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Limpkin, *Aramus guarauna* (L., 1766) (Gruiformes, Aramidae), extralimital breeding in Louisiana is associated with availability of the invasive Giant Apple Snail, *Pomacea maculata* Perry, 1810 (Caenogastropoda, Ampullariidae)

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Abstract
We document the first breeding record of Limpkin, *Aramus guarauna* (Linnaeus, 1766) (Gruiformes, Aramidae), for Louisiana, describe an additional unpublished breeding record from Georgia, as well as a possible record from Alabama, and associate these patterns with the concurrent establishment of the invasive Giant Apple Snail, *Pomacea maculata* Perry, 1810 (Caenogastropoda, Ampullariidae). We predict that an invasive prey species may facilitate range expansion by native predator species, which has ramifications for conservation and management.

Keywords
Biological control, invasive species, predator-prey relationship, range expansion, species distribution.

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Introduction

The Giant Apple Snail, *Pomacea maculata* Perry, 1810 (hereafter referred to as GAS) is a freshwater snail native to South America, but widely introduced globally (Hayes et al. 2015), and invasive in freshwater wetlands across the northern coast of the Gulf of Mexico, where its range has been expanding since the year 2000 (US Geological Survey 2018, Benson 2019). Apple snails, *Pomacea* spp., represent a major food source for the Limpkin, *Aramus guarauna* (Linnaeus, 1766), both throughout its Neotropical range and in Florida (Harper 1936, Bryan 2002), where Limpkin breeding distribution is historically closely associated with, and perhaps limited by, that of the native Florida Apple Snail, *Pomacea paludosa* (Say, 1829) (Stevenson and Anderson 1994). Although Limpkin historically occurred as far north as southeastern Georgia, the core of the Limpkin's geographic range in the USA is currently peninsular Florida; the species is locally-distributed in the northern tier of Florida counties, west to Wakulla Co. in the panhandle (Stevenson and Anderson 1994, Bryan 2002). Limpkin is also prone to wandering north of (presumably from) Florida and vagrants have occurred as far north as Nova Scotia (American Ornithologists' Union 1998, Bryan 2002). The frequency of vagrant Limpkin records in the eastern USA appears to be increasing in recent years (eBird 2019), and recent work demonstrates an association between extralimital Limpkin occurrences and GAS abundance (Marzolf et al. 2019).

Louisiana's first documented occurrence of Limpkin was at Lake Boeuf (Lafourche Parish) in December 2017 (Dittmann and Cardiff 2018); this record consisted of a group of 4 individuals. Soon thereafter, on 31 January 2018, a pair was discovered at Lake Houma (Terrebonne Parish), Louisiana, approximately 20 km to the southwest (eBird 2019). The authors were able to document successful breeding by this Limpkin pair. Extralimital breeding records from Louisiana and Georgia, and possibly Alabama, include observations of the birds eating apple snails (authors' observations; eBird 2019), which prompted us to hypothesize that the Limpkin's historical inability to persist and expand its breeding range along the northern coast of the Gulf of Mexico, outside of Florida, has been due to a lack of abundant, preferred *Pomacea* spp. prey. Although Limpkins will eat other species of freshwater snails and mussels, apple snails represent the species' primary food source throughout its range (Bryan 2002). We suggest that establishment of GAS populations preceded recent incidents of extralimital Limpkin breeding on the northern Gulf coast. Here we describe the first documented breeding record of Limpkin in Louisiana, and compare the spatial and temporal overlap of extralimital Limpkin breeding records to GAS occurrence on the northern Gulf coast. Regarding the latter, we asked the question: In watersheds with evidence of Limpkin breeding, were GAS present prior to and within 5 km of the Limpkin breeding localities?

Methods

Limpkin field observations. We observed Limpkin activity on the southern edge of Lake Houma (29.611, –90.721), Terrebonne Parish, Louisiana during 8 observation periods, averaging 64 min in duration (range 18–197 min) and generally occurring in the afternoon, between 2 February and 7 May 2018. During each observation period, we conducted continuous focal-animal sampling (Altmann 1974, Martin and Bateson 1995) to observe the birds from a distance of 20–150 m, using binoculars and spotting scopes, and classified breeding-related behaviors displayed by the birds following Laughlin et al. (1990). We supplemented our observations with those reported to the eBird database (eBird 2019), where they provided novel information.

Apple snail and Limpkin data compilation. We acquired GAS occurrence records sourced from the Nonindigenous Aquatic Species (NAS) database (US Geological Survey 2018) and Limpkin occurrence and breeding records from the eBird database (eBird 2019; see also Sullivan et al. 2009). We compared the locations and timing of GAS arrival in southeastern watersheds to records of Limpkins breeding outside the species' traditional range (hereafter referred to as extralimital) in the states of South Carolina, Georgia, Alabama, Mississippi, Louisiana, and Texas (west to Brazoria County, Texas; hereafter referred to as northern Gulf coast), all of which lack recent (in the last 100 years) Limpkin breeding records. We made comparisons at the scale of the US Geological Survey's 6-digit Hydrologic Unit Codes (HUC), which are designations for delineated drainage basins. We did not collect GAS or Limpkin specimens and thus have no voucher material; we comment on identification of both taxa below. To further place recent Limpkin breeding observations within the context of Limpkin vagrancy patterns and GAS range expansion, we compiled documented and otherwise verified records of extralimital Limpkins, through the year 2018, from the ornithological literature, state bird records committee databases and reports, and the eBird database. The historical status of Limpkin in Georgia is unclear, but it may have been a rare local resident at one time (Bryan 2002); we limited our review of Georgia Limpkin records to more recent times, when it has been considered accidental in the state (Beaton et al. 2003).

