THE GREEN TREEFROG, HYLA CINEREA (SCHNEIDER), IN INDIANA

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ABSTRACT. The Green Treefrog, *Hyla cinerea*, is widely distributed in the southeastern quadrant of the United States. Although it did not occur historically in Indiana, it was recorded from Vanderburgh County in extreme southwestern Indiana in 2003. From 2003 to 2013 we documented this hylid's range expansion in Indiana as part of a rapid and recent range expansion in adjoining states in the middle Mississippi Valley. Likely dispersal mechanisms for its appearance and colonization in southwest Indiana are discussed. In addition to distributional records, its status, relative abundance, and potential for additional colonization within the state are reviewed. Our findings indicate that *H. cinerea* arrived in the state as part of a natural range expansion and that it appears to be permanently established as member of the state's herpetofauna.

Keywords: colonization, dispersal, distribution, Hyla cinerea, Indiana, treefrog, range expansion

INTRODUCTION

The Green Treefrog, Hyla cinerea (Schneider), is a moderate sized elongate anuran, native to lowlands in the southeastern United States. It is a wide-ranging hylid, occurring historically on the Atlantic Coastal Plain from the Delmarva Peninsula and Chesapeake Bay region southward, throughout all of Florida and the Gulf Coastal Plain, westward through east Texas, and northward up the Mississippi Embayment to extreme southern Illinois and extreme western Kentucky (Conant & Collins 1998; Redmer & Brandon 2005). While the species is known from southern Illinois and western Kentucky, its historic occurrence there has been restricted to a few localities on the lower Mississippi and Ohio River floodplains. Published range maps reflect this limited distribution (Barbour 1956, 1971; Smith 1961). Prior to 2003, H. cinerea was not known from Indiana. It does not appear in any of the published accounts of the state's herpetofauna (Hay, 1886, 1892; Minton 1972, 2001; Minton et al. 1983).

In spite of the historical geographic hiatus between H. cinerea populations in the middle Mississippi Valley and Indiana, H. cinerea was discovered in the state in 2003 (Lodato 2003; Lodato et al. 2004). This discovery raised a number of questions about this species in Indiana: a) how did it come; b) its status, i.e., a native but previously overlooked species, a natural range expansion, or an introduction; c) its distribution; d) its ecological niche; e) its natural history and how it compares with its natural history elsewhere; and f) its future? Interest in addressing these questions led to collaboration between the senior author and personnel from the Indiana Department of Natural Resources Wildlife Diversity Program.

METHODS

We reviewed the published literature, unpublished reports, and corresponded with regional herpetologists and naturalists knowledgeable about *H. cinerea*. In mapping the historical distribution, we relied on published

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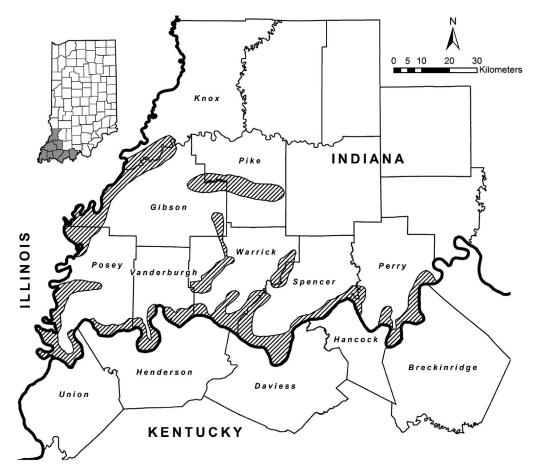


Figure 1.—Counties surveyed for *Hyla cinerea* in southwest Indiana, 2003-2013. Crosshatching depicts primary search areas along major rivers and tributaries in eight southwest Indiana counties.

and unpublished reports prior to 1985. We adopted this cut-off based on the analysis of Brainard Palmer-Ball, formerly of the Kentucky Nature Preserves Commission (Pers. Comm.), who used this date, and Redmer et al. (1999), who generally state that new and extra-limital Illinois populations were first noted in "the 1980s" and thereafter. Distribution records after that time were considered as current. Beginning in 2003, we surveyed for populations of H. cinerea by listening for breeding choruses and male advertisement calls during the active season, typically from the first week of May through the last week of July, with 4 May the earliest survey date and 1 August the latest. Surveys were conducted during evening and night, typically between 18:30 and 24:00 hours CDT. We conducted systematic field surveys annually from 2003

through 2013. Both known *H. cinerea* sites and potential sites were revisited each year in order to detect new populations and changes to known populations. Sites chosen for survey included known natural wetlands along stream corridors and river bottoms, and other wetland sites based on our experience with the species outside the state. More than 150 sites in eight counties in southwest Indiana (Gibson, Knox, Perry, Pike, Posey, Spencer, Vanderburgh, and Warrick) were surveyed (Fig.1). In addition to auditory surveys, we opportunistically examined vegetation adjacent to wetlands and surveyed roadways adjacent to potential sites. The geographic coordinates were recorded when H. cinerea was detected. When located in a new county, either a voucher specimen was collected or a photographic voucher was taken. Specimens were deposited at the University of Michigan Museum of Zoology in Ann Arbor, Michigan, and photographic vouchers were deposited in the Illinois Natural History Survey in Champaign, Illinois. The natural features and vegetation at each site as well as relative abundance of the population were noted.

