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Geographic variation in a restricted-range endemic dragonfly *Gomphurus ozarkensis* (Odonata: Gomphidae), with description of a new subspecies

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Abstract

The geographic distribution of *Gomphurus ozarkensis* (Westfall, 1975), a species described to science only four decades ago, is confined to a four-state area in the central United States: southeastern Kansas, eastern Oklahoma, western and northern Arkansas, and southern Missouri. Its small range has led some to classify it a species of conservation concern. We examined geographic variation in the species, which despite its small range exists in three distinct subpopulations: one in the Ouachita Mountains of western Arkansas and southeastern Oklahoma; one on the Ozark Plateau of northeastern Oklahoma, southeastern-most Kansas, southern Missouri, and northern Arkansas; and one in the Osage/Flint hills of southeastern Kansas and northeastern Oklahoma. Clinal variation is evident in the extent of yellow on the terminal abdominal segments and the extent to which certain thoracic stripes are fused. A population in a separate watershed basin in the southern Osage Hills of Oklahoma is taxonomically distinct, with some phenotypic characters tending toward *G. externus* (Hagen, 1858). We describe this population as a new subspecies of *G. ozarkensis*.

Key words: clinal variation, dragonfly, *Gomphurus*, new subspecies, Osage Hills, United States

Introduction

Phenotypic, ecological, genetic, or physiological variation across a species' geographic range underpins basic aspects of evolutionary potential: without variation, there can be no evolution. Exposition on intraspecific geographic variation in insects has a long history (Hubbell 1956; Chown & Gaston 2010), even if attention lags behind that given to vertebrates and has been focused in certain taxonomic orders, such as Lepidoptera, Orthoptera, and Diptera (in which details on variation in *Drosophila*, for example, are legion). Moreover, broad ecogeographic rules have been applied to body size variation in insects, albeit with mixed results (Chown & Gaston 2010; Shelomi 2012), as have comparable ideas about how elevation drives variation in body size (Hawkins & DeVries 1996; Pérez-Valencia & Moya-Raygoza 2015). Yet intraspecific geographic variation extends well beyond body size: color, shape, and pattern vary, too; for example, color and pattern feature prominently in studies of geographic variation in Lepidoptera (Gillham 1956; Braby *et al*. 2012), and color-based ecogeographical rules have been applied to Collembola (Rapoport 1969).

Studies of patterns of geographic variation in Odonata, the damselflies and dragonflies, often have considered size and shape (e.g., Stewart 1982; Battin 1992; Kenner 2000; Sagedhi *et al*. 2009), although for species with a long flight season, studies of body size are confounded by time of year, with individuals that emerge earlier larger than those that emerge later (McCauley 2010; Stewart & Vodopich 2018). Nonetheless, color and pattern have been assessed, too, often through the prism of infraspecific taxonomy. The subspecies rank has not played a prominent role in Odonata taxonomy, at least relative to other orders or classes: only perhaps 10% of the >6,300 described species have described subspecies, although those that have vary in pattern and color.

Geographic variation and subspecies in the odonate family Gomphidae, the clubtails, have been elucidated and named in a number of instances (e.g., Donnelly 1987; Catling & Hughes 2008; Kosterin 2014). Often, subspecies descriptions increase as a taxon's phenotypic complexity increases (Páll-Gergely *et al*. 2019) and as its geographic range increases (Phillimore *et al*. 2007). By contrast, species with small geographic ranges rarely exhibit any measurable degree of geographic variation.

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Gomphurus ozarkensis is a dragonfly endemic to the central United States that was described relatively recently (Westfall 1975). Adults are active only early in the flight season, chiefly late March through June (Susanke & Harp 1991; Smith-Patten & Patten 2017). It is largely confined to the Ozark Plateau and Ouachita highlands of a four-state area from southeastern Kansas and southwestern Missouri south to southeastern Oklahoma and western Arkansas. Because of its small geographic range, Bick (1983) considered the species to be of high conservation concern, although he later (Bick 2003) revised his assessment downward, and we (Patten & Smith-Patten 2013) categorized it as vulnerable in Oklahoma, the state with perhaps the largest population size.