Results

New record—Limpkin breeding in Louisiana. Upon discovery by M. Autin on 31 January 2018, 2 adult Limpkins at Lake Houma (29.611, −90.721) behaved as though they were a mated pair, frequently calling back-and-forth, and exhibited courtship behavior in the form of courtship feeding, in which one adult presented the other with food items—often GAS, but also including other mollusks (e.g., bivalves) (eBird 2019; Table 1). On 21 February 2018 we discovered that the pair had an active nest located just inside the edge of a homogenous patch of giant cutgrass, *Zizaniopsis miliacea* (Michx.), which was surrounded by water and floating vegetation, e.g., water hyacinth, *Eichhornia crassipes* (Mart.) Solms, and positioned between and ca 10–15 m from 2 wooded spoil banks. Incubation continued until 21 March, or shortly thereafter, and during our subsequent observation (26 March), we observed 6 downy young ca 50–80 m away from the nest (Table 1, Fig. 1). At least 2 juveniles survived to 7 May 2018, at which time they were near adult-size and foraging independently; we did not attempt to monitor the birds after 7 May 2018. We did not quantify snail capture or consumption by the Limpkins, nor did we quantify snail availability at the site. Anecdotally, however, the vast majority of prey items that we observed the Limpkins capture, handle, and eat were GAS, and the birds were often able to spend little time searching between GAS captures, suggesting that GAS were very abundant at the site (authors personal observations). Empty GAS shells littered the ground in numbers, occasionally in piles, in places along the fringes of the wetland.

Apple snail and extralimital Limpkin occurrence patterns. Our review found the first reports of GAS along

Table 1. Results of Limpkin observations at Lake Houma, Terrebonne Parish, Louisiana (observations by authors, except where noted).

Date	Observation start time	Observation duration (min)	Number of Limpkins observed	Highest breeding code[†] observed	Details
2 Feb. 2018	0715	43	2	Courtship	Both adults eating apple snails, calling, and 1 adult Limpkin passing apple snails to the other adult[‡]
7 Feb 2018[‡]	1542	42	2	Courtship	Birds continued to behave as if a mated pair, calling back-and-forth.
21 Feb. 2018	1334	197	2	Nest containing eggs	2 adults spent over 2 h and ca 1 h, respectively, sitting low and tight on an active nest, apparently incubating. Eggs were not visible from our vantage point, but 1 adult stood above and appeared to turn eggs with its bill.
12 Mar. 2018	1450	31	1	Nest containing eggs	1 adult sitting low and tight on nest for duration of our visit, apparently still incubating
21 Mar. 2018	1424	104	2	Nest containing eggs	1 adult sitting low and tight on nest for 1 h, except for standing up twice to rearrange nest material
26 Mar. 2018	1813	42	8	Recently fledged young[§]	We observed 2 adults with 6 downy young, ca 50–80 m from nest site (Fig. 2)
4 Apr. 2018[¶]	1652	37	4	Recently fledged young[§]	We observed 1 adult with 3 young
7 May 2018	1503	18	4	Juveniles	We observed at least 2 juveniles, which were nearly adult-size, foraging seemingly independently

[†] Laughlin et al. 1990.
[‡] Bracketing this date, J. Romano (6 Feb. 2018) and J. Rogers (12 Feb. 2018) observed the birds copulating (eBird 2019).
[§] Equivalent to downy young for nidifugous species (e.g., Limpkin).
[¶] On 1 Apr. 2018 K. Cunningham documented 7 juveniles, which was the maximum number of young birds observed at the site (eBird 2019).

Figure 1. Adult Limpkin and downy young, Lake Houma, Louisiana, 26 March 2018 documents first breeding record for Louisiana. Photo by J.L. Schulz.

the northern coast of the Gulf of Mexico, outside of Florida, in Houston, Texas in 2000. By 2008, all 5 states with watersheds that flow into the Gulf of Mexico, not including Florida, had at least one watershed with a reported GAS observation (Table 2, Fig. 2). The number of 6-digit HUC watersheds with reports of GAS increased from 0 in 1999 to 82 in 2017 for all states in the northern Gulf of Mexico basin except Florida (Table 2). As of 2017, every 6-digit HUC watershed that borders the Gulf of Mexico between Galveston Bay, Texas and the Lower Suwannee National Wildlife Refuge, Florida had at least 1 record of GAS. Concurrent with the increase in the number of unique watersheds occupied, the number of new locations reported within those watersheds also increased.