GENERAL DESCRIPTION

Hyla cinerea is usually bright green with a rather streamlined, slender build (Fig. 2). The only other treefrogs in Indiana that may occasionally be confused with *H. cinerea* are the gray treefrogs of the *Hyla versicolorchrysocelis* complex. Treefrogs of these sibling species, while usually gray, with a heavily mottled pattern on the dorsum, occasionally also display a bright green dorsal coloration. However, the body shape of gray treefrogs is stockier than *cinerea*, and the snout is blunt and rounded. Additionally, there is invariably a unique white blotch below the eye, and an orange or yellow wash is always present in the hidden area of the groin.

The advertisement call of males of *H. cinerea* is distinctive, easily detected, and is the best field indicator of its presence, particularly during the breeding season. Large choruses of singing males have considerable carrying power. Individual calls have a distinct metallic sound (Smith 1961), and several authors liken the call to the clanging of a bell, sometimes more specifically to a cowbell (Garman 1892; Wright & Wright 1949; Smith 1961). While the cowbell comparison may be dated, the metallic clanking sound is accurate. We describe the call as a monotonous and repetitive "wank, wank, wank ... " and others describe it similarly (Wright & Wright 1949; Smith 1961). The call is repeated at a rate of between 0.27 and 1.1 calls per second (Oldham & Gerhardt 1975). An aggression call, described by Elliot et al. (2009) is said to be a harsh but quickly repeated "quarr-quarr-quarr."

RANGE EXPANSION IN NEARBY STATES

A number of authors note a range expansion for this species (e.g., Dodd 2013, Green et al. 2014). The distribution maps for *H. cinerea* in this paper (Figs. 3 & 4) update recent maps in Dodd (2013) and Green et al. (2014). On a more local level, regional authorities, referenced below, provide a more detailed description of range expansion and the species' current distribution.

We estimate that this range expansion began about 15 years before H. cinerea appeared in Indiana, perhaps in the mid- to late-1980s. The expansion appears to have been pronounced at the northern periphery of the historical range for the species in the middle Mississippi Valley, and is well documented. In adjacent Illinois, Redmer et al. (1999) report an extraordinary range expansion beginning in the mid-1980s. In his monograph on Illinois amphibians and reptiles, Smith (1961) reports H. cinerea from just four localities in two counties in the extreme southwestern tip of the state, and he states, "I have been unable to find the species anywhere north of Union County" (p. 89). In contrast, Redmer et al. (1999) plots 127 localities including several new counties. A distribution map published that year for Illinois indicates that it was then present in nine counties in the southwestern corner of the state (Phillips et al. 1999). Subsequent to this, an undated online revision to the distribution map by the Illinois Natural History Survey (IHNS 2012) added Clinton and Monroe Counties. These records are based on collections in 2001 (Christopher Phillips, Pers. Comm.). Another major range expansion, to Jersey County (Tucker et al. 2008) brings to twelve the number of counties with populations of H. cinerea in Illinois. This range expansion, for the most part, occurred very rapidly, perhaps in little more than one or two decades. It is all the more remarkable when one considers that, as recently as the mid-1970s, H. cinerea was classified as a rare and/or endangered species in Illinois (Dyrkacz 1974; Ackerman 1975).

In adjoining Kentucky, John MacGregor of the Kentucky Department of Fish and Wildlife Resources, and Brainard Palmer-Ball of the Kentucky State Nature Preserves Commission (Pers. Comm. & unpublished distribution data) have data showing a rapid and continuing range expansion northward and eastward into the west Kentucky coal field and beyond, including Ohio River border counties adjacent to southwest Indiana. Historically *H. cinerea* was unknown outside the Jackson Purchase region of Kentucky, and even there it was restricted to the western edge of four counties bordering the Mississippi River (Dury & Gessing 1940; Barbour 1956, 1971). *Hyla*



Figure 2.—Photographs of *Hyla cinerea* from Indiana. Top: Specimen from Vanderburgh County, voucher for state of Indiana. Bottom: Photographic voucher of specimen from Warrick County.