In the course of our work with *Gomphurus ozarkensis* in Oklahoma and Arkansas, we noted apparent geographic variation in phenotype—chiefly in terms of pattern, but to an extent in body size—despite the species' small geographic range. Herein we describe and assess that variation across the whole of the species' range, with particular attention paid to an outlying population.

Material and methods

We quantified phenotypic characters of 30 ♂ and 19 ♀ specimens of *Gomphurus ozarkensis*, principally from the Smith/Patten collection (housed at the Oklahoma Biological Survey, University of Oklahoma) but supplemented with specimens from CSUC, FSCA, OMNH, SEMC, and USNM (see Acknowledgments for museum abbreviations). We likewise quantified characters on 23 ♂ and 11 ♀ specimens of *G. externus* (Hagen, 1858) for comparative purposes.

We used digital calipers for length and span measurements, to the nearest 0.1 mm. Measured traits were forewing length, hindwing length, abdominal length (anterior of abdomen to terminal appendages), and total length (frons to tip of longest terminal appendage). We quantified the amount of yellow on abdominal segments S7–S10 (dorsally and laterally) as surface area from standardized photographs taken with a Moticam 3.0 MP digital camera attached to a Motic SMZ-171 stereo microscope. Specifically, we estimated extent (mm^2) using ImageJ software, in which we used the line segment tool to measure linear structures and the freehand selection tool to measure areas. We likewise used standardized photographs to quantify (to the nearest 0.1 mm) ♂ and ♀ reproductive structures. On ♂ cerci, we measured, in lateral view, 1) length, both from the posterolateral edge of S10 to dorsal tip of cercus and along the ventral base of the cercus to the tip, 2) depth (distance from dorsal to ventral cercus tip), and 3) span (distance between outer edges of cercus tips). On ♂ epiprocts, we measured 1) length, both from the posterolateral edge of S10 to dorsal tip and from the edge of S10 to an imaginary vertical line extending down from tip of epiproct, and, in dorsal view, 2) depth, both along a vertical line between the epiprocts and along the distal edge of S10 to edge of epiproct center, and 3) span, the distance between outer edges of epiproct tips. On the ♀ subgenital plate, we measured the span of tips of the lobes, width of the base, narrowest point, length, and depth of the distal cleft. We measured each trait twice; these measurements correlated highly ($r = 0.98$), so we used in analyses the mean trait values of the replicates.

Our analyses focused on differentiation of a geographically isolated population of putative *G. ozarkensis* along Salt Creek at the fringe of the Osage Hills in western Osage County, Oklahoma, that seemed to differ from individuals elsewhere in the species' geographic range. Osage specimens suggested a tendency toward *G. externus* in some characters, so our first analyses were to determine whether the population was intermediate (potentially implying hybridization) or whether it could be diagnosed as one species or the other. To answer this question, we performed linear discriminant analysis (via R package 'MASS'; Venables & Ripley 2002) in two ways: three groups *a priori* (*G. externus* vs. *G. ozarkensis* vs. Osage) and two groups *a priori* (*G. externus* vs. *G. ozarkensis*, with Osage individuals classified *a posteriori*). For these analyses we used only ♂ specimens because they provided a larger sample size. We considered on ten characters that varied enough (determined via coefficients of variation) to suggest an ability to discriminate: 1) hindwing length, 2) total length, 3) cercus length, 4) cercus depth, 5) epiproct span, 6) epiproct depth, 7) extent of yellow dorsally on S8, 8) extent of yellow dorsally on S9, 9) extent of yellow laterally on S7, and 10) extent of yellow laterally on S8.

Subsequent analyses focused on assessing variation within *G. ozarkensis*, for which we explored patterns of clinal variation and determined the extent to which the Osage population could be differentiated from individuals collected elsewhere. For the latter, we ran two-group (*G. ozarkensis* vs. Osage) discriminant analyses 1) with the same ten characters enumerated above and 2) with measures of the cerci and epiprocts excluded because we did not expect these characters to differ. We further assessed variation and overlap via Bayesian analogs to two-sample *t*-tests (Kruschke 2013) for each character, analyses that included estimates of effect size in terms of diagnostic ability (custom JAGS code run via R package 'rjags'; Plummer 2003). Here, too, we used only ♂ specimens because there is only a single

♀ specimen from the Osage population, yet we were able to estimate a mean and Bayesian highest posterior density intervals around that mean for other ♀ specimens and show where the Osage ♀ plotted for two key features of the subgenital plate.