In addition to the first record of Limpkin breeding in Louisiana, our review of Limpkin data in the eBird database revealed breeding near Albany, Dougherty Co., Georgia (31.604, −84.182) in 2016, 2017, and 2018 (eBird 2019; Table 3, Fig. 2). Near Albany, W. Schaffner documented successful nesting, from copulation and nest building through incubation and young reaching fledging age, during April-June in both 2016 and 2017 at a site known as the Kingstown–Gardens Pond; this pair produced 6 and 5 juveniles in 2016 and 2017, respectively, at that pond (eBird 2019; Schaffner personal communication). Limpkins at the Kingstown–Gardens Pond fed almost exclusively on apple snails, which were abundant in 2016–2017 (eBird 2019; Schaffner personal communication). Schaffner's photos of apple snail egg masses from the site indicate GAS, of which there is a confirmed population in the Albany area (US Geological Survey 2018). Apple snail abundance at the Kingstown-Gardens Pond declined dramatically after 2016–2017. Concurrently, the Limpkins moved among a number of ponds in the immediate area in search of apple snails, and nested at the nearby Argonne-10th Pond, producing 2 juveniles, in 2018 (eBird 2019; Schaffner personal communication). Schaffner's observations suggest that the Limpkins' movements and shifts in breeding sites were a response to changing availability of apple snails in this complex of storm water management ponds.

In both Louisiana and Georgia, Limpkin breeding was documented where GAS populations had been present for several years in the same watershed at a location within 15 km of the nesting site. In Louisiana GAS was first documented in the Houma area in 2008. Since the initial report, GAS has spread throughout the Houma area and have now been noted throughout the watershed (6-digit HUC: Central Louisiana Coastal 080903). The Limpkin nesting site at Lake Houma was 15 km from the initial GAS report. Near Albany, Georgia, the first report of GAS was in 2011 and the first report of breeding by

Limpkin was in 2016, 5 km from the initial GAS locality. Note that historic records of Limpkin in southeastern Georgia, including suspected breeding, suggests that the species' natural range may have extended farther north than it does currently (summarized in Bryan 2002).

Six Limpkins occurred at Gantt Lake, Covington Co., Alabama (31.450, −86.418) in May to July 2017, with 2 of the birds representing a possible mated pair (eBird 2019; G. Jackson personal communication; Table 3, Fig. 2). Breeding was not confirmed at Gantt Lake, nor is GAS known to occur at the site (US Geological Survey 2018). Gantt Lake, however, has harbored an introduced population of Florida Apple Snails since 1970 (Benson 2018), and has hosted at least one extralimital Limpkin in the past (McConnell 2009), leading some to suspect that breeding may occur at the site (E. Soehren personal communication). Gantt Lake represents one of few known extralimital Limpkin localities to harbor multiple Limpkin individuals, repeated occurrences over time, and a prolific population of apple snails, characteristics which are consistent with the only known extralimital breeding sites in Louisiana and Georgia.

Table 2. Year of first report of GAS for 6-digit HUCs on the northern coast of the Gulf of Mexico, from years 2000 (00) through 2017 (17) (data from US Geological Survey 2018).

HUC	States†	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17
030402	SC									●									
030502	SC											●							
030601	GA									●									
030702	GA						●												
030801	FL						●												
031102	FL/GA								●										
031200	FL			●															
031300	FL/GA/AL										●								
031401	FL/AL												●						
031602	AL									●									
031700	MS/AL				●														
031800	LA/MS									●									
080702	LA													●					
080703	LA																		●
080801	LA																●		
080802	LA																●		
080902	LA									●									
080903	LA							●											
120301	TX									●									
120302	TX								●										
120401	TX								●										
120402	TX	●																	
120904	TX																		●
120701	TX								●										
SUM‡		1	0	1	1	0	2	1	4	6	1	1	1	1	0	0	2	0	2
CUM§		1	1	2	3	3	5	6	10	16	17	18	19	20	20	20	22	22	24

† Six-digit HUC watersheds of the northern Gulf Coast, which include portions of the states of South Carolina (SC), Georgia (GA), Florida (FL), Alabama (AL), Mississippi (MS), Louisiana (LA), and Texas (TX). For Florida, we only included HUC watersheds north of 29°30′ N latitude.
‡ SUM is the number of new 6-digit HUC watersheds invaded in a given year.
§ CUM is the cumulative number of 6-digit HUC watersheds invaded since the year 2000.

Extralimital breeding by Limpkins in Louisiana and Georgia, and possibly Alabama, during the 2016–2018 period coincided with widespread wandering by Limpkins in the southeastern USA (Table 3). Extralimital occurrences of nonbreeding Limpkins, however, have been increasing in general since the early 2000s, at least in Alabama, Georgia, and South Carolina (Table 3). Over this same time period, these states have experienced colonization by GAS (Table 2). In Georgia and South Carolina, most Limpkin records and all but one of those pertaining to multiple individuals, are from watersheds known to harbor GAS (Table 3). Alabama follows the same trend if one expands the Limpkin-GAS relationship to include the invasive Florida Apple Snail (Table 3). These patterns further support the hypothesis that an invasive prey species may facilitate range expansion by a native predator species.