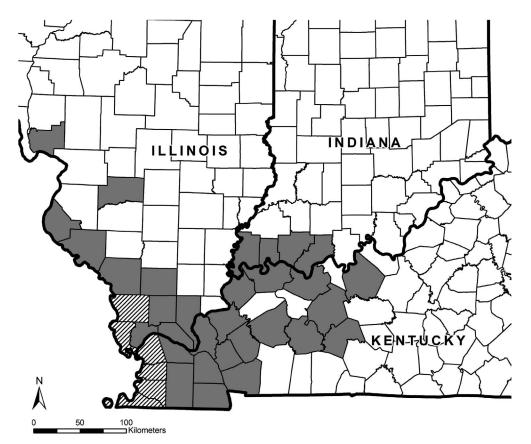


Figure 3.—Counties harboring populations of *Hyla cinerea* in Illinois, Indiana, and Kentucky. Slant lines depict counties with historical populations of *H. cinerea*; grayscale depicts range expansion for the species in the region since about 1985. Two counties in eastern Kentucky containing artificially introduced populations of *H. cinerea* are not included in this figure.

cinerea is currently known from at least 19 counties, 15 of which are east and north of the species' historical range, and four of these (Breckinridge, Daviess, Henderson, and Union) border Indiana (Kentucky Department of Fish & Wildlife Resources 2014; and John MacGregor, Pers. Comm.). Additionally, field work by MacGregor confirms the species in Hopkins County (Pers. Comm.). Independent field work by Noah Gordon and his students confirms the species in Caldwell County (Pers. Comm.). Twenty-one counties harbor *H. cinerea* in western Kentucky (Fig. 3).

In Missouri, Powell et al. (1995, 1996) document substantial range expansions from the historical range in the lowlands of the Missouri "bootheel." Jeff Briggler of the Missouri Department of Conservation reports new populations in central Missouri well outside the species' historical range (Pers. Comm.). In Tennessee, *H. cinerea* "appears to be expanding its range upstream along the Cumberland River, as well as along the Tennessee River Valley west of Chattanooga...." (Reynolds 2013, p. 276).

The senior author has herpetological field experience dating from the 1960s in the middle Mississippi Valley region of southern Indiana and Illinois, western Kentucky and Tennessee, and southeastern Missouri, and field experience with *H. cinerea* in this region and throughout its range dating from the early 1970s. It is undeniable that *H. cinerea* has rapidly expanded its range from a few highly restricted localities at the northern edge of the Mississippi Embayment to a much larger landscape in suitable aquatic sites in multiple eco-regions and physiographic provinces, and now including some in extreme southwest Indiana. The rate of this range expansion,

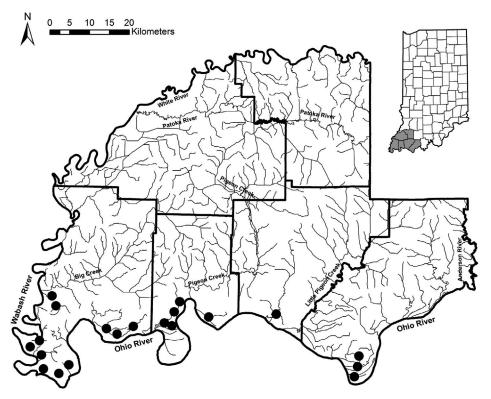


Figure 4.—Distribution of breeding colonies of Hyla cinerea in Indiana as of 2014.

observed firsthand, has been nothing short of remarkable.

The range expansion of *H. cinerea*, primarily northward and eastward in the middle Mississippi Valley, is not restricted to that region. Significant range expansions have been recently confirmed along the Atlantic Coastal Plain, northward into the Piedmont in South Carolina (Snyder & Platt 1997) and in both Georgia and South Carolina along the Savannah River drainage (Platt et al. 1999).

The impetus for this range expansion is unknown. In Illinois, it may be facilitated by climate change (Tucker et al. 2008) and possibly aided to by human activities (Phillips et al. 1999; Redmer et al. 1999); however, the consensus of these authors is that the range expansion is a natural phenomenon. Range expansion in Kentucky is likely similar in nature, although there are documented instances where the frogs have been inadvertently introduced with fish hatchery stock, probably as tadpoles, in at least two eastern Kentucky localities (John MacGregor, Pers. Comm.). In Indiana, there is no evidence of artificial introduction at any of our sites. Indeed, all known Indiana populations occur in natural lowland habitats or on adjacent terraces and nearly all of these sites are remote, seldom visited locations on the floodplains of the lower Wabash and Ohio Rivers (Fig. 4). Redmer & Brandon (2003) suggest that the species' ability to reproduce in wetlands and other aquatic situations with predatory fish has greatly aided its rapid colonization of new sites.

APPEARANCE OF HYLA CINEREA IN INDIANA

Hyla cinerea was first confirmed in Indiana based on specimens collected on 14 June 2003 by Jim Horton of Indianapolis and Scott Kramer of Evansville, Indiana (Lodato 2003). These original specimens were retained by Mr. Horton in a private, living collection. The collection site was Howell Slough, an oxbow pond on the Ohio River floodplain and adjacent to Carpenter Creek. Howell Slough is located in Perry Township, Vanderburgh County, and at the southwestern limits of the city of Evansville. Subsequent to the first collection of specimens by Horton and Kramer, voucher specimens were collected for deposit in a museum collection (Lodato et al. 2004).

