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Status and Distribution of the Gopher Frog (*Rana capito*) in Florida, USA

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Abstract.—**We determined the occurrence in Florida, USA, of the Gopher Frog (*Rana capito*) primarily by conducting dipnet surveys of 1,330 potential breeding ponds on 113 conservation lands in 44 counties and 23 ponds on private lands in 12 counties. We compared recent and historical records to determine distributional trends, and we developed a Maxent Potential Habitat Model to gain a better picture of its possible distribution in unsurveyed areas. This model identified 1,177,002 ha on the peninsula and 292,751 ha in the Panhandle; 30.1% of the habitat was on conservation lands. While conducting dipnet surveys, we found Gopher Frog tadpoles in 356 ponds on 59 conservation lands in 31 counties and in six ponds on private property in five counties. Across public and private property, dipnet surveys found 294 new breeding ponds; frogs heard calling accounted for 38 new breeding ponds; and incidental observations accounted for four new breeding ponds. Historical and recent records show that Gopher Frogs have been reported from 109 conservation lands and 488 ponds, and populations are presumably extant on 96 conservation lands. We estimated that at least 114 metapopulations were likely extant by combining records within 7 km of each other provided they were not separated by barriers to movement. Gopher Frogs have been recorded from 56 of 67 counties of Florida, and we suspect populations are extant in at least 44 counties. Urbanization, however, may have eliminated populations at the southernmost extent of the range of the species in Palm Beach, Broward, and Collier counties.**

Key Words.—amphibian; conservation; metapopulations; potential habitat model; survey

Introduction

The Gopher Frog (*Rana capito*) occurs in the southeastern Coastal Plain of the USA from southern Alabama to North Carolina, with disjunct populations in central Alabama and the Cumberland Plateau in Tennessee (Jensen and Richter 2005). The Center for Biological Diversity petitioned the U.S. Fish and Wildlife Service (USFWS) in 2012 to list the Gopher Frog as Endangered or Threatened, and the USFWS (2015) found that the petition presented substantial scientific information that listing may be warranted based on four factors. The Gopher Frog is one of many at-risk species designated for status reviews under the U.S. Endangered Species Act (Smith et al. 2018). Florida represents the largest portion of the global range of the Gopher Frog, which historically occurred throughout Florida except for the Everglades region (Krysko et al. 2019). Populations have declined significantly throughout much of the range of the species (Jensen and Richter 2005; Vanessa Terrell and John Maerz, unpubl. report). The most cited management concerns for Gopher Frogs are infrequent fire regimes and declines in populations of the Gopher Tortoise (*Gopherus polyphemus*) and Southeastern Pocket Gopher (*Geomys pinetis*), whose burrows, along with those of other mammals and stumpholes of decayed trees, are used as underground retreats by frogs to minimize the threat of predation or desiccation (Gentry and Smith 1968; Franz 1986; Blihovde 2006; Roznik and Johnson 2009a; Roznik et al. 2009). Other potential causes of declines are habitat degradation from silviculture, urbanization, road mortality, groundwater withdrawal, drought, and disease (Jensen and Richter 2005; Blihovde 2006; Roznik 2007). More than 9.3 million acres of wetlands in Florida were destroyed from 1780 to 1980, and 90% of remaining Longleaf Pine (*Pinus palustris*) habitats and 51% of remaining herbaceous wetlands were lost between 1936 and 1995 (Dahl 1990; Kautz 1998). About 30% of the land area of Florida is protected in conservation lands, some of which have xeric uplands with embedded isolated wetlands and apparently robust Gopher Frog populations.

Extensive surveys are lacking from much of the range of the species (Jensen and Richter 2005), but two such surveys were conducted previously in Florida. Richard Franz and Lora Smith (unpubl. report) found Gopher Frogs at only three of 63 historical sites visited

in 1990−1995 but found 83 new sites in 19 counties, including four new county records. Based on the lack of recent activity at many historical breeding sites, they concluded that populations declined east of the Apalachicola River in 1975–1995, particularly in coastal counties and in the southern peninsula, where human population concentrations are largest. Wigley et al. (1999) sampled 444 ponds on forest industry lands in Florida and Georgia in 1996–1998 and identified Gopher Frogs in only 16 ponds (14 of them in Florida), suggesting that intensive silviculture is unfavorable for the species.

The main objective of our study was to determine the present occurrence on public lands in Florida of the Gopher Frog and four other winter-breeding amphibian species listed as Species of Greatest Conservation Need (Enge et al. 2014). We accomplished this primarily by conducting, from November 2005 through May 2020, dipnet surveys of potential breeding ponds, which are typically temporary or semipermanent shallow ponds that lack predatory fish and have an open canopy and emergent vegetation (Jensen and Richter 2005). Gopher Frogs are explosive breeders that often breed after heavy rains from September to April (Palis 1998; Branch and Hokit 2000; Blihovde 2006), although they can breed in any month of the year in Florida, with summer breeding being more common in southern Florida because of weaker winter frontal systems there (Godley 1992; Dale Jackson, unpubl. report). Before our study, voucher specimens existed from 43 counties and unvouchered records from an additional seven counties. We gained insights on population trends and status of the species by comparing the historical and present distribution. We determined the number of extant metapopulations by combining locality records within 7 km of each other and not separated by barriers to movement. We used recent locality records to develop a Maxent Potential Habitat Model that provided a more complete picture of the possible distribution of Gopher Frogs in Florida, particularly in areas that we could not survey, such as private lands. The Gopher Frog was formerly listed as a Species of Special Concern in Florida, but, partly as a result of our study, the Florida Fish and Wildlife Conservation Commission (FWC) delisted it in January 2017 after a biological status review determined it did not meet criteria for state listing as Threatened (FWC 2011).

