher frogs as increasing temperatures and changes in the hydrologic

617   cycle fueled by climate change are predicted to increase the duration and intensity of droughts

618   (U.S. Global Change Research Program [USGCRP] 2018). Furthermore, a recent habitat

619   suitability model classified only 8.6% of habitat with the gopher frog's range as either moderate

620   or highly suitable for the species suggesting a need for habitat restoration throughout the species'

621   range (Crawford et al. 2020a).

622   This work precedes research that will (i) incorporate breeding frequency into a population

623   viability analysis (PVA) for the gopher frog that could be adapted for other pond-breeding

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624 amphibians and (ii) use the PVA to evaluate the effects of stressors and management alternatives

625 on breeding frequency and population persistence to inform conservation decisions at local to

626 range-wide scales. Although we expect the PVA to initially require expert opinion and thus have

627 high uncertainty around certain parameters, effective monitoring of breeding activity using

628 information from this study could allow future predictions of population persistence to be

629 iteratively updated and improved. Rigorous predictions of gopher frog population persistence,

630 which account for breeding dynamics, can inform forthcoming assessments of extinction risk and

631 designation of the species' conservation status by the U.S. Fish and Wildlife Service.

632

633   **Supplemental Material**

634 All data and model code used in this study are provided in Supplemental Material, Data S1 to S7.

635 **Data S1.** Dataframe of detection-non-detection data for Florida wetlands (N = 96) sampled

636 between 2015 and 2018 in the southeastern United States. Fields (columns) include wetland

637 identification number (ID), state name, and detection histories by season and sample for gopher

638 frogs.

639 **Data S2.** Dataframe of detection-non-detection data for non-Florida wetlands (N = 96) sampled

640 between 2009 and 2019 in North Carolina, South Carolina, Georgia, and Alabama in the

641 southeastern United States. Fields (columns) include wetland identification number (ID), state

642 name, and detection histories by season and sample for gopher frogs.

643 **Data S3.** Dataframe of wetland-specific information for sampled wetlands in Florida (N = 96)

644 between 2015 and 2018. Fields (columns) include wetland identification number (ID),

645 metapopulation identification number (Pop_ID), state name, mean Habitat Suitability Index

646 (HSImean_1000), standardized precipitation index data for each season of the study (column

647   names begin with "spi"), the site's regional group for the study (Region), and the site's EPA

648   ecoregion group (EPA_LICAP).

649   **Data S4.** Dataframe of wetland-specific information for sampled wetlands in North Carolina,

650   South Carolina, Georgia, and Alabama (N = 96) between 2009 and 2019. Fields (columns)

651   include wetland identification number (ID), metapopulation identification number (Pop_ID),

652   state name, mean Habitat Suitability Index (HSImean_1000), standardized precipitation index

653   data for each season of the study (column names begin with "spi"), the site's regional group for

654   the study (Region), and the site's EPA ecoregion group (EPA_LICAP).

655   **Data S5.** Dataframe summarizing the year, season, and number of samples for the Florida data

656   (sampled for 96 wetlands between 2015 and 2018).

657   **Data S6.** Dataframe of wetland identification number (ID), state name, and detection histories by

658   season and sample (see column names) for any fish observed during dipnet sampling for Florida

659   wetlands (N = 96) sampled between 2015 and 2018.

660   **Data S7.** R code to reproduce models and outputs for estimating gopher frog *Rana capito*

661   breeding dynamics in wetlands (N = 192) between 2009 and 2019 in the southeastern United

662   States. The code uses all dataframes included in Data S1-6.

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693   purposes only and does not imply endorsement by the U.S. Government.

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871

Table 1. Parameter estimates (means and 95% Bayesian credible intervals [2.5 to 97.5 percentile of the posterior distribution]) from the integrated model using an occupancy framework of gopher frog *Rana capito* breeding in wetlands (N = 192) between 2009 and 2019 in the southeastern United States.

Parameter	Mean	95% BCI
Breeding (seasonal)		
μ_{breed}	0.256	(0.197, 0.316)
β_{fish}	-0.568	(-0.871, -0.286)
β_{HSI}	0.036	(-0.146, 0.222)
β_{SPI}	0.272	(0.144, 0.404)
$\beta_{HSI.SPI}$	-0.073	(-0.209, 0.060)
β_{lag}	1.006	(0.824, 1.189)
σ	0.799	(0.533, 1.127)
Detection		
μ_p	0.694	(0.658, 0.729)

Parameter notations: μ – intercepts for breeding and detection (presented on the probability scale); β – covariate effects on breeding (presented on the logit scale); and σ – standard deviation of the metapopulation random effect on breeding.

872

873 **Figure 1.** Distribution of sampled gopher frog *Rana capito* wetlands (N = 192) between 2009

874 and 2019, grouped into connected metapopulations (N = 67), across seven regions defined by

875 four NOAA Climate Divisions in Florida and groups of similar EPA IV ecoregions in the

876 remainder of the species' range in the southeastern United States. Wetlands (blue) are shown in

877 the inset but not range-wide.

41

878   **Figure 2.** Partial response curves showing the mean (± 95% credible intervals) predicted
879   probability of breeding for gopher frogs *Rana capito* as a function of fish presence, seasonal
880   Standardized Precipitation Index (SPI), and low (left panel) vs. high (right panel) Habitat
881   Suitability Index (HSI) of the area surrounding a wetland in the southeastern United States.
882   These results were based on data from 192 wetlands sampled between 2009 and 2019.

883   **Figure 3.** Mean (± 95% credible intervals) percentage of sampled gopher frog *Rana capito*
884   wetlands (N = 192) with breeding each season (between Fall 2009 and Summer 2019) across
885   seven regions within the species' range in the southeastern United States. Cross marks indicate
886   the mean seasonal Standardized Precipitation Index (SPI) of wetlands in each region. Region
887   abbreviations: UCP (Carolinas) – Upper Coastal Plain in North and South Carolina; UCP
888   (AL/GA) – Upper Coastal Plain in Alabama and Georgia; ACP (Carolinas) – Atlantic Coastal
889   Plain in North and South Carolina; and all others refer to Florida regions based on cardinal
890   directions.

891   **Figure 4.** Probability of failing to detect gopher frog *Rana capito* breeding at a wetland (± 95%
892   credible intervals) after one to five samples, given prior breeding probabilities of a wetland in the
893   southeastern United States. One sample refers to conducting timed dipnet and visual surveys for
894   egg masses and tadpoles. These results were based on data from 192 wetlands sampled between
895   2009 and 2019.

Figure 1. Study site map

Figure 1. Study site map

Figure 2. Response curves

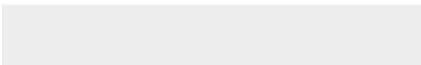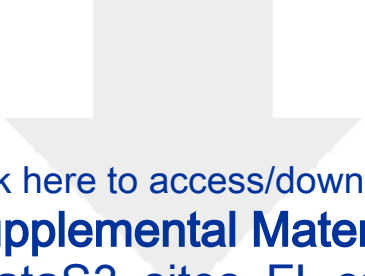Figure 3. Breeding by region_season

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