The appearance of H. cinerea in Indiana, while surprising, was not completely unexpected. In his revised monograph on Indiana amphibians and reptiles, Minton (2001) suggests that this species might be found in the state based on a recent record for *H. cinerea* from adjacent Henderson County, Kentucky (Lodato & Grannan 1990). Henderson County lies on the Ohio River and borders all of Vanderburgh County, Indiana, as well as portions of Warrick and Posey counties in Indiana. The original Henderson County collection site is a large cypress swamp on the Ohio River floodplain just west of the confluence with the Green River. The record is of interest because Ralph Gessing, a collector associated with the Cincinnati Museum of Natural History, states in correspondence with Philip Smith of the Illinois Natural History Survey that he and others collected H. cinerea in Henderson County in the 1940s (Smith 1966). This claim was dismissed at the time because the locality was so far out of range from known populations in southwest Illinois and western Kentucky (Smith 1966). The Cincinnati Museum of Natural History has no specimens of *H. cinerea* from Henderson County (Pers. Comm.).

Subsequent to the 1989 discovery and verification of *H. cinerea* in Henderson County, the senior author surveyed for the species in suitable habitat in adjacent Indiana in Posey, Vanderburgh, and Warrick Counties. In 2000, Brodman (2003) conducted anuran call surveys in both Posey and Spencer Counties during times when H. cinerea is seasonally active. No green treefrogs were located in Indiana during any of these surveys. In 1998, H. cinerea appeared for the first time in the western portion of Henderson County in a bottomland wetland complex about 18 km west and downstream of the original collection site in Henderson County. This area, immediately north of Smith Mills, is known as "the sloughs." The senior author, in conjunction with Michael Kerr, had extensively surveyed the anurans of this area dating back to 1973, and no H. cinerea were present (Lodato & Kerr 1974). However, by 2000, we noted that H. cinerea was firmly established in these wetlands on and adjacent to the Ohio River floodplain in western Henderson County, and by 2002 it had begun to saturate available habitat. At that time one could drive from the town of Geneva westward along Kentucky State Route 268 on a warm evening in June and not be out of earshot of chorusing H. cinerea. Much of this area is immediately adjacent to the Ohio River, and the Indiana shore to the north is visible for much of the way. We believe that a larger range expansion of H. cinerea (described below) is underway in the middle Mississippi Valley and, more particularly, the rapid expansion of nearby populations in adjacent Henderson County and perhaps in more easterly, upstream locales in the state, was an important prelude to its eventual appearance in Indiana.

We surmise that Kentucky is the most likely source of the Indiana populations of H. cinerea. The circumstantial evidence for this conclusion is compelling, from both a spatial and temporal point of view. While the species was rapidly expanding its range in both Kentucky and Illinois, only in Kentucky did populations establish themselves at localities proximate to Indiana. In Illinois, this treefrog has expanded its range no further east than Pope County (Christopher Phillips, Pers. Comm.). Thus, there remains a considerable hiatus between the easternmost Illinois populations of H. cinerea in the Ohio Valley and the Indiana border. Further, the senior author has surveyed suitable habitat along the Illinois side of the lower Wabash River (bordering Posey County, Indiana) from White and Gallatin counties southward into Hardin County and has not located any *H. cinerea*. However, on these same surveys, H. cinerea was heard chorusing in adjacent Union County, Kentucky. Union County lies directly south of Posey County and both counties share an Ohio River border (Fig. 1).

From a temporal standpoint, it is clear that *H. cinerea* was first confirmed proximate to Indiana in 1989, in adjoining Henderson County, some 14 years before the first Indiana collections in 2003 (Lodato & Grannan 1990). Our field observations in the intervening years revealed a substantial expansion in both range and in population size in adjacent Henderson County wetlands prior to the first reports of the species in Indiana. In addition, by 2003 *H. cinerea* had been reported even further east along the Ohio River, in Breckinridge County, Kentucky (John MacGregor, Pers. Comm.). Each of these Kentucky localities is upstream

from the earliest collection site of *H. cinerea* in Indiana.

The above timeline and account strongly suggests that *H. cinerea* successfully moved from adjacent Kentucky into southwest Indiana. A question arises as to how this occurred. As Sherman A. Minton, Jr., (1972) suggests, "[T]he Ohio River may be a formidable barrier to small amphibians...." We submit that, despite the river presenting such a barrier, these treefrogs did in fact cross the Ohio River to colonize Indiana and that the likely mechanism for doing so was rafting on drift and other flotsam during warm season flooding and during the time the treefrogs were active. The proposed evidence for this is as follows:

- Population locations.—All of the known Indiana populations are on annual floodplains or on sites immediately adjacent to floodplains, either of the Ohio or Wabash rivers. These sites communicate with the Ohio River during flooding and indirectly connect Kentucky floodplain wetland habitats harboring *H. cinerea* and Indiana floodplain wetland habitats.
- Chronology.—We have noted that dis-2) coveries of some new populations of H. cinerea in Indiana have occurred subsequent to high water events on the Ohio River. Pulses of high water occur primarily in spring, but may occur at any time of year (Fig. 5) (National Oceanic and Atmospheric Administration 2000-2013). These surges of water pick up and carry drift and flotsam and deposit such materials when waters recede. Such drift and flotsam may serve as a rafting medium for H. cinerea and facilitate colonization of new sites. Our field experience has shown that H. cinerea is locally active anytime between March and October, a period that includes frequent high water events on the Ohio River, as measured at the Evansville Gauge Station (Fig. 5). In particular, 2011 was a wet year with sustained spring high water at Evansville from the end of February until the end of May (Fig. 5) (National Oceanic and

Atmospheric Administration 2000-2013). Several new colonies were discovered in Posey and Vanderburgh counties in 2011 after high water had receded. This sequence provides circumstantial evidence that spring high water and warm season flooding contribute to dispersal and colonization of new sites by *H. cinerea*.