Materials and Methods

We initially compiled records of Gopher Frogs from various databases, museums, reports, scientific literature, and other surveys. Because we were interested in the number of extant populations, we deleted records that likely represented specimens from the same population. Gopher Frogs heard calling in ponds accounted for most records of ponds in databases that we searched. Richard Franz and Lora Smith (unpubl. report) conducted call surveys to document ponds because they were unsuccessful at identifying Gopher Frog tadpoles. Locations of breeding ponds associated with incidental observations from roads, in traps or Gopher Tortoise burrows, or after prescribed burns were usually unknown, and locations of breeding ponds found prior to the common use of GPS sometimes could not be accurately identified from the information provided. We recorded the first and last years in which the species was observed at a location, along with the name of the observer or other source of the information. Conservation land names and boundaries came from the Conservation Lands database of the Florida Natural Areas Inventory (FNAI; https://www.fnai.org/conslands/conservation-lands), which contains > 2,500 federal, state, local, and private managed lands. We individually named disjunct units of conservation lands when presenting survey results, but this was not possible when presenting area of modeled potential habitat because these units had been combined in the FNAI database.

We identified suitable-looking wetlands for dipnet surveys by overlaying GIS landcover layers (Cooperative Land Cover classification) of sandhill, upland pine, scrub, and scrubby flatwoods habitats on Google Earth satellite imagery. We also used Google Earth imagery to assess whether historical Gopher Frog records occurred near suitable uplands and wetlands, suggesting the likelihood of extant populations. In some cases, we used the timeline feature of Google Earth to determine whether wetlands had hydroperiods suitable for Gopher Frog reproduction and to identify land-use changes. During droughts, this timeline feature was particularly important at identifying ponds with longer hydroperiods that likely contained water and could be sampled for tadpoles. Because the Gopher Frog is an explosive breeder, we sometimes used precipitation data from Florida Forest Service weather stations to determine when frogs likely bred in response to large rainfall events and then typically waited > 45 d to give tadpoles time to grow and become distinguishable from those of the Southern Leopard Frog (*Rana sphenocephala*).

We initially conducted dipnet surveys primarily on the northern peninsula but expanded our efforts into the southern peninsula in 2012, when many ephemeral wetlands dried in the northern peninsula. We began surveying the Panhandle in 2013. We dip netted some ponds multiple times, particularly November 2015 through 2018 during an occupancy modeling study of 100 known breeding ponds (Crawford et al. 2022). We tried to dip net a pond for at least 30 person-minutes

but sampled shorter periods when ponds contained little water, dipnetting conditions were difficult, or large, predatory fish species were observed. In some cases, we terminated dipnetting once a Gopher Frog tadpole was captured. We did not count a pond visit as a survey if fewer than 10 person-minutes were spent dip netting unless Gopher Frog tadpoles were detected. We conducted dipnet surveys in all months, but 71.0% of 3,054 surveys were conducted February-June.

We assigned all records thought to represent extant populations to metapopulations using a potential dispersal distance (radius) of 3.5 km based on Gopher Frog telemetry data from North Carolina (Humphries and Sisson 2012) and the same methodology as used by Crawford et al. (2022). We considered records as representing the same metapopulation if the 7-km-diameter circles intersected and barriers such as high-traffic divided highways, (functional classes 1–3, lane category 2+, and speed 50+ mph in the 2016 NAVTEQ Streets for Detailed Coverage Area 9), named rivers or > 20-km-long continuous streams in the 2016 National Hydrographic Dataset (NHD) Streams of Florida at 1:24,000 scale (https://www.usgs.gov/national-hydrography/national-hydrography-datase) were absent. Determining barriers between metapopulations was somewhat subjective because we do not know frog survival in relation to road width and traffic volume or how wide a stream and its riparian vegetation must be to deter frogs from crossing. Because we could not determine the width of small streams using Google Earth imagery, we typically considered riparian vegetation ≥ 50 m wide to be a barrier to frog movements. Unsuitable land cover such as urban areas and extensive poorly drained habitats also served as barriers to movement. We considered nonintersecting circles within 3 km to be part of the same metapopulation if we determined the intervening area to contain suitable upland habitat and potential breeding ponds based on our experience. For example, when viewing Google Earth imagery, we considered low-density housing subdivisions with some areas of natural habitat, pastures, pine plantations with low stocking densities, and mesic pine flatwoods to constitute suitable upland habitat if they were part of a landscape matrix containing xeric uplands with embedded ephemeral wetlands (wetland permanence was determined using the timeline feature). We included all records after 1990 unless aerial imagery showed that suitable upland or breeding habitat no longer existed in the area or multiple unsuccessful surveys of the breeding pond or ponds suggested that the metapopulation had been extirpated. Only seven records for which the last observation was made in the 1980s were considered to have extant populations based on the continued presence of suitable habitat.

To develop a potential habitat map for the Gopher Frog, we used a Maximum Entropy Model (Maxent v3.3.3k; https://www.cs.princeton.edu/~schapire/maxent/) with default parameters and tenfold cross validation. We used Maxent because it is the best option for predicting habitat suitability using presence-only records from digital databases (Valavi et al. 2022). We compared 482 known occurrence records from 2000 through 2019 with about 4,300 random background locations within the range of the species in Florida. We used the following data layers: 2017 CLC version 3.2.5 state level classes of FNAI and FWC, distance to freshwater marshes < 20 ha in area, distance to xeric soils from Fish and Wildlife Research Institute (FWRI) of FWC 2011 soils, FWRI of FWC 2015 landform, and the 2016 percentage forest canopy cover of the U.S. Forest Service. We applied a nonhabitat mask to exclude NHD 2019 water bodies > 20 ha in size, including a 200-m buffer around lakes, ponds, and reservoirs and along NHD major flow ways (e.g., streams, rivers, and canals). To create a binary model output, we used the 10^{th} percentile training presence to obtain a threshold value (0.172) above which we defined potentially suitable habitat.