Identification. Limpkin is a distinctive, rail-like wading bird, unlikely to be confused with other species: sexes are alike, and juvenal plumage resembles definitive plumage (Bryan 2002). Similar species include: immature ibises, including White Ibis, *Eudocimus albus* (Linnaeus, 1758), Glossy Ibis, *Plegadis falcinellus* (Linnaeus, 1766), and White-faced Ibis, *P. chihi* Viellot, 1817, which are superficially similar to Limpkin, but Limpkin is easily distinguished by its overall brown plumage with white spots, and straighter, more horn-orange colored bill. Immature Black-crowned Night-Heron, *Nycticorax*

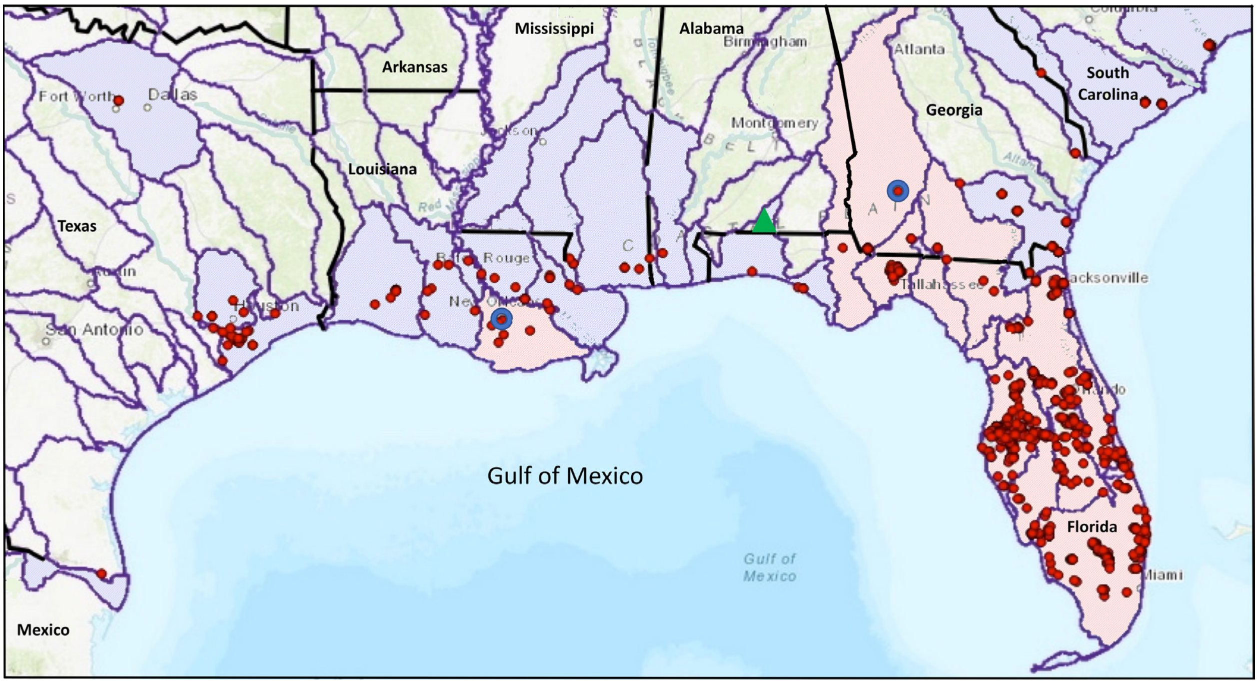

Figure 2. Six-digit HUC watersheds occupied by GAS in the states of South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, and Texas, with those lacking Limpkin breeding records shaded light purple and those containing Limpkin breeding records shaded pink (as of April 2018). Red dots represent cumulative reported GAS localities (2001-2017; US Geological Survey 2018). Blue dots and the green triangle represent confirmed and suspected Limpkin breeding localities, respectively, outside of Florida. Note that the green triangle represents a locality that contains an introduced Florida Apple Snail population, but whose 6-digit HUC (031403) currently lacks documented Giant Apple Snail occurrence (locality only ca 2.5 mi from HUC (031401), which does contain GAS records).

Table 3. Verifiable records of vagrant Limpkins in the eastern USA.