Direct observation.-Eagle Slough, in 3) southern Vanderburgh County, Indiana, had been surveyed annually for H. cinerea without success. However, in 2011, southwest Indiana experienced record-setting annual precipitation of more than 177.8 cm (National Weather Service Forecast Office 2011), and warm season flooding persisted until the end of June. During the peak of flooding, Eagle Slough was completely inundated by floodwater, and strong currents flowed over the site. On a visit to the slough on 9 July, after floodwaters had receded, we noted, for the first time, widely scattered calls of H. cinerea at the site. In this instance all were calling from isolated pools left by receding floodwater. Most of these temporary pools were situated under mature forest canopy. No H. cinerea were heard at the margins of an open cypress swamp at the northern end of this site. The following year (2012) we heard singing males in typical breeding choruses in the open buttonbush zones and vegetation at the margin of the open-canopied cypress swamp at this site. They appeared to have been deposited by the receding floodwaters. The following season they apparently migrated to the more open margins of the permanent cypress pond and began typical breeding activities (chorusing). The Eagle Slough site is both downstream and directly across the Ohio River from established Kentucky populations near the mouth of the Green River, as well as from other upstream Kentucky populations along the Ohio

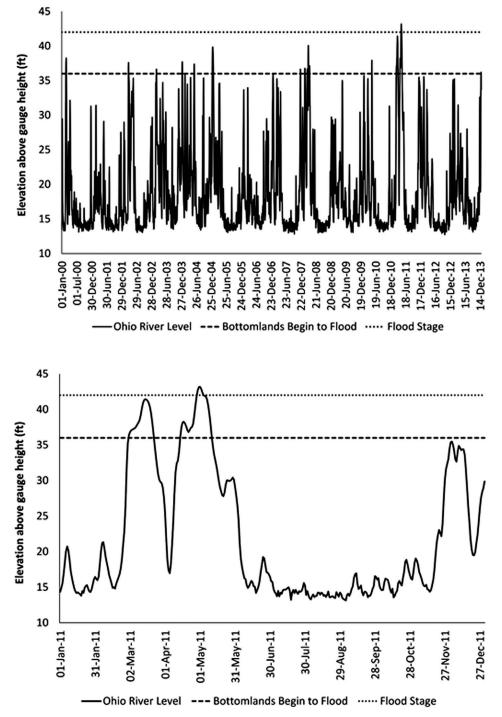


Figure 5.—Ohio River levels measured at the Evansville, Indiana gauge station. Top: Trimester Ohio River levels, 2000-2013. Bottom: Detail of periodic Ohio River stages for calendar year 2011. Pulses of high water occur at times when *Hyla cinerea* is active, March-October. Rafting under such conditions may facilitate dispersal and new colonization at floodplain sites.

River as far east as Breckinridge County (Fig. 3).

- 4) Rafting as potential dispersal mechanism for another Indiana species.-In the past decade, a reproducing colony of the common wall lizard, Podarcis muralis, a species of lizard native to Europe, was discovered in Clark County, Indiana, at Falls of the Ohio State Park (Walker & Deichsel 2005). These lizards were in rip-rap and drift along the river bank below the state park. Testing determined these lizards were genetically identical to a long established P. muralis colony upstream on the Ohio River riverfront at Cincinnati, Ohio (Walker & Deichsel 2005). While not completely excluding an introduction, rafting on river flotsam is believed to be the likely mechanism of dispersal. This theory is supported by a report documenting the dispersal of the lizard Lacerta agilis on river flotsam and new colonization during a substantial flood that occurred on the Elbe River near Meisen, Germany, in 2002 (Prokoph 2003).
- Additional, parallel vertebrate range 5) expansion.—It is also noteworthy that at least one other southern terrestrial vertebrate species, the nine-banded armadillo (Dasypus novemcinctus) invaded Indiana from the south and west at about the same time as H. cinerea appeared in Indiana (Whitaker 2010) and occupied virtually the same region as that now occupied by *H. cinerea* in southwest Indiana. Although Whitaker notes that the armadillo has expanded its range in the Southeast and appeared in Illinois and Kentucky prior to its arrival in Indiana, he does not speculate on its means of dispersal.

INDIANA DISTRIBUTION RECORDS BY COUNTY

The following is an account of *H. cinerea* in each of the four counties where it has become established, in chronological order of discov-

ery, based on field work during this study. During the course of the study, additional localities (other than the original site in each county) have been confirmed in three of the four Indiana counties harboring *H. cinerea* (Fig. 4). Although isolated treefrog vocalizations initially were recorded, we focused our attention on the location of breeding colonies, as determined by aggregations of chorusing males assembled in suitable aquatic habitats.