Results

Before our study (i.e., pre-2006), 161 Gopher Frog breeding ponds were known from 24 Florida counties (Supplemental Information Table S1), and records not associated with a breeding pond existed from an additional 25 counties. We identified 323 new breeding ponds, including the first breeding ponds known for 14 counties. Of these new ponds, we found 91.0% by dip netting, 7.7% from calls, and 1.2% incidentally. Citizen reports of seeing (verified by photographs) or hearing Gopher Frogs identified 13 new breeding ponds on private property. Call surveys detected Gopher Frogs for the first time on three conservation lands (one by an automated recorder), and incidental observations detected frogs for the first time on eight conservation lands and on private property in Jackson County. Of 493 known breeding ponds that probably have extant populations, dip netting for tadpoles was responsible for obtaining the most recent record for 80.9% of ponds. Reports of calling frogs, primarily from other observers, accounted for 15.4% of records since 1990. Incidental observations of frogs accounted for 3.7% of records since 1990. We discounted reports of calling Gopher Frogs from John M. Bethea State Forest in Baker County and Pine Log State Forest in Bay County because of unsuitable upland or wetland habitat. A sighting in Pellicer Creek Conservation Area represented the first record from Flagler County.

We compiled records of Gopher Frog presence cataloged from 2005 through 2020 from 73 conservation lands, including 390 ponds on 61 conservation lands. From November 2005 through May 2020, we dip netted

1,330 ponds on 106 public and seven private conservation lands in 44 counties and 23 ponds on private property in 12 counties (Supplemental Information Table S2). During these dipnet surveys, we found Gopher Frog tadpoles in 356 ponds (27.2% of ponds surveyed) on 59 conservation lands in 31 counties and in six ponds on private property in five counties (Fig. 1; Supplemental Information Table S2). Overall, we detected Gopher Frog tadpoles during 27.8% of 3,054 visits to ponds. We discovered breeding ponds on 45 conservation lands where ponds had previously not been identified. As many as four breeding events occurred in some ponds, as evidenced by different size cohorts of tadpoles (Fig. 2).

The potential habitat model developed for the Gopher Frog had a very good model fit (area under the curve [AUC]) of 0.91. The variables distance to freshwater marshes < 20 ha in area, distance to xeric soils, and land cover (isolated freshwater marsh, mesic flatwoods, unvegetated wetland, natural lakes and ponds, dry prairie, sandhill) had the greatest influence on the model (36.8%, 37.3%, and 15.3% permutation importance, respectively). Of the 338 Gopher Frog locations used, 49.4% were in freshwater marshes, 12.1% in sandhill, 8.6% in scrub, and 6.8% in mesic flatwoods. The potential habitat model identified 1,177,002 ha on the peninsula and 292,751 ha in the Panhandle. In the Panhandle, Okaloosa, Walton, Leon, Jackson, and Washington counties contain the most Gopher Frog habitat (Fig. 3). On the peninsula, Polk, Lake, Marion, Pasco, and Osceola counties contain the most habitat (Fig. 3). Conservation lands contain 30.1% of the total potential habitat, and 182 conservation lands contain at least 50 ha of potential habitat (Supplemental Information Table S1). Ocala National Forest (ONF) has 3.6 times the potential habitat of Eglin Air Force Base (EAFB), the conservation land with the second greatest amount of habitat (Supplemental Information Table S1). Duette Preserve in the under-surveyed southwestern peninsula is the only conservation land ranked in the top 10 in amount of potential habitat that lacks an identified breeding pond, but it has a Gopher Frog record (Supplemental Information Table S1).

Gopher Frogs have been reported from 56 counties but from only 43 counties since 2000 (Fig. 4). Seven counties have not had records since 1960 (Fig. 4). Six counties with only pre-2000 records contain at least 10,000 ha of potential habitat and likely have extant populations: Charlotte, DeSoto, Jefferson, Okeechobee, Palm Beach, and Washington (Supplemental Information Table S3). We did not conduct dipnet surveys in Charlotte, DeSoto, and Palm Beach counties. We also did not survey Bay, Escambia, and Holmes counties, which have at least 10,000 ha of potential habitat but lack Gopher Frog records (Supplemental Information Table S3). We did not survey some counties because most of the potential habitat was found on private lands. When historical and recent records are combined, Gopher Frogs have been reported from 107 conservation lands, on which 449 breeding ponds have been identified, but 30 of the 107 conservation lands have no records since 2000 (Supplemental Information Table S1). Breeding ponds have not been identified on 36 conservation lands where Gopher Frogs have been observed (Supplemental Information Table S1). Conservation lands with the largest number of known breeding ponds are ONF (n = 85), Apalachicola National Forest (ANF; n = 58), Camp

