DISTRIBUTIONAL PATTERNS AND THEIR INTERPRETATION
IN HETAERINA (ODONATA: CALOPTERYGIDAE)

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ABSTRACT

The geographical distribution, north of Mexico, for damselflies in the genus Hetaerina appears by county for each state and nearest community for 2 Canadian provinces. Hetaerina americana (Fabricius), H. titia (Drury), and H. vulnerata Hagen occur in 41, 24, and 4 U.S. states respectively, and H. americana exists also in Quebec and Ontario, Canada. Likely explanations of these geographic patterns follow the distributional data. Temperature probably controls the northern limits in H. americana and H. titia; adult behavioral preferences affect western limits of H. titia; drought severely limits distribution of H. vulnerata in the southwestern U.S. A well-isolated, pleistocene relict describes the single Florida colony of H. americana. Isolated colonies of H. americana also characterize part of its southwestern distribution. Flight season data show a 12 month adult activity period in tropical climes dropping to an approximately 3 month interval in northern colonies of H. americana, and an even shorter time in populations of northern H. titia.

This paper summarizes distributional data north of Mexico for damselflies of the genus Hetaerina, and tentatively interprets boundary limits noted in the geographical patterns. The subfamily Hetaerinae occurs only in the Western Hemisphere with center of diversity in the neotropical region. Only 3 species range northward beyond Mexico, H. americana (Fabricius), H. titia (Drury), and H. vulnerata Hagen. The species are stream to riverine inhabitants, occurring about lakes only when attributes of flowing water exist. Diagnostic characters for their determination are in Calvert (1901-1908) and Johnson (1972a).

Most damselflies are known specifically only to specialists; however, the widely distributed, large and colorful H. americana possesses a well-known popular name, Common Ruby Spot, reflecting a familiarity uncommon with Zygoptera. The traits of large size, brightly colored wings, and non-secretive reproductive behavior also make hetaerinas attractive topics for ecological and behavioral studies (Johnson 1961, 1962, 1963, 1966; Bick and Sulzbach, 1966). While behavioral and ecological attributes are becoming better known, a crude picture of their distribution still exists. Most general works on U. S. Zygoptera give readers the impression that H. americana, particularly, occurs almost everywhere. For example, Muttkowski (1910) “... Canada to Guatemala.”, Needham and Heywood (1929) “N. Am. Generally”, Hyers (1930) “Canada to Guatemala”, with Montgomery (1947) being somewhat more specific, “Quebec and California to Guatemala”. Only Walker (1953) briefly noted the need for a more precise description. Many papers giving

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distributional data have accumulated in the past 112 years since Hagen's pioneering Synopsis in 1861. Specimens representing a wealth of unpublished data also exist in various collections. A combination of these sources produced data discussed here. Published sources are in the Literature Cited and recognition appears in Acknowledgements for correspondents giving freely of time and information. A documented statement of the U.S. distribution in *Hetaerina* is now both possible and timely as better-defined questions emerge on ecology and evolution. All 3 species occur south of the U.S., *H. vulnerata* at least to southern Mexico, possibly Brazil (Calvert 1901-1908), and *H. americana* and *H. titia* to Guatemala and possibly southward (Williamson 1923). Specifics on these southern distributions remain incomplete but do not adversely affect the value of a well-defined northern distribution.

**Major Distributional Patterns**

Data exist for *Hetaerina americana* in 41 states of the U.S. and 2 Canadian provinces; likewise, *H. titia* and *H. vulnerata* occur in 24 and 4 states respectively. The distributions appear below by county for each state, and the Canadian distribution is that of Walker (1953). These localities appear graphically, 1 symbol per county, in the maps of Fig. 1 and 2; Calvert (1901-1908) gave the few *H. americana* localities shown for northern Mexico. Where only county data exist, the species symbol appears in the center of the respective county; otherwise, the symbol is on the collection site. This practice is mainly helpful for western states having large county size. Smaller counties in the eastern states are only partially responsible for the larger number of localities; collecting in the eastern U.S. occurred over a substantially longer period, and suitable habitats are more abundant. Data reported here trace back to 1861, 1873, 1893, etc., and industrial regions have probably polluted or eliminated some earlier habitats. The literature, listed chronologically, personal communication sources, and collection(s) yielding documentation for each state follow county lists. Only literature sources giving specific localities within a state appear; therefore, the earliest reference cited usually does not represent the first published recognition of the species in the state. For instance, Hagen (1861) initially listed several states but without other localities. The collections cited carry the following abbreviations: CJ Coll.—author’s coll., Mauff. Coll.—W. Mauffrey Coll., Tenn. Coll.—K.J. Tennessen Coll., U.A. Coll.—University of Arkansas Coll., Clem. U. Coll.—Clemson University Coll., Corn. U. Coll.—Cornell University Coll., U.N. Coll.—University of Nebraska Coll., USNM Coll.—U.S. National Museum of Natural History Coll., and FSCA—Florida State Collection of Arthropods. *Hetaerina americana* distributional records.