A report of a specimen of *H. cinerea* from Kirklin, Clinton County, was brought to our attention by former DNR employee Angie Garcia Miller. The specimen was found on 22 September 2009 and photographed by Wendell Zetterberg, Jr. The treefrog was perched on ornamental grasses in a garden setting near a residence. Given the latitude of the locality, its urban/residential setting, and the circumstance of discovery we consider this isolated record as a waif, likely escaped or released from captivity or accidentally transported by human agency.

Vanderburgh County.—The first records for Indiana were on 14 and 16 June 2003. Voucher specimens: University of Michigan Museum of Zoology (UMMZ 230109–230110) (Lodato et al. 2004).

Vanderburgh County was the site of the first collection of H. cinerea in Indiana. Since 2003 the species has colonized new sites in the county. At the present time, there are five breeding localities, all located on the Ohio River floodplain in Knight, Perry, and Union townships (Fig.4). Based on voice surveys, H. cinerea has sporadically occurred in wetlands on higher terraces adjacent to the floodplain, most notably in and around Burdette Park in Perry Township. Most of these are in artificial wetlands (e.g., farm ponds and impoundments), but none have persisted or established breeding colonies. The lack of welldeveloped vegetation about the margin of these sites may be the reason for this. The largest aggregations of H. cinerea in Vanderburgh County, and perhaps the most easily observed, are found along Bayou Creek, a shallow, sluggish backwater drain that forms the boundary between Perry and Union Townships. Here a paved road parallels the bayou for a portion of its course, with forest on one side of the road and cropland on the other. After dark, H. cinerea frequently move from the forested bayou margin to row crops across

the road and vice versa, and the treefrogs can often be found on the road surface.

Posey County.—First recorded in the county on 10 June 2005. Photo vouchered: Illinois Natural History Survey (INHS 2005a) (Walker et al. 2006).

Hyla cinerea was first located in Posey County at the Gray's Woods-Goose Pond cypress slough and at Rail Marsh on the west side of Hovey Lake, both in Point Township. It is of interest that the senior author and Roger Hedge of the Indiana DNR Division of Nature Preserves checked these sites in early July 2003 and no H. cinerea was found. Additional populations were discovered in 2005, 2006, 2008, 2011, and 2012. There are now eleven known breeding sites in Posey County, and these occur on both the Ohio and Wabash River floodplains (Fig.4). The species began to ascend the Wabash River floodplain in 2008 following extensive June flooding (National Weather Service 2011). We surveyed for H. cinerea in July 2008 after the Wabash floodwaters had receded and noted widely scattered, individual calling males in the rural countryside well away from breeding sites. Some of these calling stations were from lawns of rural homesteads and nearby roadside ditches. During this survey we heard calling *H. cinerea* for the first time from the vicinity of Half Moon Pond. Based on this observation, it appeared that the warm season flooding had facilitated dispersal and colonization of new sites from established populations. Following additional June flooding in 2011 (National Weather Service 2011), H. cinerea appeared further north in an extensive buttonbush swamp east of Pitcher Lake in Black Township. Since that population was discovered, we have recently (in 2014) documented a range extension of about 1.5 km to the north where the treefrogs inhabit shrub swamp along a bayou northeast of Pitcher Lake. This site, northwest of Mt. Vernon and north of State Route 62, is currently the northernmost population along the Wabash River. The population of *H. cinerea* at the Gray's Woods/Cypress Slough Swamp near the confluence of the Ohio and Wabash Rivers in Point Township is perhaps the largest and most robust in the state.

Warrick County.—First noted on 15 July 2005. Photo vouchered: Illinois Natural History Survey (INHS 2012K) (Lodato 2013).

Hyla cinerea was discovered in Warrick County along an old meander of Cypress Creek in Anderson Township. While H. cinerea was first noted at the site in 2005, and has been monitored each year since, a voucher was not taken until 2012. It is noteworthy that the senior author repeatedly checked this site in 1989 and 1990 after H. cinerea was discovered in adjacent Henderson County, Kentucky, but the species was not found. Despite seemingly good habitat elsewhere along Cypress Creek and in shrub swamp along Pigeon Creek in the western portion of the county, this remains the only known site for H. cinerea in Warrick County. Mature forest surrounds this site, and the embankments adjacent to the watercourse are somewhat steep-sided. However, the aquatic environment itself provides favorable H. cinerea habitat, with bald cypress (Taxodium distichum), buttonbush (Cephalanthus occiden*talis*) and mats of spatterdock (*Nuphar advena*).

Spencer County.—First recorded on 11 June 2013 (voice record). Vouchered with photograph and with archived audio recording: Illinois Natural History Survey (INHS 2013b) (Lodato & Gordon 2013).