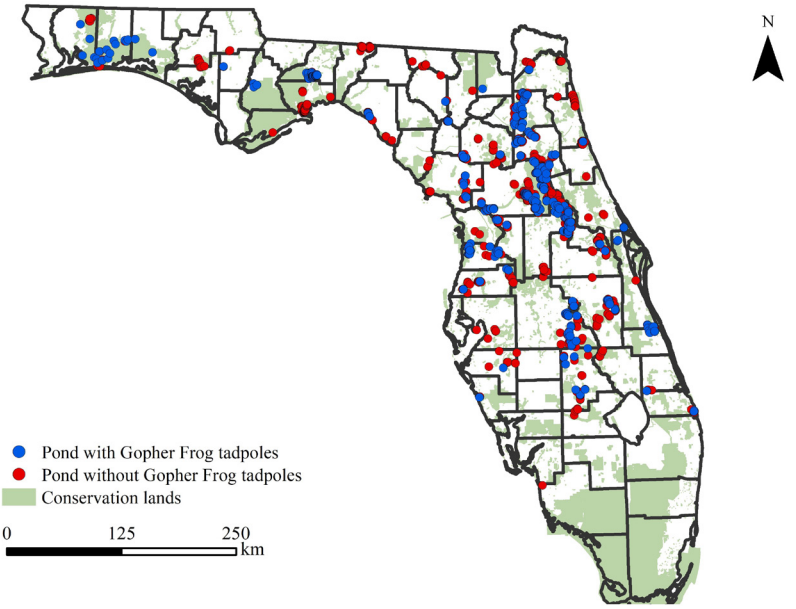

Figure 1. Results of 2005–2020 dipnet surveys for Gopher Frog (*Rana capito*) tadpoles in Florida, USA.

Figure 2. (A) Gopher Frog (*Rana capito*) tadpoles and metamorphs from Merritt Island National Wildlife Refuge, Volusia County, Florida, USA. (B) A small sinkhole pond (0.008 ha) used by Gopher Frogs in sandhill habitat on Chassahowitzka Wildlife Management Area, Hernando County, Florida, USA. (C) A depression marsh (0.78 ha) used by Gopher Frogs in a pine plantation (now a sod farm) on private property in Calhoun County, Florida, USA. (D) Kemmons Pond, a 14.0-ha basin marsh used by Gopher Frogs on Eglin Air Force Base, Okaloosa County, Florida, USA. (Photographed by Kevin Enge).

Blanding Military Reservation (CBMR; n = 32), and EAFB (n = 25; Supplemental Information Table S1).

Of the 493 identified breeding ponds in 39 counties, 30.0% are near or on the Trail and Mount Dora Ridges in Clay, Putnam, Marion, and Lake counties. These four counties contain 15.9% of potential habitat on the peninsula (Supplemental Information Table S3). The Brooksville Ridge, which lies primarily in Gilchrist, Levy, Citrus, Hernando, and Pasco counties, contains 15.9% of the known breeding ponds, and these five counties contain 13.1% of potential habitat on the peninsula (Supplemental Information Table S3). The Lake Wales Ridge, which lies primarily in Polk and Highlands counties, has 9.0% of the known breeding ponds, and these counties contain 11.6% of potential habitat on the peninsula (Supplemental Information Table S3). In the Panhandle, the Munson Sandhills in ANF has 11.5% of known breeding ponds, and Leon County has 11.2% of potential habitat (Supplemental Information Table S3). Outside of ANF and EAFB, we found Gopher Frog tadpoles in only three of 84 ponds surveyed in the Panhandle, two in Blackwater River State Forest (BRSF) and one on private property in Calhoun County (Supplemental Information Table S2). We dip netted some ponds in the Panhandle as many as three times without detecting Gopher Frogs.

We estimated that at least 114 Gopher Frog metapopulations are probably extant in Florida based upon our surveys and habitat condition (Fig. 5). The Panhandle probably contains only 18 extant metapopulations. All 57 ponds in the Munson Sandhills of ANF are in one metapopulation, whereas EAFB has nine metapopulations comprising 25 breeding ponds widely dispersed across three counties (Fig. 5). Ocala National Forest contains three metapopulations, two of which contain at least 40 ponds each (Fig. 5).

Discussion

Geographic population trends.—We documented the presence of Gopher Frogs in 43 of 56 historical counties and two additional counties. Post-2000 records do not exist from four Panhandle counties and nine peninsular counties with historical records. Peninsular populations are genetically distinct from populations in the Panhandle and elsewhere in the range of the species (Devitt et al. 2023). Gopher Frog populations are presumably extant on 96 Florida conservation lands, where 388 breeding ponds have been identified (Supplemental Information Table S1). We suspect Gopher Frog populations on the peninsula persist on many private lands, which we seldom surveyed. In the Panhandle, two public conservation lands, ANF and EAFB, contain most of the known breeding ponds, although about 67% of modeled potential habitat occurred on private lands.

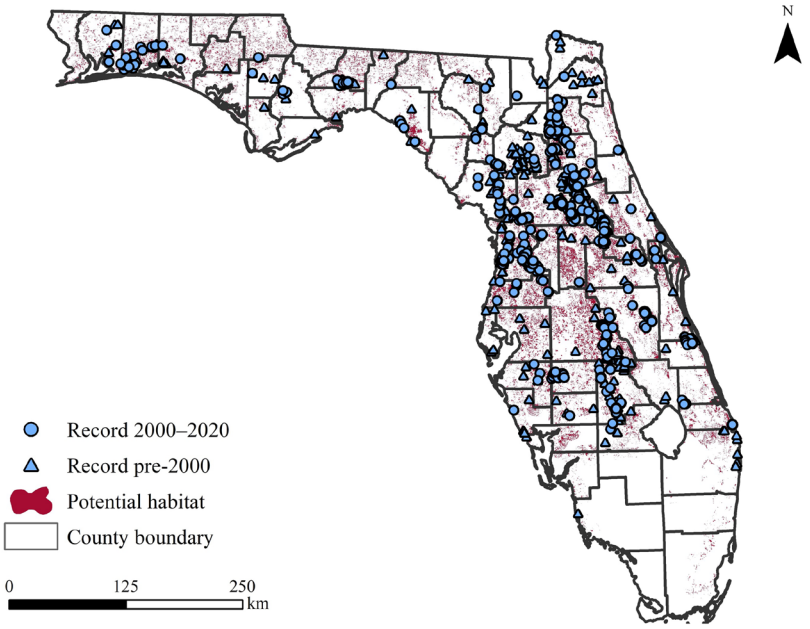

Figure 3. Potential habitat and records of the Gopher Frog (*Rana capito*) in Florida, USA.

