

Phenotypic Distribution of *Nerodia erythrogaster* in Extreme Southeastern Illinois, Western Kentucky, and Adjacent Western Tennessee, USA

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ABSTRACT

To investigate anecdotal range distributions for *Nerodia erythrogaster*, a total of 130 adult specimens from southern Illinois, western Kentucky, and adjacent western Tennessee were scored for ventral color and dorsal pigment invasion onto the ventral scales. Analysis of these characters revealed that true *N. erythrogaster flavigaster* populations do not exist in Kentucky and also may be absent from Tennessee. The region is instead dominated by morphs intermediate between *N. e. flavigaster* and *N. e. neglecta*. Furthermore, the range of *N. e. neglecta* should be extended along the Ohio and Cumberland rivers.

KEY WORDS. *Nerodia, erythrogaster, flavigaster, neglecta, transversa*, phenotype, intergrade

INTRODUCTION

There are four recognized subspecies of *Nerodia erythrogaster* (Forster) in the United States: the yellow-bellied watersnake, *N. e. flavigaster* (Conant); red-bellied watersnake, *N. e. erythrogaster* (Forster); copper-bellied watersnake, *N. e. neglecta* (Conant); and blotched watersnake, *N. e. transversa* (Hallowell). (See Conant 1949 for detailed descriptions of each subspecies.) The distinctions between these subspecies are based primarily on three characters: ventral coloration, the presence of dorsal pigment encroaching onto the ventral scales, and the persistence of juvenile pattern into the adult stage. However, the range of ventral colors and degree of encroaching dorsal pigment for each subspecies has been defined arbitrarily (Brandon and Blanford 1995).

Nerodia erythrogaster is cryptic and occupies habitats that are not easily traversed by humans, which makes collecting an adequate sample size from a variety of locations difficult

(Conant 1934; Ernst and Ernst 2003). This is perhaps why delineation of *N. erythrogaster* subspecies ranges have been based mostly on the analysis of preserved specimens. This is problematic because the colors of *Nerodia erythrogaster* fade in preservative (Conant 1949). Red and yellow pigments on the bellies of *N. erythrogaster* often completely disappear in a relatively short period of time, and even dark dorsal colors are affected to some degree. The geographic distribution of *N. erythrogaster* is further confounded because many early museum specimens were miscatalogued as *Nerodia sipedon* (L.) (Gibbons and Dorcas 2004).

In 1997, due to habitat loss and degradation, *N. e. neglecta* was listed as endangered by the states of Indiana, Ohio, and Michigan, and all *N. e. neglecta* populations above the 40th parallel were listed as threatened by the U.S. Fish and Wildlife Service (Pruitt 1997). More southerly populations (below the 40th parallel) were conferred special protection by the states of Illinois and Kentucky (Kingsbury 1998). Populations of *Nerodia erythrogaster* in

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extreme western Kentucky and adjacent western Tennessee are currently recognized as *N. e. flavigaster*, and populations of extreme southeastern Illinois are recognized as *N. e. neglecta* (Conant and Collins 1998). However, populations in Kentucky and Tennessee located west of the Tennessee river have received only anecdotal analysis (but see Bufalino 1999). The arbitrary nature of *Nerodia erythrogaster* taxonomy and the conservation issues surrounding *N. e. neglecta* warrant a thorough investigation of *N. erythrogaster* throughout its range. Herein, we present a quantitative description of the phenotypic variation exhibited by *N. erythrogaster* from the Ohio and Mississippi river systems of southern Illinois, western Kentucky and adjacent western Tennessee, and we provide an updated range map of the study area with insight on the consistency of separating specimens into phenotypic classes (i.e., subspecies) using Conant's (1949) diagnostic characters.

MATERIALS AND METHODS

Study Area and Sampling Methods

The study was conducted in portions of southern Illinois, the Jackson Purchase area of extreme western Kentucky (between the Mississippi and Tennessee Rivers), portions of Land Between The Lakes (LBL) National Recreation Area, and throughout adjacent western Tennessee (Figure 1). We captured 130 adult specimens (minimum SVL 480 mm; average SVL 792.77 ± 11.51 SE) by hand and between March 2002 and June 2004 and analyzed data from a minimum of 10 specimens from each of 11 sample sites. In order to avoid problems with color fading in preserved specimens, only living and recently killed specimens were analyzed. Live specimens were released unharmed at their site of capture.