Region/state	County	Locality[†]	Date[‡]	No.[§]	Source	Basin–GAS?[‖]
Middle Atlantic						
Maryland	Frederick	Buckeystown	May 1971	1	MOS 2019[#]	Potomac
	Howard	Benson	May 1985	1[¶]	MOS 2019[#]	Upper Chesapeake
	Howard	Dayton	Jun 2018	1[¶]	eBird 2019	Upper Chesapeake
Virginia	Lynchburg	Lynchburg College	Apr 1971	1[¶]	Scott 1971[#]	James
	James City	Near Williamsburg	Jun 2017	1[¶]	VARCOM 2019[#]	James
Southern Atlantic						
North Carolina	Columbus	Lake Waccamaw SP	Sep 1975	1	LeGrand 1990[#]	**Lower Pee Dee**
	Bladen	Smith Mill Pond	May 1983	1	LeGrand 1990[#]	Cape Fear
	Craven	New Bern	Jun 1998	1[¶]	LeGrand 2001[#]	Cape Fear
	Pender	Roan Island	Aug 1998	1	LeGrand et al. 2019	Neuse
	Catawba	Lake Norman	Jul 2015	1[¶]	Piephoff 2016[#]	Santee
	Pender	Black River	Jul 2018	1	LeGrand et al. 2019	Cape Fear
South Carolina	Aiken	Dead River	Oct 1890	2[††]	Post and Gauthreaux 1989	**Savannah**
	Charleston	Charleston	Jul 1904	1[††]	Post and Gauthreaux 1989	**Edisto–SC Coastal**
	Jasper	Savannah NWR	Apr 1971	1[¶]	Metz and Forsythe 2004	**Savannah**
	Jasper	Savannah NWR	Mar 2001	1[¶]	Glover 2002[#]	**Savannah**
	Horry	Little Pee Dee River	May 2001	2[¶]	Glover 2002[#]	**Lower Pee Dee**
	Charleston	Magnolia Gardens	May 2001	1[¶]	Cely et al. 2003	**Edisto–SC Coastal**
	Sumter	Upper Santee Swamp	Sep 2001	1[¶]	Cely et al. 2003	Santee
	Colleton	Green Pond	May 2003	1[††]	Davis 2003	**Edisto–SC Coastal**
	Lancaster	Cane Creek	Aug 2005	1[¶]	Slyce 2006[#]	Santee
	Charleston	Magnolia Gardens	Apr 2007	1[¶]	eBird 2019	**Edisto–SC Coastal**
	Jasper	Savannah NWR	Jul 2012	1[¶]	eBird 2019	**Savannah**
	Marion	Little Pee Dee River	Jul 2015	1[¶]	Hill 2016[#]	**Lower Pee Dee**
	Sumter	Sparkleberry Swamp	Sep 2015	1[¶]	eBird 2019	Santee
	Greenville	Lake Robinson	May 2017	1[¶]	Given 2018[#]	Santee
	Orangeburg	Santee SP	May 2017	1[¶]	Given 2018[#]	Santee
	Laurens	Lake Greenwood	Jul 2017	1[¶]	Given 2018[#]	Santee
	Georgetown	Waccamaw NWR	Jul 2017	1[¶]	Given 2018[#]	**Lower Pee Dee**
	Sumter	Lake Marion	Apr 2018	1	SCBRC unpubl.[#,‡‡]	Santee
	Richland	Congaree NP	Apr 2018	1[¶]	SCBRC unpubl.[#,‡‡]	Santee
	Jasper	Savannah NWR	Jul 2018	1[¶]	SCBRC unpubl.[#,‡‡]	**Savannah**

Table 3. Continued.