United States.

Alabama: Colbert, Dallas, Lee, Perry, and Tallapoosa counties. Williamson (1903); Wilson (1909); H. B. Cunningham (personal communication 1972); CJ Coll.

Arizona: Cochise, Coconino, Gila, Maricopa, Pima, Pinal, Santa Cruz, Yavapi and Yuma counties. Calvert (1901-1908); Williamson (1914a); Ahrens (1938); H. R. Rush, T. Donnelly, C. Cook, W. R. Enns (personal communication 1972); CJ Coll., FSCA.

Arkansas: Conway, Garland, Greene, Logan, Madison, Marion, Monte-
Fig. 1.—Distributional pattern of *Hetaerina americana* north of Mexico. See text for locality details.
Fig. 2.—Distributional patterns of *Hetaerina titia* and *H. vulnerata* north of Mexico. See text for locality details.
gomery, Newton, Polk, Randolph, Scott, Stone, and Washington counties. Adams (1900); Bick (1959); C. Cook (personal communication 1972), Mauff. Coll.

California: Alameda, Butte, Colusa, Fresno, Imperial, Inyo, Kern, Los Angeles, Monterey, Placer, Riverside, Sacramento, San Bernardino, San Diego, Santa Cruz, Tulare, and Ventura counties. Calvert (1901-1908); Kennedy (1917a); Seeman (1927); Ahrens (1938); T. Donnelly, H.R. Rush, P.D. Harwood (personal communication 1972), FSCA.

Colorado: Adams, Arapahoe, Boulder, and Yuma counties. Calvert (1901-1908); Williamson (1913); W. F. Barr, P.J. Clausen (personal communication 1972).


Florida: Calhoun and Jackson counties. Byers (1930); Johnson and Westfall (1970); CJ Coll., FSCA.

Georgia: Bartow, Madison, Monroe, Pike, Rockdale, and Walton counties. J.B. Wallace (personal communication 1972); CJ Coll., FSCA.


Iowa: Adair, Black Hawk, Boone, Des Moines, Dubuque, Floyd, Hamilton, Muscatine, and Story counties. Elrod (1898); Whedon (1914); Wilson (1909, 1920); Wells (1917); P.D. Harwood, W.R. Enns (personal communication 1972).


Massachusetts: Barnstable, Essex, Middlesex, Norfolk, and Worcester counties. Hagen (1873b); Calvert (1905); Howe (1917-1921); CJ Coll.


Missouri: Boone, Calloway, Carter, Crawford, Lawrence, Osage, Pike, Pulaski, Shannon, St. Louis, and Taney counties. Williamson (1932); P.D. Harwood, W.R. Enns (personal communication 1972); FSCA.

Montana: Hagen (1873a, 1874a) reported on 3 broken male specimens taken during the U.S. Geological Survey of 1872. He determined the specimens as Hetaerina californica Hagen in Selys, 1859, a name recognized as a junior synonym of H. americana by later writers. The only locality data was “...the Yellowstone.” This term referred, presumably, in the 1870’s, to the Yellowstone River occurring largely in Montana. Hagen (1875) again referred the specimens only to the “Yellowstone”; however, Calvert (1901-1908) listed H. americana from Montana on the basis of Hagen’s specimens. J.H. Lowe and N.L. Anderson searched collections at the University of Montana and Montana State University respectively to no avail. C. H. Bick (personal communication 1972) collected Odonata in Montana extensively during the summer of 1972 without encountering the species. Apparently no evidence currently exists for colonies of H. americana in Montana.