Spencer County has been surveyed annually for H. cinerea since 2003. Our searches have focused on bottomlands near the confluence of Little Pigeon Creek and the Ohio River (east of Yankeetown, Warrick County). Periodic surveys were also conducted in wetlands on the Ohio River floodplain in the southern lobe of the county (Luce and Ohio townships), but all of these surveys had been without success. However, in June 2013 H. cinerea was heard calling from an unnamed slough along Garrett Creek and from points immediately south of this site (Lodato & Gordon 2013). It is not known precisely when the treefrogs first colonized these sites because the specific area had not been surveyed since 2009 and H. cinerea was not present at that time. On 25 July 2013 two small groups of chorusing males were heard calling from artificial ponds on terraces immediately adjacent to the annual floodplain. These sites were in Luce Township, west of the 11 June 2013 vouchered locality. These treefrogs are of recent origin as these sites were checked in 2012 and no H. cinerea were detected.

The authors have made extensive surveys north and east of the four counties now known to harbor breeding populations of *H. cinerea* (Fig. 3). Numerous visits to buttonbush swamps and other wetlands at the mouth of Poison Creek and Oil Creek in Perry County have been unsuccessful. However, a breeding colony is known from a buttonbush swamp just across the Ohio River in Breckinridge County (John MacGregor, Pers. Comm.). Likewise we have periodically surveyed seemingly good sites along the Wabash, White, and Patoka Rivers in Knox, Gibson, and Pike Counties without success. However, it is clear that populations of H. cinerea are dynamic and the history of colonization and range expansion noted in adjacent Kentucky and Illinois could be repeated in Indiana. For this reason, continued surveys and monitoring of known populations are warranted.

OBSERVATIONS ON *HYLA CINEREA* IN INDIANA

Phenology.—The earliest date we observed *H. cinerea* was 14 March, and the latest date was 16 October. These observations were made at Eagle Slough in Vanderburgh County. The treefrogs were not calling at this time but were found perched on vegetation on sites elevated well above the breeding wetland. The March sighting was about 100 m from the breeding site while the October sighting was about 50 m distant.

Breeding Dates.—The earliest breeding chorus we have heard was 6 May, and the latest date was 28 July. This breeding period may be somewhat shorter than the "early May to early August" given for a population in southwestern Illinois (Garton & Brandon 1975) and is decidedly shorter than the March through September breeding period for a population in northwest Florida (Gunzburger 2006).

Indiana choruses begin to increase in intensity from early May and peak with the approach of the summer solstice. Choruses remain level for several days and then begin to decline until the end of July, when males cease calling. There is an order of magnitude increase in volume, frequency, and intensity between the first choruses in early to mid-May and the peak of such activity in mid- to late-June. Thus, mid-June through early July is the optimal time to survey for new populations. A number of authors report that *H. cinerea* has a rain call that portends inclement weather, particularly in the south (Wright & Wright 1949; Conant & Collins 1998; Elliott et al. 2009), but we have not noted any spontaneous calling in local populations in response to approaching rainstorms.

Amplexing pairs have been noted on various dates in Vanderburgh County, as early as 7 June and as late as 13 July. Recently metamorphosed juveniles have been found from mid- to late-September.

Multiple egg clutches per season have been shown for *H. cinerea* in Georgia (Perrill & Daniel 1983) but evidence for such in Indiana populations is lacking.

Habitat.-To date all of the breeding localities for *H. cinerea* occur within the Southern Bottomlands Natural Region of the state, a region of southwest Indiana along the floodplains of the major rivers and with natural communities of flora and fauna that have affinities with the lower Mississippi Valley and the Gulf Coastal Plain (Homoya et al. 1985). Hyla cinerea requires aquatic habitat in order to reproduce, and all of the Indiana populations are tied to particular wetland sites within this natural region. We have found the species in a variety of wetland habitats, including floodplain sloughs, swamps, oxbow ponds, bayous, and occasionally in flooded fields, ditches, and artificial ponds. However, based on our call surveys, preferred breeding habitat for the species here appears to be a natural, permanent or semi-permanent, shallow slough, pond, or swamp with an open, sunlit canopy with exposed shrub thickets and borders and with ample emergent and floating vegetation. We have observed that these aquatic sites often have scattered bald cypress, thickets of buttonbush, and mats of spatterdock (Fig. 6). An open canopy is essential as sites with mature swamp forest with a closed canopy are avoided. In Point Township, Posey County, H. cinerea is abundant in the open canopied Gray's Woods/Goose Pond Cypress Slough, but absent in the nearby heavily forested, closed canopied wetlands of the Twin Swamps Nature Preserve.

Our observations show that in Indiana, *H. cinerea* is essentially dependent on an opencanopied shrub swamp for its breeding sites. These observations are consistent with those of Redmer et al. (1999) in adjacent Illinois. It is noteworthy that when this treefrog colonized Indiana it found habitats not unlike those it occupies in its historical range in the southeastern United States. These open floodplain



Figure 6.—Breeding habitats for *Hyla cinerea* in Indiana. Top: Bayou Creek, Union Township, Vanderburgh County. Note bank-to-bank mat of spatterdock (*Nuphar advena*). Shrub borders are dominated by buttonbush (*Cephalanthus occidentalis*) and swamp rose mallow (*Hibiscus palustris*). Bottom: Unnamed cypress pond, Marrs Township, Posey County. Note bald cypress trees (*Taxodium distichum*) and widely spaced buttonbush shrubs. Water surface covered by duckweed (*Lemna spp.*) and mosquito fern (*Azolla caroliniana*).

wetlands favored by *H. cinerea* as breeding sites constitute an ecological niche scarcely used by any other Indiana hylid.