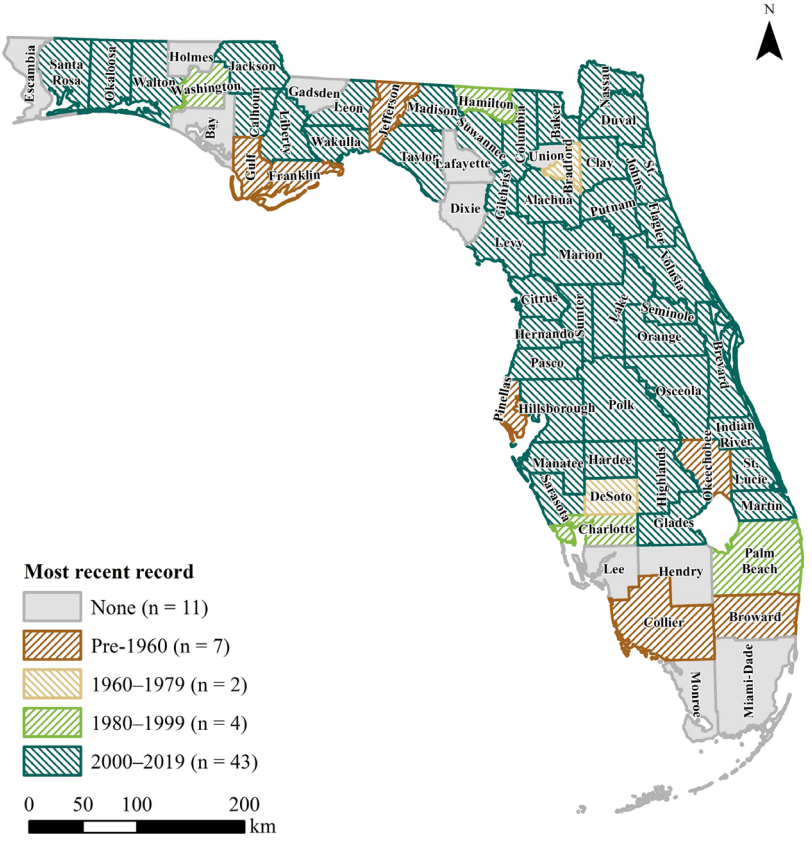

Figure 4. The most recent record of the Gopher Frog (*Rana capito*) by time period for each county of Florida, USA.

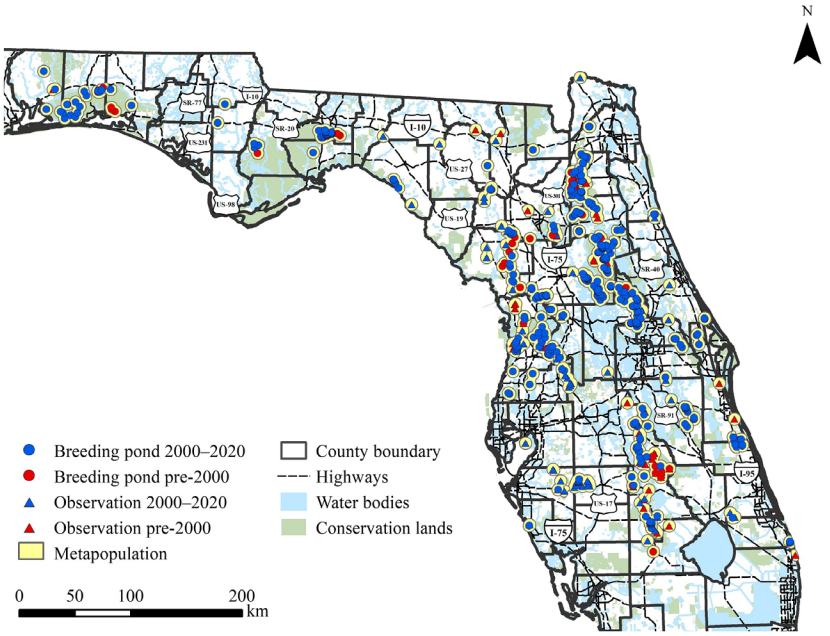

Figure 5. Presumably extant Gopher Frog (*Rana capito*) metapopulations in Florida, USA.

The Panhandle has only 18 known metapopulations, half of them on EAFB, which has 27% of the known breeding ponds with extant populations in the Panhandle. We assumed that three metapopulations in the Panhandle with post-1990 records have been extirpated: Econfina Creek Water Management Area, BRSF near Goose Ponds, and Santa Rosa Outlying Landing Field (Supplemental Information Table S2). In 1993–1994, John Palis and John Jensen (unpubl. report) found 22 breeding ponds on EAFB, whereas we recorded frogs in 15 known ponds and in two new ponds. The metapopulation in the Munson Sandhills of ANF would appear to be the most secure because it comprises 57 known breeding ponds, and we discovered a new metapopulation in the Liberty County portion of ANF. But the significant, inexplicable decline in ANF populations of the Striped Newt (*Notophthalmus perstriatus*), which breeds in the same types of wetlands in xeric uplands as the Gopher Frog, suggests that Gopher Frog populations should not be considered secure there, even in apparent strongholds. Only one of 18 known Striped Newt breeding ponds in ANF still contains a natural, nonaugmented population (Farmer et al. 2017). Also, Gopher Frogs apparently no longer occur in the nearby Panacea Unit of St. Marks National Wildlife Refuge (Dodd et al. 2007), which contains 4,124 ha of potential habitat. Outside of ANF and EAFB, we found Gopher Frog tadpoles in only three ponds in the Panhandle. We suspect a pond on private property in Jackson County supports a population, despite our lack of success in detecting tadpoles. A citizen reported observing a Gopher Frog in a Gopher Tortoise burrow there, and upland and wetland habitats were suitable. Four central Panhandle counties (Bay, Calhoun, Jackson, and Washington) contain 78,982 ha of potential habitat, but Gopher Frogs are now rare or absent there. Neill (1957) often heard choruses in Calhoun and Gulf counties.