Nebraska: Antelope, Blaine, Cass, Cherry, Hamilton, Lancaster, Lincoln, Scotts Bluff, Sioux, and Thomas counties. UN Coll. Montgomery (1967) is the only published report known for Nebraska; however, he gives no specific localities.

New Hampshire: Clark and Lincoln counties. La Rivers (1940).


New Mexico: Bernalillo, Catron, Chaves, Dona Ana, Eddy, Grant, Quay, Rio Arriba, and Socorro counties. Needham and Cockrell (1903); Ahrens (1938); Johnson (1963, 1966); P.D. Harwood, T. Donnelly (personal communication 1972); CJ Coll.; FSCA.


Oklahoma: Alfalfa, Beaver, Beckham, Caddo, Canadian, Cleveland, Comanche, Cotton, Custer, Garvin, Harmon, Harper, Jackson, Johnston, Le Flore, Major, Marshall, McLain, McCurtin, Murray, Muskogee, Roger Mills, Sequoyah, Washita, and Woods counties. Williamson (1914b); Bird (1932); Bick (1951); Bick and Bick (1957); Rick and Sulzbach (1966).

South Carolina: Aiken, Darlington, Lexington, and Oconee counties. Montgomery (1940); Clem. U. Coll.


Tennessee: Anderson, Benton, Bledsoe, Blount, Bradley, Carter, Cheatham, Cocke, Coffee, Davidson, Dickson, Dyer, Fentress, Greene, Hancock, Hawkins, Henry, Jackson, Johnson, Knox, Lincoln, Loudon, Maury, Monroe, Morgan, Obion, Overton, Putnam, Scott, Sequatchie, Sevier, Smith, Sullivan, Summer, Tipton, Unicoi, Washington, and Wilson counties. Byers (1931); Williamson (1934); Wright (1938); Kormondy (1957); Trogdon (1961); C. Cook (personal communication 1972).


Virginia: Fairfax, Giles, Loudoun, Madison, Montgomery, Orange, Prince George, Prince William, Russell, Shenandoah, Tazewell, and Warren counties. Williamson (1903); Donnelly (1961); Johnson (1963); P.D. Harwood, C. Cook (personal communication 1972); C.J. Coll.


Wisconsin: Bayfield, Burnett, Clark, Crawford, Dane, Grant, Green, Iowa, Jefferson, La Crosse, La Fayette, Marquette, Milwaukee, Ozaukee, Pierce, Richland, Rock, Sheboygan, Vernon, Walworth, Waukesha, and Waupaca counties. Muttkowski (1908); Wilson (1909); W. Hilsenhoff (personal communication 1972); Tenn. Coll.


Canada.


Quebec: Montreal.
**Hetaerina titia** distributional records.

Alabama: Colbert and Dallas counties. Williamson (1903); CJ Coll.
Florida: Alachua, Bradford, Clay, Columbia, Gadsden, Gilchrist, Highlands, Jackson, Lee, Levy, Liberty, Manatee, Marion, Orange, Polk, Santa Rosa, Suwannee, Union, and Wakulla counties. Calvert (1901-1908); Byers (1930); Davis and Fluno (1938); Needham (1946); Johnson and Westfall (1970); CJ Coll.; FSCA; Tenn. Coll.
Georgia: Bibb, Brantley, Burke, Decatur, Floyd, McDuffie, Pierce, and Union counties. Byers (1931); Williamson (1934); CJ Coll.; FSCA.
Iowa: Cherokee County. Whedon (1914).
Mississippi: George, Hancock, Jackson, Lafayette, Marion, Monroe, Pearl River, Pike, and Stone counties. Mauff. Coll.
North Carolina: Buncombe, Cherokee, Henderson, Madison, Robeson, Stokes, Transylvania, and Wake counties. Brimley (1903); Williamson (1934); B.E. Montgomery (personal communication); FSCA.
New Jersey: Montgomery (1947) cites New Jersey for *H. titia* without a specific locality. I have been unable to confirm this report or locate other specimens from this state.
Ohio: Brown, Fairfield, and Williams counties. Kellicott (1895); Borror (1937); P.D. Harwood (personal communication 1972).
Oklahoma: Bryan, Johnston, Le Fore, Murray, and Muskogee counties. Williamson (1912); Bick and Bick (1957).
Pennsylvania: Bedford, Butler, Cumberland, Fayette, and Philadelphia counties. Hagen (1861); Calvert (1893); Williamson (1912); Ahrens and Beatty (1968); Beatty, Beatty and Shiffer (1969); C. Cook (personal communication 1979).
South Carolina: Aiken, Chesterfield, Greenville, and Pickens counties. Williamson (1934); FSCA.
Texas: Angelina, Bexar, Bosque, Brazos, Caldwell, Colorado, Comal, Dallas, Denton, Fayette, Goliad, Gonzales, Grimes, Guadalupe, Hays,
Jackson, Jim Wells, Kendall, Kimball, McLennan, Polk, Presidio, San Jacinto, San Patricio, Robertson, Travis, Uvalde, Victoria, and Webb counties. Calvert (1901-1908); Williamson (1912, 1914b); Ferguson (1940); Johnson (1961, 1963, 1972).