Field Observations

In the field, snakes were classified as *flavigaster*, *neglecta*, or *neglecta* $\times$ *flavigaster* (specimens not falling within the acceptable range of variation for either *N. e. neglecta* or *N. e. flavigaster*) based on observations of the diagnostic characters described by Conant (1949). The anterior-most 10 belly scales (posterior to the chin), the 10 belly scales at mid-body, and the 10 posterior-most belly scales (anterior to the anal plate) of each snake were

scored with a Pantone Graphic Arts Color Key® (Pantone Inc., Carlstadt, New Jersey, USA) under natural lighting by holding the color tabs next to the darkest area of the snake's belly scales and selecting the corresponding tab. The proportion (%) of red hue present in the color score was recorded from lightest (yellow) to darkest (dark red). The color-scored belly segments also were digitally photographed on a neutral gray background under natural lighting.

Image Analysis

Photographs of the color-scored belly segments taken in the field were downloaded into Microsoft Photo Editor® (Microsoft Corporation, Mountain View, California, U.S.A.) for image analysis. The four best (free of scars and obscurities) belly scales of each 10-scale photograph were cropped and enlarged to 400 $\times$ actual size. The total area (%) (in pixels) of the dorsal pigment present on each belly scale was determined, and the mean of the four-scale segment was recorded and used (along with the ventral color scores) in quantifying the differences among specimens assigned to phenotypic groups in accordance with Conant's (1949) qualitative methods (SAS Institute Inc., Cary, North Carolina, U.S.A.).

RESULTS

Phenotypic Variation

Adult *Nerodia erythrogaster* specimens from this region exhibited subtle variations in dorsal pattern prominence and ground color. Dorsal patterns ranged from inconspicuous to a slight remnant of the juvenile pattern. Dorsal ground colors ranged from chocolate brown to olive/gray and from gray to black. Because of the high variability and absence of an observable color gradient in the dorsal phenotypes (e.g., similar to the yellow to red gradient on the venter), we focused our efforts on the belly scales. Specimens assigned to the *neglecta* group (as defined by Conant 1949) exhibited ventral phenotypes that ranged from light orange to fire red-orange with dorsal pigment invasion that ranged from moderate/heavy to profuse (almost melanistic). Specimens classified as *flavigaster* exhibited ventral phenotypes that ranged from pale yellow to a yellow/light orange mixture with little to no dorsal pigment invasion along the anterior