Region/state	County	Locality[†]	Date[‡]	No.[§]	Source	Basin–GAS?[ǀ]
Georgia	Monroe	Russellville	Sep 1994	1[¶]	Adrien 1994[#,§§]	Altamaha
	McIntosh	Harris Neck NWR	Apr 2001	1[¶]	Bell 2001, Cely et al. 2003	Ogeechee
	Cook	Reed Bingham SP	May 2003	1[¶]	GCRC records[#,‖]	**Suwannee**
	Henry	Lake Blalock	Jun 2004	1[¶]	GCRC records[#,‖]	Altamaha
	Cook	Reed Bingham SP	Jun 2006	1[¶]	GCRC records[#,‖]	**Suwannee**
	Wayne	Alex Creek	Jul 2006	1[¶]	GCRC records[#,‖]	Altamaha
	Henry	Lake Blalock	Jul 2006	1[¶]	eBird 2019	Altamaha
	Dougherty	Chickasawhatchee WMA	Jul 2006	4[¶]	Davis 2007a	**Apalachicola**
	Wayne	Sansavilla WMA	Sep 2006	1[¶]	Davis 2007b	Altamaha
	Tattnall	Big Hammock WMA	Jun 2007	1[¶]	Davis 2008	Altamaha
	Crisp	Georgia Veterans SP	Dec 2007	1[¶]	GCRC records[#,‖]	**Apalachicola**
	Charlton	Okefenokee NWR	Apr 2011	1[¶]	GCRC records[#,‖]	**Suwannee**
	Liberty	Fort Stewart	Apr 2011	1[¶]	LeGrand et al. 2014	Ogeechee
	Jenkins	Millen	Apr 2013	1[¶]	GCRC records[#,‖]	Ogeechee
	Crisp	Georgia Veterans SP	May 2014	3[¶]	GCRC records[#,‖]	**Apalachicola**
	Crisp	Georgia Veterans SP	Jul 2015	2[¶]	GCRC records[#,‖]	**Apalachicola**
	Colquitt	Reed Bingham SP	Mar 2016	1[¶]	GCRC records[#,‖]	**Suwannee**
	Dougherty	Near Albany	Jun 2016	8[¶]	eBird 2019	**Apalachicola**
	Colquitt	Reed Bingham SP	Aug 2016	1[¶]	GCRC records[#,‖]	**Suwannee**
	Colquitt/Cook	Reed Bingham SP	Jan 2017	2[¶]	eBird 2019	**Suwannee**
	Dougherty	Near Albany	Feb 2017	7[¶]	eBird 2019	**Apalachicola**
	Clayton	Clayton Co. Water Authority	May 2017	3[¶]	eBird 2019	Altamaha
	Camden	St Marys	May 2017	1	eBird 2019	**St Marys–Satilla**
	Tift	Undisclosed	Jun 2017	1[¶]	eBird 2019	**Suwannee**
	Crisp	Georgia Veterans SP	Jun 2017	1[¶]	eBird 2019	**Apalachicola**
	Decatur	Stones Landing	Jul 2017	1[¶]	eBird 2019	**Apalachicola**
	Brooks	Quitman Country Club	Aug 2017	1[¶]	eBird 2019	**Suwannee**
	Seminole	Ray's Lake	Sep 2017	1[¶]	eBird 2019	**Apalachicola**
	Decatur	Lake Seminole–Woodruff Dam	Jan 2018	1[¶]	eBird 2019	**Apalachicola**
	Calhoun	Chickasawhatchee WMA	Apr 2018	1[¶]	eBird 2019	**Apalachicola**
	Dougherty	Near Albany	May 2018	6[¶]	eBird 2019	**Apalachicola**
	Glynn	Clayhole Swamp WMA	May 2018	1[¶]	eBird 2019	Altamaha
	Muscogee	Cooper Creek Park	May 2018	1[¶]	eBird 2019	**Apalachicola**
	Cook	Reed Bingham SP	Jul 2018	1[¶]	eBird 2019	**Suwannee**
Central southern						
Tennessee	Davidson	Radnor Lake	Jun 1961	1	Morlan 1961	Lower Cumberland
	Haywood	Hatchie NWR	Sep 1999	1[¶]	Somershoe and Sloan 2015	Hatchie–Obion
	Marion	Tennessee River Gorge Trust	May 2017	1	eBird 2019	Middle Tennessee–Hiwassee
Alabama	Cullman	Smith Lake	Sep 2000	1[¶]	McConnell and Wells 2002; Gardella 2004[#]	Black Warrior-Tombigbee
	Lee	Opelika	Aug 2000	2	McConnell 2006[#]	Coosa–Tallapoosa
	Covington	Gantt Lake	Sep 2007	1[¶]	McConnell 2009[#]	Escambia
	Barbour	Eufaula NWR	May 2012	1[¶]	McConnell 2013[#]	**Apalachicola**
	Houston	Cottonwood	Nov 2016	2	Kittle et al. 2016	**Apalachicola**
	Covington	Gantt Lake	May 2017	6[¶]	eBird 2019	Escambia
	Tallapoosa	Near Alexander City	May 2017	1[¶]	eBird 2019	Coosa–Tallapoosa
	Barbour	Eufaula NWR	Jun 2017	2[¶]	eBird 2019	**Apalachicola**
	Autauga	Near Prattville	Jun 2017	1[¶]	Kittle et al. 2017	Alabama
Mississippi	Alcorn	Waukomis Lake	May 1956	3	Warriner 1962	Hatchie–Obion
	Lowndes	Near Columbus	Jun 1972	1[¶]	Turcotte and Watts 1999	Black Warrior–Tombigbee
Louisiana	Lafourche	Lake Boeuf	Dec 2017	4[¶]	Dittmann and Cardiff 2018[#]	**Central Louisiana Coastal**
	Terrebonne	Lake Houma	Jan 2018	9[¶]	eBird 2019; this study	**Central Louisiana Coastal**

† Locality abbreviations: State Park (SP), National Wildlife Refuge (NWR), Wildlife Management Area (WMA).
‡ Initial sighting date.
§ Maximum number of individual Limpkins observed.
ǀ Six-digit HUC basin containing Limpkin record; bold text signifies that NAS database also indicates GAS occurs in basin (US Geological Survey 2018). Note that this is not applicable for historical records, as GAS first appeared, in the NAS database, north of Florida in 2003 (US Geological Survey 2018).
¶ Record documented with photograph.
# Record endorsed by state bird records committee.
†† Record documented by specimen.
‡‡ South Carolina Bird Records Committee (SCBRC) data; SCBRC removed Limpkin from its review list in 2018 (fide A. Given, SCBRC Chair).
§§ Davis (1995) noted that this was the first record in Georgia in 19 years. We did not include predating this record because Limpkin historically occurred in southeastern Georgia (see Bryan 2002, Beaton et al. 2003).
‖ Georgia Ornithological Society Checklist and Records Committee (GCRC) data; GCRC removed Limpkin from its review list in 2018 (fide J. Flynn, GCRC Chair).

nycticorax (Linnaeus, 1758) and Yellow-crowned Night-Heron, *Nyctanassa violacea* (Linnaeus, 1758) are also superficially similar to adult Limpkin, but, again, are easily differentiated by bill shape and color, and plumage details. Voices of all of these species differ from that of Limpkin. The Limpkin pair vocalized during our observations, particularly in the early nesting stages. Vocalizations were unique, loud series of bugling "krreeeow" calls with a crane-like quality, unlike vocalization of any other Louisiana bird. Based on the large, broad shape of the white spots on the birds' wing coverts and scapulars, and the lack of white at the base of the secondaries (Bryan 2002), the Limpkins reported herein are of subspecies *A. g. pictus* (Meyer, 1794). This subspecies occurs in Florida, the Bahamas and the Greater Antilles (Bryan 2002) and is the expected taxon to occur in the southeastern USA, assuming that the birds would most likely originate in the Florida population.