Virginia: Henrico and Tazewell counties. Williamson (1903); Gloyd (1951).


*Hetaerina vulnnerata* distributional records.

Arizona: Cochise, Coconino, and Gila counties. R.W. Garrison (personal communication 1972); CJ Coll.; FSCA.

New Mexico: Catron, Grant, and Sandoval counties. CJ Coll.; FSCA.


**Factors Limiting Distribution**

The range of *hetaerinas* doubtlessly expands and contracts along peripheries as conditions dictate. A number of observations reflect the instability of northern colonies. Kormondy (1958) commented on Evans' (1914) northernmost Michigan record of *H. americana* as "... undoubtedly were strays." W.L. Hilchhoff (personal communication 1972) described *H. americana* as uncommon in northern Wisconsin. R.L. Post (personal communication 1972) reported for the single North Dakota *H. americana* collection "... I collected 2 specimens... on August 14, 1961,... spring fed pond... a subsequent visit found the small area muddied... trampled... thoroughly disturbed." P.J. Clausen (personal communication 1972) said of *H. americana* "... not apparently a very common species in Minnesota." Garman (1927) had only 2 *H. americana* localities in Connecticut, and Howe (1917-1921) described the species as rare in Maine and Massachusetts. Hagen's questionable Montana specimens, mentioned above, may also reflect problems encountered by northern colonies. *Hetaerina titia* is less successful in colonizing northern environments. The locality records for *H. titia* terminate far south of the northernmost *H. americana* sites and are generally uncommon to the north. Kormondy (1958) described it as "... an occasional adventive in Michigan." Low temperature probably plays the major role limiting northward distribution of both *H. americana* and *H. titia*; however, its relative importance to adults and larvae is unknown.

In the xeric southwest to California, *H. americana* occurs along larger rivers serving as refuges for recolonizing smaller creeks and springs between intervals of drought. These populations experience more isolation than in the midwest and eastern states, and some completely isolated populations occur. A large spring, Ojo Caliente, produces a stream in western Socorro Co., New Mexico, flowing for approximately 1 mile before the water disappears into the desert floor. The dry stream bed follows a winding path southeast to the Rio Grande through 40 to 50 miles of dry desert terrain. The next closest *H. americana* habitats are the Tularosa and Gila Rivers, 30 to 40 miles west across the Continental Divide. Complete isolation from other populations exists for *H. americana* at Ojo Caliente probably dating from a much earlier,
humid era. Similar isolation occurs for *H. americana* about the San Bernadino Springs in the southeastern corner of Cochise Co., Arizona. The absence of *H. americana* in the northwestern sector of the U.S. perhaps involves an interaction of temperature, dispersal ability, and in some areas, extensive mountains.