Extensive Sand Pine (*Pinus clausa*) silviculture and low densities of Gopher Tortoises in the Panhandle (Diemer 1986; Enge et al. 2013) are probably the primary reason that Gopher Frogs are scarce there. Gopher Frog tadpoles occurred in only one of 85 ponds sampled in Sand Pine plantations but occurred in significantly more ponds in adjacent Longleaf Pine Forests in ANF (Means and Means 2005). Many Panhandle Gopher Tortoise populations have not recovered from past human depredation (Enge et al. 2013), and there may be too few alternative burrows to support viable Gopher Frog populations. Additional surveys are needed to investigate whether modeled potential habitat on public and private lands in the Panhandle contains more metapopulations. For example, four counties (Bay, Escambia, Gadsden, and Holmes) contain about 10,000 or more ha of modeled habitat but no records of Gopher Frogs. Conservation measures may be needed to prevent further population declines. Recent conversion of the pine plantation surrounding the breeding pond in Calhoun County to a sod farm (Michael Sisson, pers. comm.) likely extirpated that population.

The peninsula has at least 96 metapopulations, and our surveys indicate that Gopher Frogs are still widely

distributed on the peninsula and are particularly abundant on the Trail, Mount Dora, Brooksville, and Lake Wales ridges. These findings are consistent with those of Richard Franz and Lora Smith (unpubl. report), who, based on surveys of 146 ponds, considered the species to be common on protected lands along the central spine of the peninsula north of Lake Okeechobee. Peninsular strongholds are ONF (three metapopulations and 85 breeding ponds) and CBMR (two metapopulations and 32 breeding ponds). Before our surveys, only 11 breeding ponds were known in ONF, and we suspect the existence of dozens of additional breeding ponds. Although we discovered 74 new breeding ponds there, time constraints and drought prevented us from surveying most of the potentially suitable ponds, and 77.9% of 339 ponds surveyed on ONF were dip netted only once. On CBMR, we detected Gopher Frogs in 20 ponds, whereas Hipes and Jackson (1996) heard Gopher Frogs calling from 21 of 35 ponds in 1993–1994. Some public lands, such as Withlacoochee State Forest, have extensive suitable upland habitat but contain relatively few suitable wetlands for breeding Gopher Frogs.

Urbanization has severely reduced and fragmented upland habitats used by Gopher Frogs on the coastal ridges of both southeastern and southwestern Florida. Gopher Frog populations may have been eliminated in Palm Beach and Broward counties on the southeastern peninsula; only 2% of scrub habitat remains in Broward County, and < 5% of scrub habitat remains in Palm Beach County (Fernald 1989). Gopher Frogs likely never occurred as far south as Miami-Dade County (Krysko et al. 2019), despite modeling indicating the presence of 6,117 ha of potential habitat. The Maxent model likely overpredicts the extent of potential habitat, and the species does not occur in many areas with identified habitat. The habitat model does not take into account deleterious past land-use practices, presence of predatory fish species in wetlands, and lack of suitable refugia, such as Gopher Tortoise burrows; however, the model is useful in identifying suitable areas to conduct future surveys, acquire land, or reintroduce populations. We found few recent records from the southwestern peninsula in Pinellas, Hillsborough, Hardee, Manatee, Sarasota, Charlotte, DeSoto, Lee, and Collier counties. Dale Jackson (unpubl. report) trapped on 12 conservation lands in the southwestern peninsula, finding Gopher Frogs only at Oscar Scherer State Park, Sarasota County, where we documented the first two breeding ponds. We surveyed only 13 ponds in this region, finding Gopher Frogs in three ponds. Based on the amount of potential habitat, additional Gopher Frog populations are likely present in Hillsborough and Manatee counties.

Mining, agriculture, and urbanization have reduced upland habitats on the central ridges of peninsular Florida (Dale Jackson, unpubl. report; Turner et al. 2006), but substantial habitat remains. Polk, Lake, Marion, and Pasco counties on the Brooksville, Mount Dora, and Lake Wales ridges contain the most potential habitat. We surveyed some conservation lands only once and likely failed to detect Gopher Frogs in areas where they still occur. For example, we found no Gopher Frog tadpoles during a survey of Hilochee WMA in Lake County but scoping of 45 tortoise burrows detected one Gopher Frog (FWC, unpubl. report).