Pomacea apple snails are characteristically large as adults (>5 cm shell length), with globular-shaped shells, the presence of an operculum, and they lay egg masses above the water line, a combination of characteristics that differentiates them from any native snail on the northern Gulf of Mexico coastal plain west of Florida (Rawlings et al. 2007). Within *Pomacea* species, the one species that GAS may be confused with is the Channeled Apple Snail, *P. canaliculata* (Lamarck, 1828), based on shell and egg mass morphology. The 2 species, however, may be distinguished by the size of their eggs, the number of eggs in an egg mass, and subtle differences in shell morphology (Hayes et al. 2012). We identified egg masses in the immediate vicinity of our observations as those of GAS. Further, in a previous genetic study, apple snails identical to those at the Limpkin breeding site were determined to be *P. insularum* (Carter unpublished data), which has been synonymized with *P. maculata* (i.e., GAS).

For Limpkin and GAS records accessed by the eBird and NAS databases, respectively, we relied on data verification measures implemented by eBird (details in Sullivan et al. 2009) and the US Geological Survey (details in US Geological Survey 2018) personnel.

Discussion

Our breeding observation of Limpkin in Louisiana is ca 570 km (350 mi.) west of the nearest confirmed published breeding record (Wakulla Co., Florida; Florida Fish and Wildlife Conservation Commission 2003), which is essentially the western edge of the species' established range (Bryan 2002, eBird 2019). The Louisiana breeding record also coincides with other recent accounts of Limpkin breeding activity outside of the species' northern stronghold in the Florida panhandle, with the first known breeding activity in Georgia in 2016 (at least in modern times), as well as possible breeding activity in Alabama in 2017. Extralimital Limpkin breeding records and Limpkin behavior at those sites (e.g., adults collecting, extracting, eating and feeding apple snails to young birds) compared to GAS occurrence data suggests that GAS colonization of the northern Gulf coast, north and west of the Florida panhandle, may be facilitating Limpkin extralimital breeding and possibly range expansion (see also Marzolf et al. 2019). Frequency and distribution of extralimital Limpkin non-breeding records compared with GAS occurrence data are also consistent with that hypothesis.

We did not include watersheds entirely within Florida in our analysis because we wanted to avoid Limpkin breeding locations that could be considered at the margins of their traditional range, and because there was evidence of Florida Apple Snail range expansion in the state (Benson 2018). Given that there are 9 other 6-digit HUC watersheds outside of Florida along the northern Gulf of Mexico drainage basin with GAS observations, we suspect that there may be other Limpkin breeding sites outside of Florida that have not yet been discovered. Indeed the 2 confirmed extralimital Limpkin breeding sites discussed herein (Louisiana, Georgia) are near roads. Vast areas of freshwater marsh, particularly in Louisiana, are roadless and inaccessible to the vast majority of birders, begging the question: what is the true status and distribution of Limpkin within the expanding range of GAS on the northern Gulf coast?

We know of no data showing that extralimital Limpkins are unable to persist or breed on the northern Gulf coast in the absence of apple snails, other than Limpkin's current geographic range and its close association with the Florida Apple Snail. It is possible that the recent, unprecedented wandering of Limpkins north and west of Florida is a response to some unknown environmental stimulus, and may be short-lived, with extralimital Limpkins breeding to lessen the negative impacts associated with being displaced from their ideal range (as opposed to Limpkins following an ample food source opportunistically). Causes of Limpkin vagrancy have not been explored in detail, but may include response to drought in the species' core range in Florida (Cely et al. 2003) and associated negative effects on habitat conditions and food availability (apple snails, other mollusks). Extralimital Limpkins clearly rely on apple snails where they are available (authors' observations; eBird 2019). Little information is available on extralimital Limpkin diet where apple snails are not available, but reports generally involve bivalves (eBird 2019), including Giant Floater, *Pyganodon grandis* (Say, 1829) and Paper Pondshell, *Utterbackia imbecillis* (Say, 1829) in northern Alabama (McConnell and Wells 2002).

It is important to recognize that Limpkin and GAS occurrence and distribution patterns presented herein are based on data with inherent limitations. Much of our Limpkin data are from the eBird citizen science database, contributions to which have increased nearly exponentially since its inception in 2003. That period (2003–2018) presumably worked fairly well in our comparative context with GAS data from the NAS database because GAS colonization of the northern Gulf coast occurred over the same period. Nevertheless, we attempted to mitigate this potential source of temporal bias by searching literature and authoritative bird status and distribution reference material for additional Limpkin occurrence data. Literature and other reference material was particularly important in composing our more general summary of Limpkin vagrancy. Similarly, tracking GAS range expansion using the NAS database has limitations, of which under-reporting is a concern. The NAS database relies on the public and professionals to report locations of GAS, which does not always happen for a variety of reasons. More importantly for our analysis, GAS populations may become established in areas between localities documented in the NAS database, and thus their distribution within a watershed may often be incomplete. To ensure that we were not omitting other readily-available GAS occurrence data, we examined GAS locality records in the iNaturalist citizen science database (iNaturalist.org 2019); those data did not provide any novel GAS records at the scale of the 6-digit HUCs that we used in our analysis.