We supplemented quantitative analyses with a qualitative assessment of variation visible in photographs ($n = 48$) archived in Odonata Central (https://www.odonatacentral.org/), a citizen-science endeavor wherein an observer can submit photographically documented records that are vetted by regional experts. Our qualitative scoring considered only the extent of yellow dorsally on S9 (none, trace, some, much) and of yellow (fused, trace, split) between the black on thoracic stripes T1/T2, regardless of sex. These data were analyzed via a Bayesian multinomial model (custom JAGS code) such that probability of each class, as well as associated uncertainty (the highest posterior density intervals), could be estimated.

Results

We were able to discriminate *G. externus* from *G. ozarkensis* readily (Fig. 1), more-or-less purely on the basis of length and depth of the cercus and the extent of yellow laterally on S8 (Table 1). At the level of these two species, no individuals were misclassified and, indeed, none had *a posteriori* probability of correct classification <0.999. A two-group discriminant analysis, for which loadings were similar, with Osage individuals classified *a posteriori* (i.e., on the basis of discrimination of the two species), emphasized that individuals from that population cluster with *G. ozarkensis* (Fig. 2).

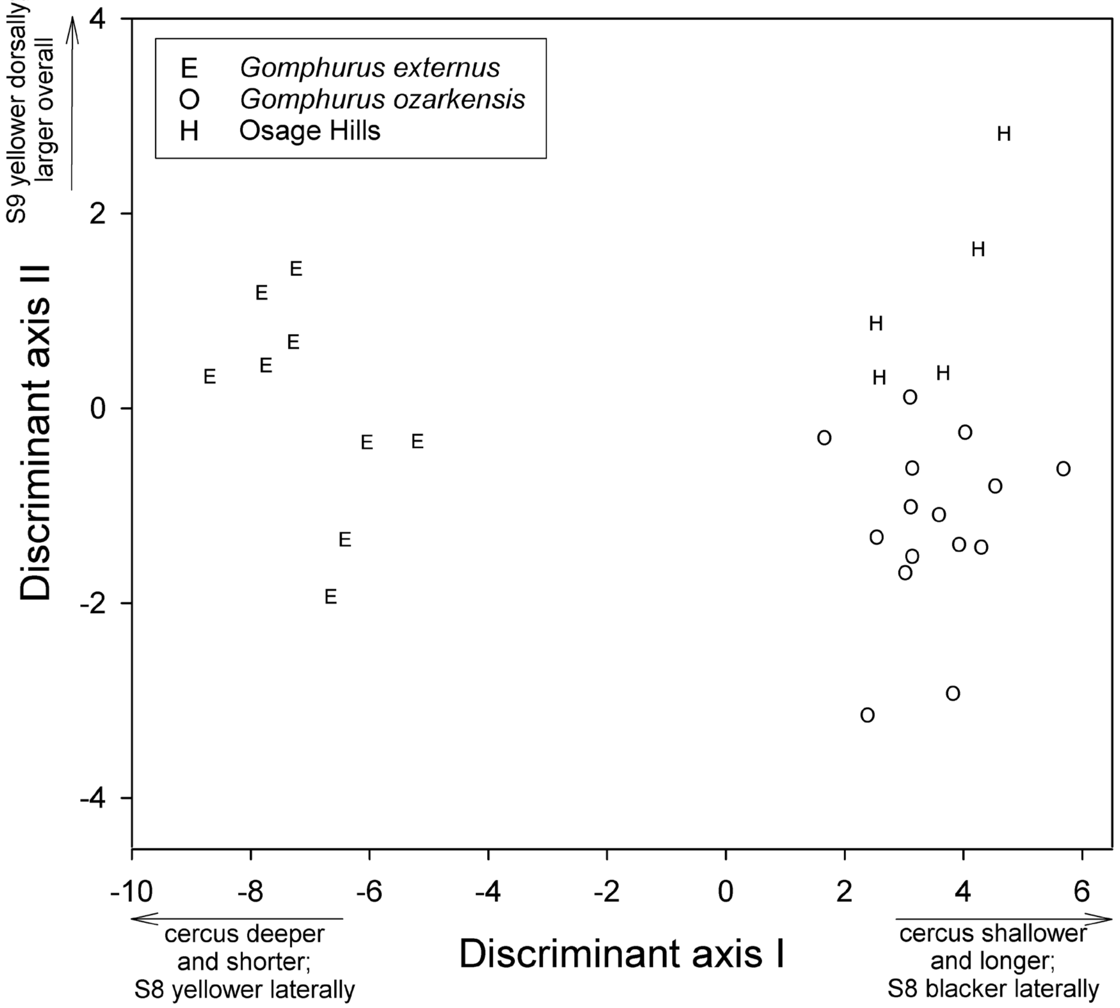

Figure 1. Scatter plot on the first two linear discriminant axes of ♂ *Gomphurus externus* and *G. ozarkensis*, including from an isolated Osage population. The Osage individuals cluster with *G. ozarkensis*, which is the species to which they had been identified since discovery in 2011, but nonetheless separate from that main cluster of that species, represented by individuals from farther east and south. Key diagnostic characters were determined from loadings of discriminant scores (Table 1).

Table 1. Loadings—Pearson correlation coefficients between variates and raw variables—for a linear discriminant analysis of ♂ *Gomphurus externus* and *G. ozarkensis*, with Osage County treated *a priori* as a third group. Higher (in magnitude, regardless of sign) correlations indicate that the synthetic variate carries more "signal" from that raw variable (i.e., trait).

trait	**axis I**	**axis II**
hindwing length (mm)	-0.379	0.445
total length (mm)	-0.193	0.575
cercus		
length (mm)	0.85	-0.383
depth (mm)	-0.965	0.026
epiproct		
span (mm)	-0.616	0.326
depth (mm)	0.181	-0.289
extent of yellow		
S8 dorsal (mm^2)	-0.534	0.487
S9 dorsal (mm^2)	-0.54	0.724
S7 lateral (mm^2)	-0.735	0.397
S8 lateral (mm^2)	-0.826	0.51

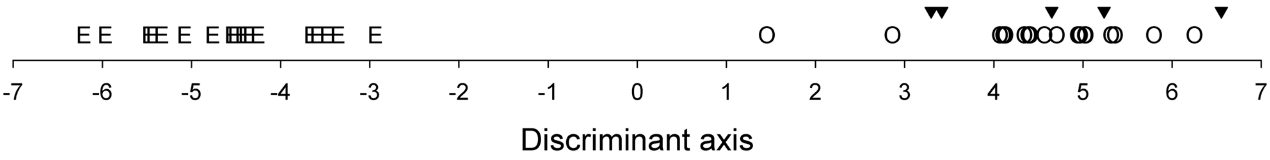

Figure 2. Linear discriminant axis of males of *Gomphurus externus* (E) and *G. ozarkensis* (O), with individuals from an isolated Osage population (downward triangles) classified *a posteriori*. On the basis of cercus length and width, epiproct span, and extent of yellow laterally on S7 and S8, Osage individuals are *G. ozarkensis*.