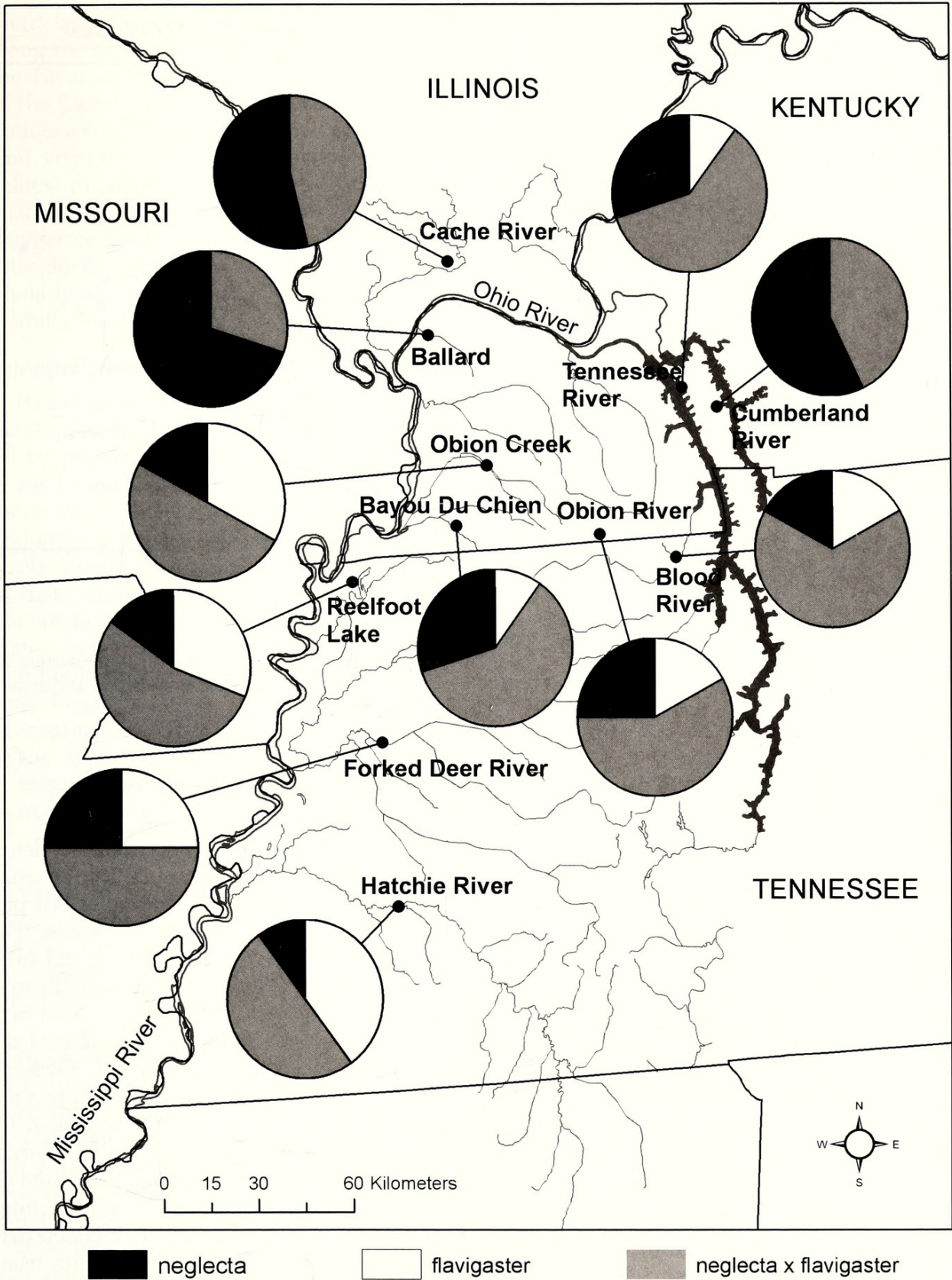


Figure 1. Study area with drainages and points indicating collection sites as well as phenotypic ratios of the populations sampled based on qualitative observations of Conant's (1949) ventral diagnostic characters.