Threats to Gopher Frog populations.—Our Maxent model identified 1,469,750 ha of potential habitat, which is similar to the 1,385,270 ha of high suitability habitat modeled by Crawford et al. (2020). Gopher Frog populations are impacted by changes in the extent and quality of both wetland and surrounding upland habitats. Crawford et al. (2022) found some evidence that wetlands surrounded by higher quality terrestrial habitat may have increased breeding probability of Gopher Frogs during drought conditions. Quality of upland habitats is probably a function of fire frequency and refugium availability. Historically, frequent, low- to moderate-intensity surface fires, started by lightning or by Native Americans, sustained open, diverse Longleaf Pine savannas in a fire climax, preventing their succession to forests dominated by fire-intolerant hardwood species (Battle and Golladay 2003; van Lear et al. 2005). These frequent fires maintained a diverse, herbaceous ground cover, which in turn supported a diverse invertebrate prey base and herpetofaunal community (Lannoo 2005). The Gopher Frog has been identified as one of the amphibian species most sensitive to hardwood invasion resulting from fire exclusion (Cathryn Greenberg et al., unpubl. report), but it is somewhat tolerant of groundcover degradation and may persist in pastures and other altered communities in peninsular Florida provided refugia and suitable wetlands are present (Dale Jackson, unpubl. report; Enge et al. 2014).

In Florida, logging, agriculture, urbanization, silviculture, and fire suppression have reduced old-growth Longleaf Pine savanna to < 1–2% of its former range (Lannoo 2005). Prescribed burns in sandhill and upland pine habitats are needed every 1–3 y to provide ideal habitat for Gopher Frogs (Johnson and Gjerstad 2006), but scrubby flatwoods and scrub have longer natural fire return intervals (Florida Natural Areas Inventory 2010). Gopher Frog populations may be responding directly to changes in upland habitat or indirectly to declines in the number of burrows of Gopher Tortoises, which are also sensitive to habitat changes associated with long-term fire exclusion (Diemer 1986; Cox et al. 1987; Ashton et al. 2008). Alternative refugia to tortoise burrows are also declining both from the silvicultural practices of stumping and short-term rotation of pines, reducing the availability of stumpholes (Means 2005; Enge et

al. 2014), and from the extirpation of Pocket Gopher populations from much of their historical range due to habitat fragmentation and urbanization (Parsons 2019).

Another factor in Gopher Frog population decline is the degradation of wetlands, which includes changes to hydroperiod, fire frequency, vegetative composition, and fish communities. Hydroperiods of isolated wetlands in the Southeastern U.S. have been altered by urbanization (McCauley et al. 2013), reduction of forest cover, and silviculture (Chandler et al. 2017; Jones et al. 2018a; Haggerty et al. 2019). Groundwater withdrawal, particularly near wellfields and cities, may reduce the hydroperiod of wetlands that are not solely filled by rainfall, eliminating population recruitment when wetlands dry before tadpole metamorphosis (Grubbs and Crandall 2007; FWC 2011; Metz 2011). Fires need to periodically burn into dry wetlands to prevent shrub invasion and excessive peat buildup that reduces emergent vegetation, water depth, and hydroperiod (Enge et al. 2014). Vegetative changes to wetlands also result from disturbance by off-road vehicles (ORVs) and foraging feral Pigs (*Sus scrofa*). The use of ORVs in pond basins (i.e., mudding) can cause direct mortality of tadpoles and adults and degrade pond habitat quality by altering contours, herbaceous vegetation, and hydrology (USFWS 2001). Loss of herbaceous vegetation decreases food and protective cover for tadpoles and stalks to which egg masses are attached (USFWS 2001). By 2010, the U.S. Forest Service closed the Munson Sandhills of ANF to ORV use to protect Striped Newt ponds (USFWS 2011), and many areas and trails have been closed in ONF. These restrictions are difficult to enforce, however, and ORV disturbance of wetlands continues in these two forests, on some other public lands, and on many private lands. Feral Pigs may root up the dried wetlands, reducing vegetation and altering microtopography, and increase eutrophication by defecating (Bentsen et al. 2014; Jones et al. 2018b). We found Gopher Frog tadpoles in wetlands that had been moderately disturbed by ORVs or feral Pigs, and the deeper holes or ruts sometimes retained the only water in drying wetlands, allowing some tadpoles to successfully metamorphose, if food and suitable water quality were present.

The impact of disease on Gopher Frog populations in Florida is not known. We observed massive tadpole die-offs in only three ponds during dipnet surveys, but die-offs are seldom detected because amphibians decay so fast. Alveolate protist parasites (*Dermomycoides* spp.) have been implicated in massive Gopher Frog tadpole die-offs in Florida (Rothermel et al. 2008; Landsberg et al. 2013; Isidoro-Ayza 2017) and are a serious impediment to augmentation programs for the federally listed as Endangered Dusky Gopher Frog (*Rana sevosa*; Cook 2008; Atkinson 2016). Gopher Frogs are highly susceptible to various ranaviruses in laboratory experiments (Hoverman et al. 2011; Sutton et al. 2014; Earl et al. 2016), and ranaviruses have been implicated in Gopher Frog tadpole die-offs in Florida (Hartmann et al. 2022). Some tadpoles successfully metamorphose during such die-offs, and these ponds are still used by breeding Gopher Frogs.

Breeding probability of Gopher Frogs at a pond is positively influenced by seasonal precipitation and negatively influenced by the presence of fish (Crawford et al. 2022). Periodic colonization or introduction of fish into isolated wetlands may increase egg and tadpole mortality and decrease recruitment rates (Gregoire and Gunzburger 2008; Liner et al. 2008). Colonization of wetlands by fish is particularly prevalent in areas of low topographic relief that experience sheet flow of water across the landscape after heavy rains (Enge et al. 2020). Stocking of sunfish (*Lepomis* spp.) and bass (*Micropterus* spp.) into ponds for fishing contributes to population declines of Gopher Frogs (FWC 2011), which apparently do not successfully reproduce in wetlands with large predatory fishes (Jensen and Richter 2005). We failed to find Gopher Frog tadpoles in ponds in which we detected gamefish species, but we found that 16.3% of occupied Gopher Frog ponds contained small, nonpredatory fish species, particularly Eastern Mosquitofish (*Gambusia holbrooki*). Gregoire and Gunzburger (2008) demonstrated that mosquitofish, which are sometimes introduced into isolated wetlands by county mosquito control agencies (Kondapaneni et al. 2021), can negatively affect Gopher Frog tadpoles by injuring the tail fins of tadpoles. Some ponds are naturally colonized by fishes during floods, but most fish species are eliminated when ephemeral ponds dry down (Moler and Franz 1988; Enge et al. 2020). Connecting wetlands by drainage ditches alters their hydrology and facilitates colonization by fish (Vickers et al. 1985; Babbitt and Tanner 2000). Cattle dugouts in wetland basins can harm Gopher Frog populations if they provide permanent water that allows survival of predatory fish, but dugouts lacking predatory fish can benefit Gopher Frog populations by allowing successful reproduction and population recruitment during dry conditions.