Within *G. ozarkensis*, proportion of yellow dorsally on S9 varied clinally with latitude for either sex (Fig. 3), and the proportion of yellow tends to be smaller on individuals in the Ouachita subpopulation (i.e., S9 is blacker) than on individuals in the Ozark subpopulation. We consider variation clinal because a two-segment piecewise regression did not improve fit (Skalski et al. 2008). On males, estimates of mean extent of yellow dorsally on S9 did not overlap between typical *G. ozarkensis* and Osage individuals, and that character as well as extent of yellow laterally on S8 and total length had a large (or greater) effect size (Table 2), with "large" interpreted to be $|\eta| \geq 0.8$ (Sawilowsky 2009). Subsequent two-group discriminant analyses with *G. ozarkensis* as one group and the Osage population as the other emphasized that the latter could be diagnosed from the former (Fig. 4). With measures of ♂ appendages included, no specimens were misclassified (Fig. 4A) and posterior probabilities of correct classification were ≥0.69 for all specimens and >0.90 for 75% of them. With measures of ♂ appendages excluded, a single *G. ozarkensis* classified with $P = 0.76$ as an Osage Hills individual (Fig 4B). On the basis of loadings, three characters largely drive the diagnoses: total length ($r = 0.88$) and extent of yellow dorsally on S9 ($r = 0.77$) and laterally on S7 ($r = 0.75$). The sole ♀ specimen from Osage was an outlier in two features of the subgenital plate: the span of the tips of the lobes and the basal width (Fig. 5). The Osage ♀ did not differ in three other features of the subgenital plate: width at narrowest point, total length, and depth of the cleft.

We were able to qualitatively score the extent of yellow dorsally on S9 and whether T1/T2 was fused on photographs (archived at Odonata Central) of 27 ♂ and 21 ♀, three of the ♂ from the Osage population. Typical *G. ozarkensis* was estimated with $p = 0.64$ [0.51, 0.78] to have S9 wholly black and with $p = 0.77$ [0.65, 0.89] to have T1/T2 fused (Fig. 5). By contrast, all three photographs of individuals from the Osage population had the dorsum of S9 extensively yellow and T1 and T2 divided with yellow from the base to ~⅓ their length. Four additional photographs from Osage archived at the Oklahoma Biological Survey exhibit much yellow dorsally on S9; further, in three images T1/T2 were definitely split, but we designated one individual as indeterminate because we were unable to determine whether the stripes fused or split partially.