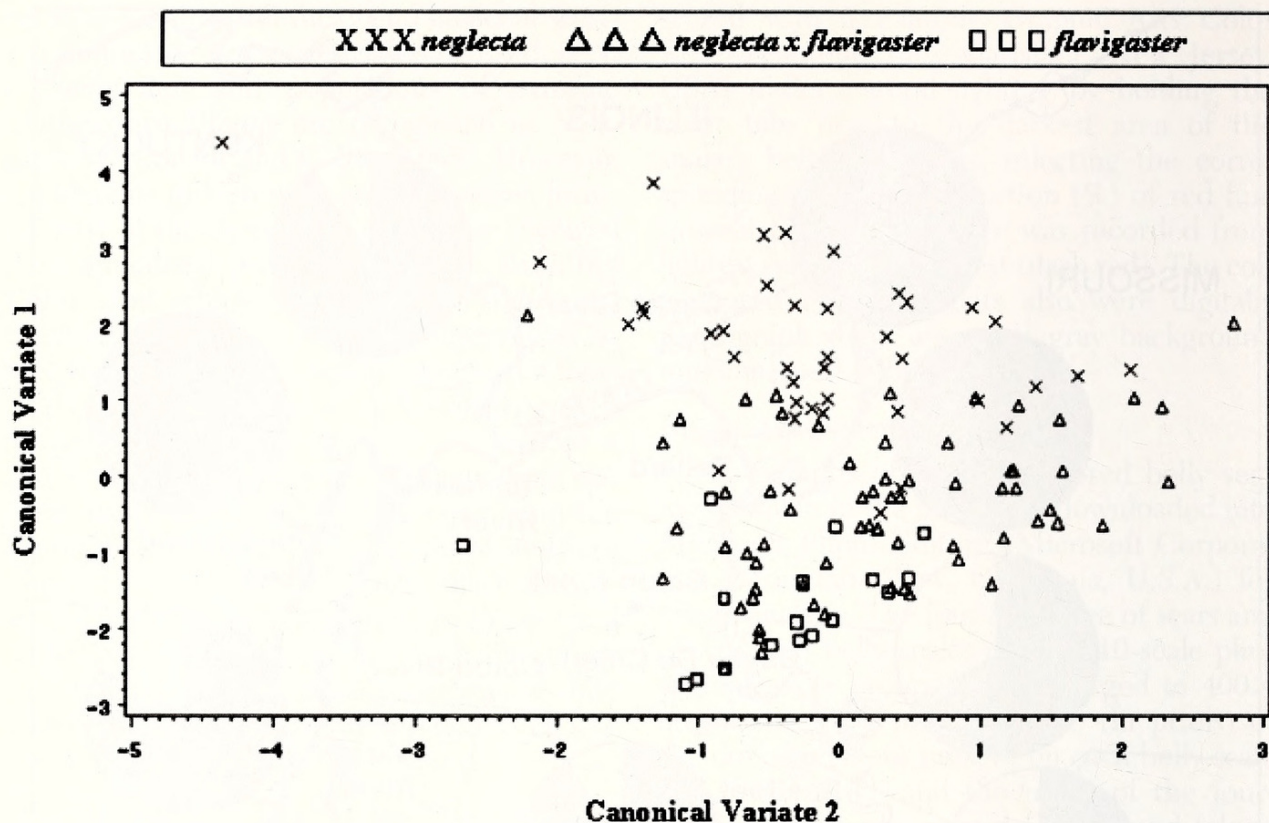


Figure 2. Plot of canonical variates created from ventral-scale data collected from each specimen illustrating the overlapping (or confusion) that can result when specimens from regions with broad phenotypic variation are assigned to phenotype groups (e.g., subspecies) using Conant's (1949) qualitative methods.

scale margin. Specimens classified as *neglecta* $\times$ *flavigaster* intermediates exhibited four general ventral phenotypes: 1) medium orange to red with little or no invading dorsal pigment (similar to *N. e. erythrogaster*), 2) a noticeably redder stripe running through the center of otherwise yellow scales, 3) the anterior half of each belly scale orange and the posterior half yellow, and 4) yellow and heavily mottled with dorsal pigment.

Phenotypic Classifications

Tukey's studentized range (HSD) ($\alpha = 0.05$) revealed that phenotype groups were most strongly differentiated with mid-ventral observations: 1) all three groups had significantly different ($F_{2,130} = 15.60$, $P < 0.001$) amounts (%) of red hue: *flavigaster* = 1.31 ± 0.23 SE; *neglecta* $\times$ *flavigaster* = 7.63 ± 0.95 SE; *neglecta* = 11.26 ± 1.01 SE and 2) all three groups had significantly different ($F_{2,130} = 78.06$, $P < 0.001$) areas (%) of dorsal pigment invading into the belly scales: *flavigaster* = 6.93 ± 0.81 SE; *neglecta* $\times$ *flavigaster* = 18.13 ± 0.64 SE; *neglecta* = 39.16 ± 0.93 SE.

Discriminant and Canonical Discriminant Analysis

Discriminant analysis was used to determine the probability of misclassification using ventral color and the total area of dorsal pigment invading onto the ventral scales. The probability of misclassification was (23.44%) with eight *flavigaster* and eight *neglecta* misclassified as *neglecta* $\times$ *flavigaster*, seven *neglecta* $\times$ *flavigaster* misclassified as *flavigaster*, and seven more misclassified as *neglecta*. However, there were no instances where a *flavigaster* and/or a *neglecta* were mistaken for one another. Canonical discriminant analysis was used to create canonical variates based on the ventral data collected from each specimen to generate a plot that visually characterizes the overlap (or confusion) that occurs when separating *N. erythrogaster* into subspecies using qualitative observations (Figure 2).