Snails in the genus *Pomacea* have the potential to cause ecosystem disruption (Carlsson and Lacoursiére 2005) and GAS may be negatively impacting wetlands on the northern Gulf Coast by reducing aquatic vegetation cover and depredating native species (Baker et al. 2010, Bonin 2016, Carter et al. 2018). There are limited management options for *Pomacea* species in non-agricultural wetland systems. Native predators, however, may play an important role in apple snail management (Yusa et al. 2006, Yamanishi et al. 2012), and there is evidence that American Alligator, *Alligator mississippiensis* (Daudin, 1802) (Elsey et al. 2017), Raccoon, *Procyon lotor* (Linnaeus, 1758) (Carter et al. 2017), and now Limpkin (this work) may utilize a new resource with the establishment of GAS. Further, the risk of GAS invading additional watersheds is high. For watersheds that drain into the Gulf of Mexico, an average of 10 new populations per year have been reported in the past 4 years (Benson 2019). Byers et al. (2013) modeled apple snail distribution based on climate and pH and suggested that, except for areas with low pH waters such as blackwater swamps, the entire coastal plain from North Carolina to Texas was at risk of apple snail invasion under the current climatic regime.

Another species whose breeding range in the United States has been limited by the range of the Florida Apple Snail, but which may have the potential to respond to expanding GAS populations, is the Florida Snail Kite, *Rostrhamus sociabilis plumbeus* Ridgway, 1874 (Cattau et al. 2016), which is listed as endangered in the United States (US Fish and Wildlife Service 2018). While the Florida Snail Kite has occasionally been found outside of its normal range and feeding on species other than apple snails (Slyce et al. 2009, Serridge 2017), its range in the USA has been restricted to southern Florida. While it was initially feared that the GAS might be too large for younger Florida Snail Kites to eat (Cattau et al. 2010) and thus its proliferation in the Florida Snail Kite's range was of concern, a recent report has documented that the kites are developing morphological adaptations to consume GAS (Cattau et al. 2017). Cattau et al. (2016) demonstrated that Florida Snail Kites adjusted their movements and local breeding distribution to track the spread of GAS in a complex of wetlands in southern Florida. Recent observations of extralimital breeding by Florida Snail Kites at GAS-occupied wetlands in northern Florida suggest that northward range expansion facilitated by GAS is a possibility (C. Poli, personal communication). Note also that Texas has 4 extralimital records of Snail Kite (Texas Bird Records Committee 2019), presumably birds originating in Mexico or Central America; vagrants of that population also have the potential to exploit a previously unavailable resource, as GAS continues to spread in Texas (Perez et al. 2017, US Geological Survey 2018).

The scenario described above is not without precedent. Range expansion by both Limpkin and Snail Kite followed the introduction and establishment of apple snails, reportedly *Pomacea flagellata* (Say, 1827) and *P. patula* (H.B. Baker, 1922), on the Pacific coast of northwestern Mexico (Hernández-Vázquez et al. 1999, 2013, Palomera-García et al. 2006). In Mexico and northern Central America, Limpkin and Snail Kite occur from Veracruz through the Yucatan Peninsula to Honduras (and beyond) on the Atlantic slope (Howell and Webb 1995). On the Pacific slope, as recently as the early 1990s, Limpkin occurred from El Salvador north only to eastern Oaxaca, and Snail Kite was locally distributed in Guatemala and in Chiapas and Guerrero, Mexico (Howell and Webb 1995). Limpkin and Snail Kite began colonizing Pacific lowland area in Colima and Nayarit, Mexico in the mid-1990s (Howell 1994). Limpkin range expansion of the region accelerated in the late 1990s (Hernández-Vázquez et al. 1999, Howell 2004), and continued in the 2000s when Palomera-García et al. (2006) documented its association with *P. flagellata* in Jalisco, Mexico. Snail Kite range expansion followed suit, but with a 5–10-year time lag relative to Limpkin range expansion (Howell 1994, Hernández-Vázquez et al. 2013).

Factors other than apple snail availability may continue to restrict Florida Snail Kites to Florida, yet there exists the possibility that they may undergo range expansion, similar to what appears to be underway with Limpkin, to areas where populations of GAS have become established along the northern Gulf of Mexico coast. The management goal to control GAS could potentially come into conflict with the management goal to conserve Florida Snail Kite, if kites expand to new breeding areas along the northern Gulf coast. On the other hand, Limpkin and Florida Snail Kite may eventually play important roles in the management of GAS in these same areas. Extralimital interactions between Limpkin and GAS, as demonstrated in this study, represent the possibility that an invasive species may support native species (Rodriguez 2006, Schlaepfer et al. 2011).

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Authors' Contributions

RCD, JC, and JLS conceived and wrote the manuscript; RCD and JLS made the field observations; JLS produced the figures.

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