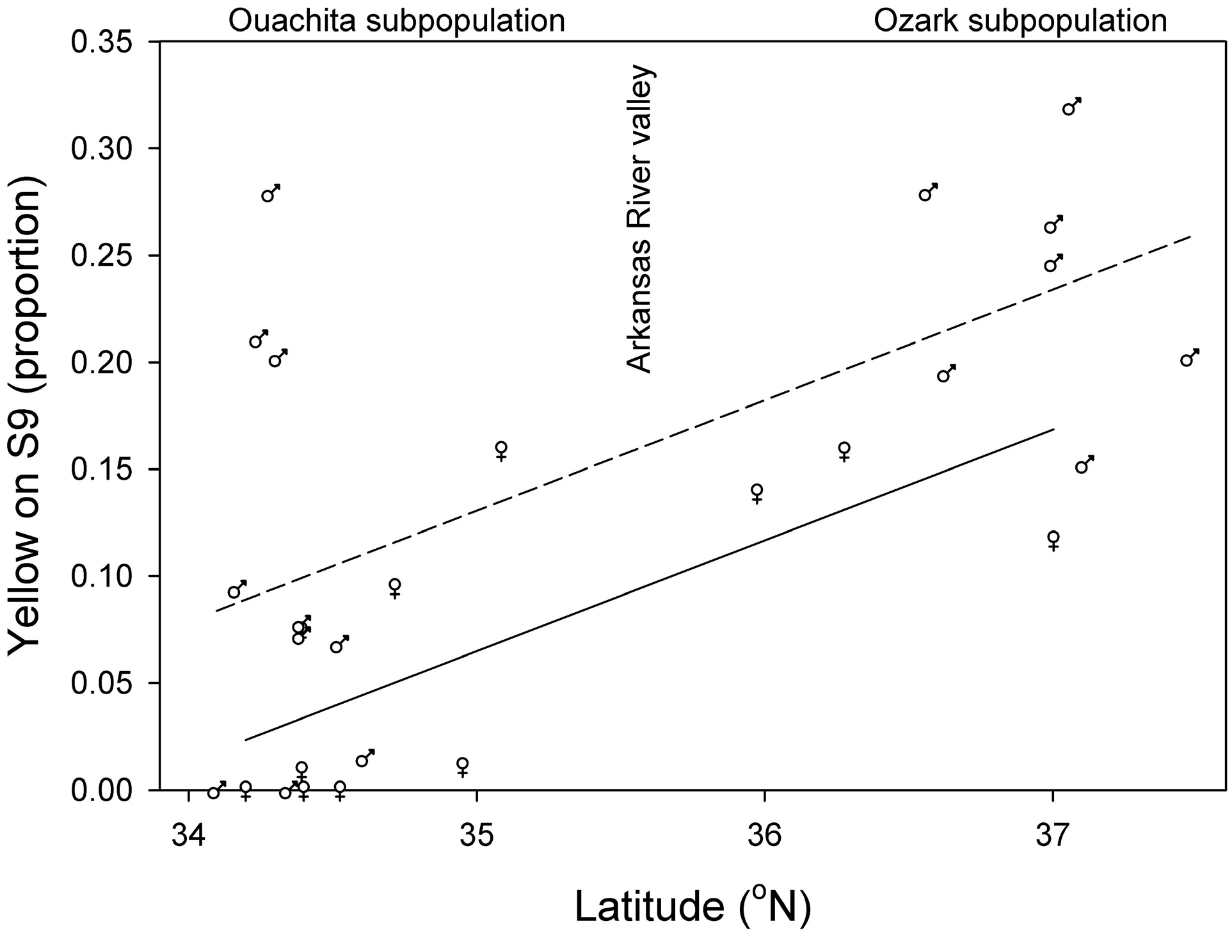

Figure 3. Apparent clinal variation of the extent of yellow on S9 in *Gomphurus ozarkensis*. For either sex, yellow increases with latitude: individual variation is considerable, but both males and females in the Ozark subpopulation average yellower than those in the Ouachita subpopulation, with males tending toward slightly yellower than females. Lines are simple linear regressions fit separately to ♂ and ♀ data. In each case, the proportion of yellow on S9 increases ~0.047 mm^2 / ° latitude.