Phenotypic Distribution

The ventral characters associated with *neglecta* (greater red coloration and dorsal pig-

ment invasion) reached their greatest values along the Ohio River and east of the Tennessee River. A transition occurred through most of the Jackson Purchase and adjacent western Tennessee as these values became smaller. The ventral characters reached their lowest values in southwest Tennessee where the characters became more associated with the *flavigaster* phenotype (yellow coloration with little dorsal pigment invasion) (Figure 3). The phenotypic ratios at each sample site reflected a similar trend (Figure 1).

Intergradation Zone Delineation

Based on qualitative observations of specimens collected during this study and supported by population means of the ventral diagnostic characters described by Conant (1949), there was evidence of intergradation in all drainages but the Cumberland, Ohio, and Cache rivers. Intergradation may be occurring in these drainages as well, but no *flavigaster* phenotypes were observed, and the intermediates were visually much closer to *neglecta*. The findings suggested that the intergradation zone began south of the confluence of the Mississippi and Ohio rivers and extended east to the Tennessee River side of LBL, running at least as far south as the Hatchie River Bottoms of southwest Tennessee (Figure 4).

DISCUSSION

Nerodia erythrogaster populations of extreme western Kentucky and adjacent Tennessee exhibit a variety of phenotypes including individuals that are typical of all four United States subspecies. Within the study area, *N. e. neglecta* influence is greatest in the northern and eastern portions along the Ohio and Cumberland rivers. *N. e. neglecta* influence then gradually gives way to *N. e. flavigaster* influence in southwest Tennessee along the Mississippi River. The dominant phenotype class in the region, however, is a highly variable *neglecta* $\times$ *flavigaster* intergrade.

Brandon and Blanford (1995) suggested that a *neglecta* population will contain individuals typical of that subspecies as well as questionable forms that still bear a resemblance to *neglecta*. If so, the range of *N. e. neglecta* should be extended through the Ohio River (down to Ballard County, Kentucky) and through the northern half of the Cumberland

River Basin (upstream to Trigg County, Kentucky). Furthermore, there is a large zone of intergradation south of the confluence of the Mississippi and Ohio rivers in the Jackson Purchase area of western Kentucky, east to the Tennessee River, and south to below the Hatchie River bottoms of southwest Tennessee. Thus, true *flavigaster* populations (populations consisting of individuals that only exhibit phenotypes typical of *flavigaster* or intermediate forms that favor *flavigaster*) do not occur in the state of Kentucky. Likewise, they might not occur in the state of Tennessee because the southward extent of the *neglecta* phenotype west of the Tennessee River (in some individuals) extends at least to the Hatchie River drainage and may reach as far south as northern Mississippi.

This study suggests that Conant's (1949) ventral diagnostic characters are reliable when separating specimens that are typical of *N. e. flavigaster* and *N. e. neglecta* from one another, but they lose considerable precision in regions or populations with broad phenotypic variation. Such populations can exhibit phenotypes other than those expected from a simple melding of phenotypes typical of an intergrade zone between two subspecies. For instance, in the field, 23 specimens indistinguishable from *N. e. erythrogaster* were observed, but for the needs of this study were classified as *neglecta* $\times$ *flavigaster* because the closest reported range of the red-bellied water snake subspecies (Conant and Collins 1998) is in rather distant southeastern Alabama.

With respect to *N. e. neglecta* conservation, the *Nerodia erythrogaster* populations of the Midwestern U.S.A. above the 40th parallel (regardless of subspecies) are threatened with extirpation from anthropomorphic activities and warrant each state's endangered status. *Nerodia erythrogaster* (including the *N. e. neglecta* phenotype) was well represented in the aquatic habitats investigated during this study, albeit, habitat degradation and fragmentation continue to be a concern for this or any wetland species occurring in the region. Thus, the protection currently provided by these state governments seems appropriate. However, our findings of *N. e. erythrogaster* phenotypes in western Kentucky and Tennessee along with Christiansen and Leclerc's (2002) report of an *N. e. neglecta* population in Iowa