Adult behavior may determine the western limits of *H. titia* across the central U.S. Williamson (1923, 1932) indicated a greater preference by *H. titia* for shaded streams while *H. americana* readily colonizes open sunny situations. The preferences refer to perch-site conditions selected by adults. Both species may also occur together exercising interspecific competition (Johnson 1963). My field experiences agree with Williamson; however, I have also noted the higher perch sites (tree vs. emergent grass) more frequently chosen by *H. titia*. The distribution of *H. titia* occurs largely within the forested, thus shady, areas of the eastern and southern U.S. Streams in the prairie environments of western Texas, Oklahoma and Kansas obviously are not shadeless, but the forest-type overstory of these waters is distinctly less. A short period of observation on *H. titia* reveals its marked reluctance to leave, for long intervals, tree-shade conditions. This subtle behavioral attribute may play a major role in *H. titia*’s geographical occurrence.

Drought is a major factor limiting the spotty distribution of *H. vulnerata* in the southwest. I collected *H. vulnerata* on the Rio Mimbres, Grant Co., New Mexico, on 24 August 1962. In 2 weeks, the river bed was completely dry with no Odonata. The subsequent winter snow-melt revived the river channel; however, I was unable to find *H. vulnerata* on the stream during annual visits over the next 5 years. A similar event developed on Cottonwood Creek, Catron Co., New Mexico. Both *H. vulnerata* and *H. americana* occurred on Cottonwood Creek in June 1963, with *H. vulnerata* confined to the shady, shallow, higher elevations. Drought reduced water to small puddles in this section of the stream in August of that year, and, in the following 4 years, I collected only 1 adult *H. vulnerata* where an active population previously existed. Localities in Arizona, where I have seen *H. vulnerata*, appear equally susceptible to drought. The mean adult male life expectancy of *H. americana* is approximately 15 days (Johnson 1962), and, with a maximum maturation period of 10 days, an individual has 25 days of life. Most probably live a shorter period. This time is largely for reproductive activity at the stream. Life expectancies probably are not greatly different in other *Hetaerina* species, and *H. vulnerata* also exhibits close attachment to the stream side. Little time exists for adult movement. The long distances between streams in southwestern mountainous or xeric habitats surely reduce migration to a low trickle. The utilization by *H. vulnerata* of streams, or sections of streams, subject to drought-effects combined with a low dispersal rate surely limits its U.S. distribution in large part. The Texas record for *H. vulnerata* is the first documented case of verified specimens for that state (Johnson 1972a). I have studied 2 males from the Carl Cook Collection and concur with his determinations.

The only known colony of *H. americana* in Florida occurs on the Chipola River about Florida Caverns State Park and Blue Springs immediately north and east respectively of Marianna, Jackson County, Florida. Southward on this river, the species disappears. Two males taken about 12 miles south of Marianna in Calloway County constitute the southernmost record for the state. This distribution is not an artifact of limited collecting. Numerous
entomologists concerned with aquatics, including Odonata specialists, have collected frequently in Florida and the southeast. Byers (1930) initially reported the *H. americana* colony on the basis of 1 female collected on 13 April 1928, and further evidence was lacking for 41 years until M.J. Westfall, Jr. and I collected both sexes on 15 August 1969. I have verified its presence at Marianna during the following 3 years. The colony does not occur in dense numbers noted for more optimal areas as central Texas; however, the species probably has occurred for a long period about Marianna.

The Chipola River north of Marianna becomes a small, turbid, sluggish stream known as Cowarts Creek, and I have been unable to find *Hetaerina* even 10 miles north of Florida Caverns State Park. Only the Apalachicola River to the east otherwise joins the Chipola River about 45 miles south of Marianna in rather swampy situations. Collections or observations of *H. americana* are lacking on the Apalachicola River or its tributaries in Georgia for at least 190 miles north of the Florida State line. River systems west of the Chipola River have been specifically collected for Zygoptera without encountering this species (Johnson 1972b). Isolation from other populations or drainage systems characterizes the single Florida colony. Field work in the summer of 1972 sought to clarify extent of the isolation directly to the north. Results of this work appear, in part, in Fig. 3. Habitats with colonies were: Jackson-Calhoun Counties, Florida, population discussed above; Martin Lake and Horseshoe Bend National Military Park sites on the Tallapoosa River, Tallapoosa County, Alabama; Auburn, Lee County, Alabama; Concord, Pike County, Georgia, small tributary of the Flint River; and High Falls State Park, Monroe County, Georgia, Tawaliga River. These collections occurred during the summer and well within the adult flight season. The species' colorful attributes and active breeding behavior bring it to a collector's attention if present, and its absence in southern Alabama, Georgia, and essentially all of Florida is genuine. I believe the above Alabama and Georgia colonies are quite near the southern edge of its distribution in those states. The closest sites in Alabama occur in Perry and Dallas Counties to the west on the Alabama River Drainage, and all other Georgia localities are well north of sites shown in Fig. 3.