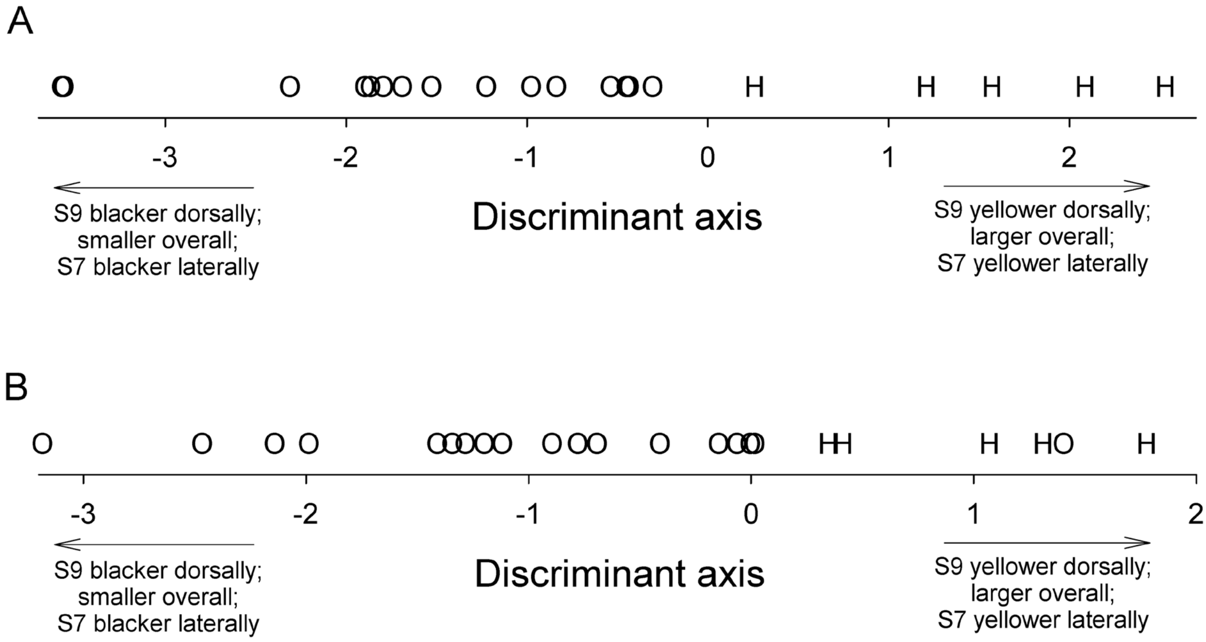

Figure 4. Linear discriminant axes of ♂ *Gomphurus ozarkensis* (O) and from an isolated Osage Hills population (H) both A) including and B) excluding measures of ♂ cerci and epiprocts. The extent of yellow on the dorsum of the ninth abdominal (S9) was especially differentiated.