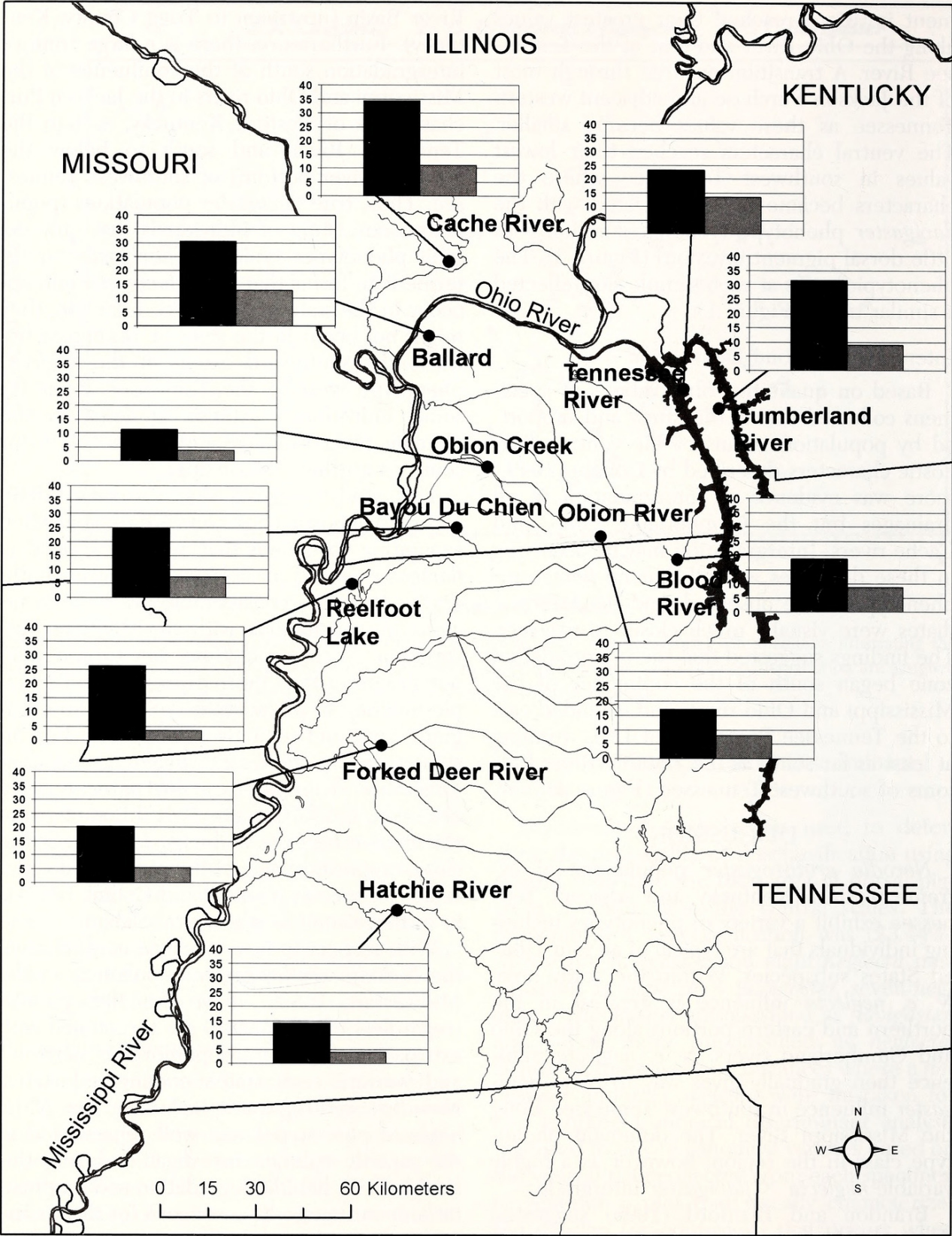


Figure 3. Mean proportion of red (gray bars), and the mean proportion of the ventral scales invaded by dorsal pigment (black bars) at the mid-ventral region for each sample population.