We have found H. cinerea perched on trees, including ash (Fraxinus spp.), bald cypress, pin oak (Quercus palustris), dogwood (Cornus florida and C. drummondii), silver maple (Acer saccharinum), boxelder (A. negundo), and willow (Salix spp.) and shrubs including buttonbush, swamp privet (Foresteria acuminata), swamp rose mallow (Hibiscus palustris), and elderberry (Sambucus nigra) in and adjacent to occupied wetland habitats. The most common aquatic plants in sites harboring H. cinerea are spatterdock and creeping yellow primrose (Ludwigia spp.). Commonly occurring floating and submerged plants have included duckweed (Lemna spp.) and hornwort (Ceratophyllum demersum). We have also found H. cinerea in cropland adjacent to breeding sites where they were perched on wheat (Triticum spp.) and soybeans (Glycine max) and in flooded fields perched on cocklebur (Xanthium spp.). Recently metamorphosed young-of-the-year were found in sedges (Carex spp.) and perched on shrub-sized roughleaf dogwood (C. drummondii) at the edge of a wetland in Vanderburgh County.

Size/Color/Pattern.—The size range given for adults of *H. cinerea* is from 32 to 57 mm, with a maximum of 64 mm (Conant & Collins 1998). Based upon snout-vent measurements (SVL) generously provided by Dale Edwards, Noah Gordon, and Anne Steele of the University of Evansville (Pers. Comm. 2013) and our own data, Indiana adult males averaged 46.2 mm SVL (N = 25). Adult females averaged 51.3 mm SVL (N = 3). Recently metamorphosed juveniles (young-of-the-year) measured 20.6 mm SVL (N = 6).

Indiana *H. cinerea* are apparently typical in color and pattern as well as size. All Indiana specimens we examined ranged from grass green to bright lime green, and all had a bright white to silver stripe from the upper lip extending down the side. Specimens lacking these light lateral stripes have been noted in some populations (Conant & Collins 1998; Elliot et al. 2009), but we have seen no patternless Indiana specimens. Many had small gold flecks on the dorsum that were either partially or completely circled in black. Recent studies indicate that the number and size of

these dorsal spots vary over time on individual frogs (Beaudry & Höbel 2014).

Stability of Populations.—The *H. cinerea* colonies that have become established in the state appear to be stable and resilient. While there seems to be some variability in chorus intensity from year-to-year at certain locations, no breeding colonies have been lost during the course of this study. In 2010 and 2012, two drought years, one colony in Posey County and one in Vanderburgh County became dormant (all chorusing ceased) by the first week of July. At these locations surface water had largely evaporated. Chorusing resumed, however, at each of these sites in succeeding years.

SUMMARY

The newly established Indiana populations of *H. cinerea* are at the northern periphery of the known range of this species. Based on the data collected in this study, and in the context of information reported from other states where the species occurs, we can now address some of the questions posed in the Introduction to this paper:

- 1) *Hyla cinerea* is thought to have arrived in Indiana as the result of a natural expansion of its range in the middle Mississippi Valley.
- 2) The most likely source of Indiana *H. cinerea* populations, based on temporal, spatial, and other factors, is adjacent Kentucky.
- Rafting on drift during warm season flooding on the Ohio River is thought to be the likely mechanism for the arrival and establishment of initial populations in the state.
- Subsequent warm season flooding seems to have facilitated colonization and saturation in suitable habitat along the lower Wabash and Ohio River floodplains in Indiana.
- 5) Upon its arrival in southwest Indiana, *H. cinerea* encountered and occupied austroriparian habitats not unlike those it occupies in its historical range in the southeastern United States. Its preference for open-canopied shrub swamp and other similar wetlands here is consistent with its habitat preference

in adjoining states. At its floodplain breeding sites, it fits into an ecological niche that is only marginally used for such purposes by any other local hylid.

- 6) Local populations have a somewhat shorter breeding period than that reported for more southern historic populations in the middle Mississippi Valley and the Gulf Coastal Plain.
- 7) In the decade since it was discovered in Indiana, this treefrog has survived northern winter temperatures; swift, roiling currents from flooding of breeding sites; and considerable drought. Under these conditions, it has continued to expand its range in the state.
- 8) This southern species now appears to be permanently established in the state and is poised for further expansion.

This documented recent range expansion of *H. cinerea* in the middle Mississippi Valley, including its recent colonization of southwestern Indiana, demonstrates the remarkable vagility of this species. It presents an intriguing biogeographic phenomenon and contrasts sharply with amphibian declines generally.

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