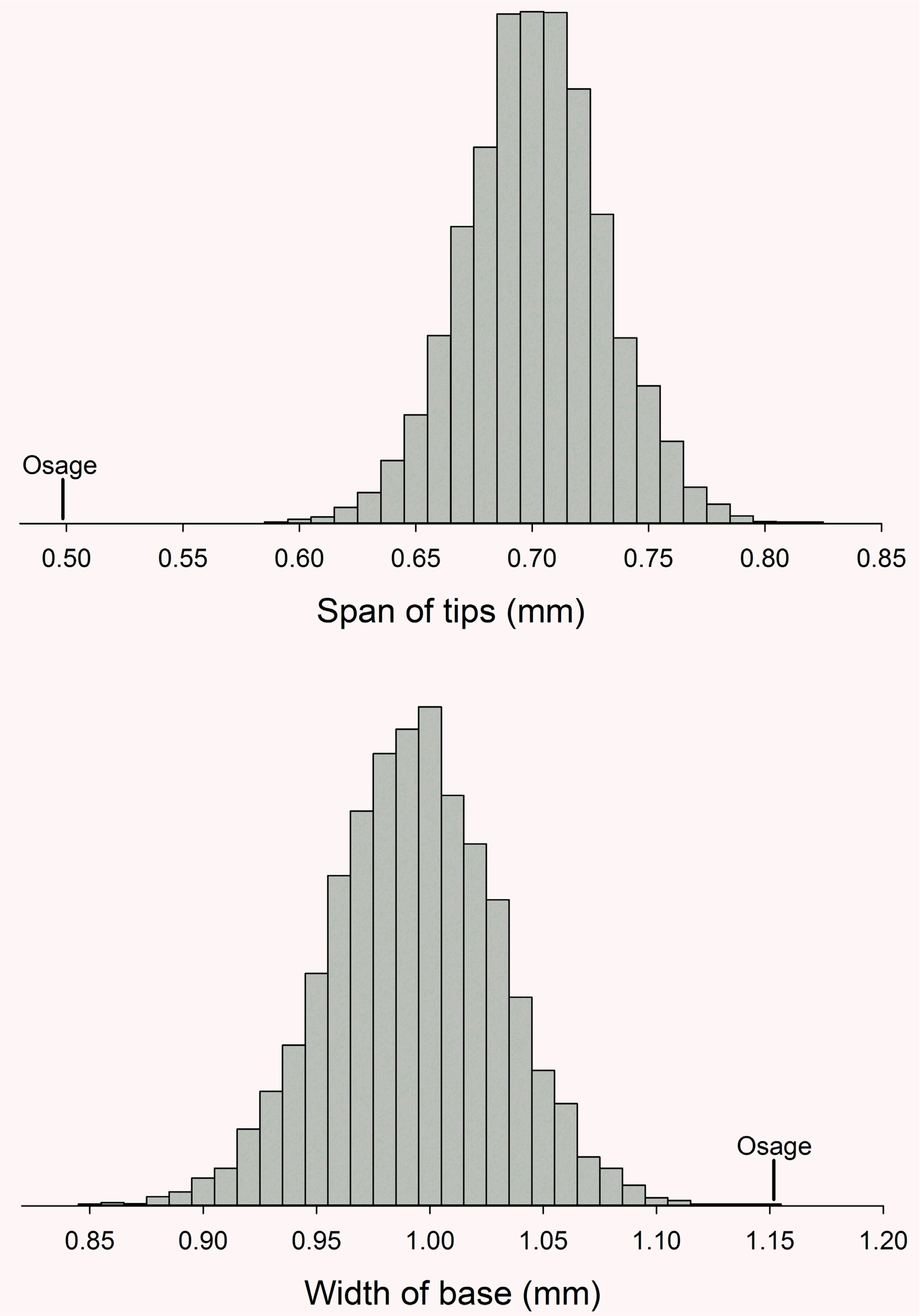

Figure 5. Bayesian posterior distribution of mean tip span and basal width of the subgenital plate of ♀ *Gomphurus ozarkensis*, with measurements for the single ♀ specimen from Osage Hills population plotted for comparison.

Table 2. Bayesian estimates of means and mean differences (from an analog of a two-sample *t*-test) between typical ♂ *G. ozarkensis* (*n* = 24) and ♂♂ from the Osage population (*n* = 5) across four key characters, as well as estimated effect sizes (η) for those differences. (Effect size is a scale-independent estimate of, in this case, the extent to which one sample differs from another, such that a larger effect size indicates a greater magnitude of difference.) "Proportion >0" refers to the extent the posterior probability density is less than zero, with typical individuals as the reference (i.e., a value can be read, for example, as "with probability 0.87, the true and underlying mean hindwing length of Osage individuals is greater than that of *G. ozarkensis* from elsewhere").

	Osage	*G. ozarkensis*	difference (HDI)	proportion >0	η
hindwing (mm)	29.4	28.9	0.5 (-0.5, 1.4)	0.87	0.56
total length (mm)	54.8	53	1.8 (0.4, 3.3)	0.99	1.66
extent of yellow					
dorsal S8 (mm^2)	1.09	0.72	0.37 (-0.22, 0.99)	0.92	0.96
dorsal S9 (mm^2)	1.81	0.97	0.84 (0.19, 1.50)	0.99	1.34
lateral S7 (mm^2)	1.01	0.68	0.33 (-0.38, 1.02)	0.87	0.73
lateral S8 (mm^2)	2.44	1.97	0.47 (0.19, 0.75)	0.99	1.35