The southeastern U.S. experienced several major environmental changes during the Pliocene-Pleistocene periods. Neill (1957) discussed the geological events and summarized effects on faunal distributions. Blair (1958) correlated Pleistocene activities with southern vertebrate life, and among Odonata, Johnson (1972b) related southeastern variation in the damselfly, *Argia apicalis*, to Pleistocene environments. The faunal responses frequently produce small relict, isolated populations of species with northern affinities occurring in northwest Florida. Similarity of the Florida colony of *H. americana* to these patterns gives support for identifying it as a Pleistocene, or possibly Pliocene, relict. The explanation for *H. americana*'s failure to remain in or later penetrate the south is unknown. The correct question here is uncertain. The species certainly shows wide ecological tolerances elsewhere. By contrast, *H. titia* colonizes far southward to Lee County, Florida, and also occurs in the West Indies. I consider the crossing of oceanic barriers by *Hetaerina* species to colonize islands inconceivable. The relatively wide distribution of *H. titia* including such islands suggests it is a relatively older species than *H. americana* and *H. vulnerata*. Speciation in this genus appears conservative as its evidence is missing in areas enjoying a rather long isolation.
Fig. 3.—Distribution of *Hetaerina americana* colonies north of the single, disjunct Florida population. 1—Jackson-Calhoun Counties, 2,3—Martin Lake and Horseshoe Bend National Military Park, respectively, Tallapoosa River, Tallapoosa County, Alabama. 4—Auburn, Lee County, Alabama. 5—Concord, Pike County, Georgia, small tributary of the Flint River. 6—High Falls State Park, Monroe County, Georgia, Towaliga River.
ADULT FLIGHT SEASONS AND LATITUDE

Williamson (1923) listed a year-round occurrence for adults of both *H. americana* and *H. titia* in Guatemala. Davis and Fluno (1938) also reported a year-round flight season for *H. titia* in Orange County, central Florida. Earliest available dates for *H. americana* adults in Texas and Louisiana are 27 March and 3 April, respectively (Bick 1957, Johnson 1961). The earliest *H. americana* dates in the central tier of states, Missouri, Illinois, Indiana, and Ohio are 9 June, 19 June, late April, and 7 May, respectively (Williamson 1932, Garman 1917, Montgomery 1947, Borrer 1937). Farther north, later comparable dates exist, 9 July and 1 July, for Michigan and Canada, respectively (Kormondy 1958, Walker 1953). The latest observations of *H. americana* in Texas and Louisiana are 10 November and 2 October, respectively (Bick 1957, Johnson unpublished). Comparable dates in Missouri, Illinois, Indiana, and Ohio are 28 August, 22 October, early October, and 7 October, respectively (Williamson 1932, Garman 1917, Montgomery 1947, Borrer 1937). Generally, seasons terminate earlier in Michigan and Canada, 24 and 30 September, respectively (Kormondy 1958, Walker 1953). Initial dates for *H. titia* in Texas and Louisiana are 30 March and 24 June, respectively (Bick 1957, Johnson 1961). Other initial dates for *H. titia* in the north are few. Williamson (1932) listed 23 July in Missouri, and Montgomery (1947) gave a graph showing mid-August for Indiana. Borrer (1937) had a single date of 28 September. Bick (1958) and I (unpublished) have latest *H. titia* dates of 1 and 15 November for Louisiana and Texas, respectively. My observations on *H. vulnerata* in southern New Mexico and Arizona extend from 13 June to 25 August. These dates reflect, in part, activities of collectors as well as the insects; however, they generally substantiate shorter adult seasons with increasing latitude and suggest *H. titia* particularly has a short adult season in the north. Adult seasons range from 12 months in the south to approximately 3 months in northern areas for *H. americana*, and even shorter northern seasons exist for *H. titia*.

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