Florida is the southern terminus of the range of the Gopher Frog, and Florida populations may be more strongly affected by climate change than those in the center of its range. The Center-periphery Hypothesis predicts that marginal populations are more prone to extinction and genetically less diverse than center populations because they tend to occur in less suitable habitats and at lower and more variable densities (Lawton 1993; Vucetic and Waite 2003). At present, many Florida populations are apparently doing better than more northerly populations, but this trend may not continue, and rear-edge populations (i.e., those residing

at the low-latitude margins of the range of a species) are vital to long-term conservation of genetic diversity, phylogenetic history, and evolutionary potential (Hampe and Petit 2005). Long-term increases in the severity and frequency of droughts and in temperature due to climate change will likely result in loss and degradation of habitats and affect reproductive success by decreasing wetland hydroperiods and causing changes in the timing of amphibian reproduction (Blaustein et al. 2010; Walls et al. 2013). In the past 120 y in Florida, average annual air temperatures have increased steadily in most months on the peninsula; on the central peninsula, the duration of droughts has increased significantly, and the severity of droughts has increased in the late fall-early winter months, when Gopher Frogs frequently breed (Enge et al. 2014). Hydroperiods of most isolated wetlands in ONF are forecast to become insufficient for recruitment of juvenile Gopher Frogs (Cathryn Greenberg et al., unpubl. report).

Conservation.—The taxonomy and geographic ranges of Gopher Frogs have undergone many revisions. Goin and Netting (1940) described the Dusky Gopher Frog (*R. sevosa*) as a separate species. In the Peterson Field Guide, Conant (1975) described three subspecies of Gopher Frog based on appearance: Dusky (*R. areolate sevosa*) from southeastern Louisiana to the western Florida Panhandle; Carolina (*R. a. capito*) from east central Georgia to North Carolina; and Florida (*R. a. aesopus*) in most of Florida and southern Georgia. Based on allozyme evidence, Young and Crother (2001) separated Gopher Frogs (*R. capito*) from Crawfish Frogs (*R. areolate*), resurrected *R. sevosa*, and failed to recognize subspecies of *R. capito*. The Dusky Gopher Frog, which historically ranged from southeastern Louisiana to Mobile County, Alabama, but is now restricted to Mississippi, was federally listed as Endangered in 2001. Based on mtDNA, Richter et al. (2014) identified a Coastal Plain lineage that occurred from North Carolina to the Florida Panhandle and two Peninsular lineages in Florida, which they recommended the USFWS consider as distinct population segments during listing evaluations. The Panhandle distinct population segment that Devitt et al. (2023) identified as occurring from North Carolina to the Florida Panhandle may warrant consideration for listing because of population loss and restriction to a few geographical areas and conservation lands, primarily EAFB and ANF. Continued habitat loss, degradation, and fragmentation may eventually restrict peninsular populations primarily to large tracts of conservation land with suitable land-management practices and multiple breeding ponds.

Although the Gopher Frog is no longer listed as Threatened in Florida, take and possession are still prohibited without a permit, and a species action plan has been developed to help conserve populations (FWC 2013). Several conservation actions could benefit Gopher Frog populations in Florida. Creation of wetlands for metapopulations in areas where there is currently only one breeding pond may enhance population persistence; Gopher Frogs will breed in man-made wetlands, including borrow pits. Gopher Tortoise burrows remain throughout much of the peninsula, including suburban and agricultural areas, but small, nonviable populations of this long-lived species (Diemer 1986) will not continue to provide refugia for the Gopher Frog and other commensal species. Upland restoration, addition of artificial burrows, or translocation of Gopher Tortoises may make some Panhandle sites, such as Econfina Creek Water Management Area in Bay and Washington counties, candidates for the reintroduction of Gopher Frogs, which has been successful in other states (LaClaire 2017; Vanessa Terrell and John Maerz, unpubl. report). Upland habitat connectivity in the form of continuous natural forests is important for dispersal of juveniles to new areas and recolonization of areas after local extinctions (Rothermel and Semlitsch 2002). Gopher Frog populations would benefit from habitat management practices, preferably frequent prescribed burns during the growing season, that create an open canopy and diverse, herbaceous ground cover similar to that of the Longleaf Pine savanna that once predominantly surrounded isolated wetlands in Florida (van Lear et al. 2005). Dispersing newly metamorphosed Gopher Frogs were highly susceptible to predation and desiccation if they did not find an underground retreat within a few days (Roznik and Johnson 2009a); they selected fire-maintained habitat with an open canopy, few hardwood trees, small amounts of leaf litter, and large amounts of Wiregrass (*Aristida stricta*) where Gopher Tortoise burrows (primary refugia) were more abundant (Roznik and Johnson 2009b, Roznik et al. 2009).

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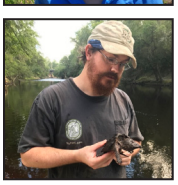

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