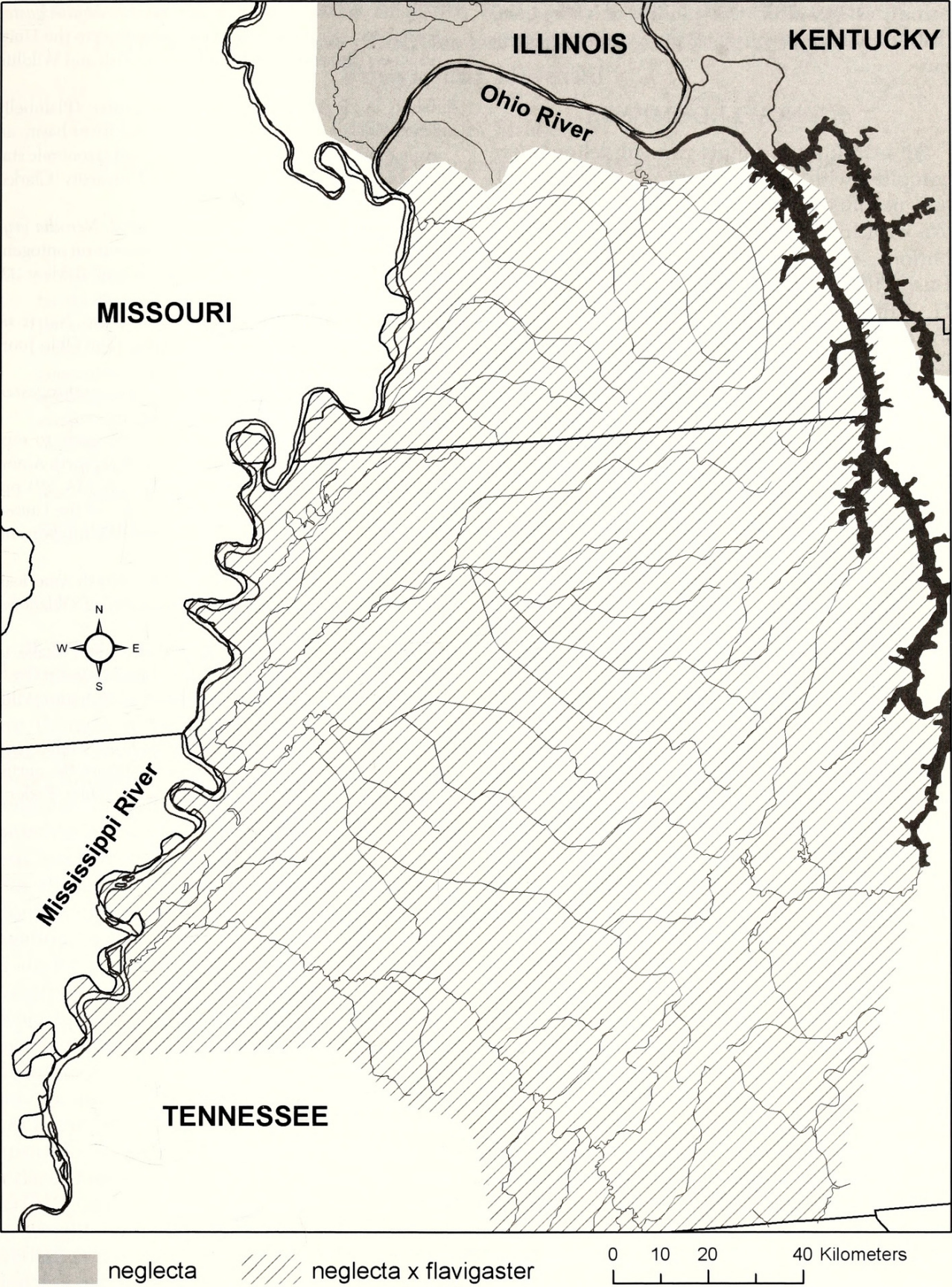


Figure 4. Revised *N. erythrogaster* range map for the study area. Only regions investigated during this study are delineated. Although perimeter areas such as southeast Missouri are visible in the figure, they were not investigated so they have been left idle.

bring into question the validity of subspecies distinctions in *Nerodia erythrogaster* altogether.

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