***Gomphurus ozarkensis howeryi*, subsp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:A907E77F-F9D6-4A42-BE17-198DD85F0AA0

Diagnosis. Like nominate *G. ozarkensis*, but more extensively yellow dorsally on S8 and S9 and laterally on S7 and S8, T1/T2 split by a pale line 1/3 or more of the suture length, and overall body size generally larger (54.0–56.8 mm, mean 55.0 mm; Fig. 6). In general, the yellow dorsally on S9 >1.75 mm^2 and that laterally on S7 will be >1.0 mm^2). Females may differ further in the narrower span of the tips of the subgenital lobes and the wider base of the subgenital plate, but there exists but a single ♀ specimen from the Osage population.

Type specimens. Holotype: ♂ from Salt Creek 4 km NNE of Burbank, Osage County, Oklahoma, collected 11 June 2016 by Brenda D. Smith (specimen 1942 in the Smith/Patten collection [SP], housed at the Oklahoma Biological Survey, University of Oklahoma, Norman); dorsal yellow S9, 1.79 mm^2, lateral yellow S7, 0.80 mm^2, total length, 56.75 mm. Allotype: ♀, locality as holotype, collected 29 May 2014 by Michael A. Patten and Brenda D. Smith (specimen SP 1212).

Paratypes: all same locality as holotype: 1 ♂, same date as holotype (SP 1943), 2 ♂, same date as allotype (SP 1210, 1211), and 1 ♂, collected on 11 May 2014 (SP 1181).

Distribution. This subspecies is known only from Oklahoma along Salt Creek on the southwestern fringe of the Osage Hills, a southward extension of the Flint Hills ecoregion of Kansas (Fig. 7). Salt Creek lies within the Arkansas–Keystone watershed basin, a separate basin from nearby populations. This population presumably has been isolated there for some time. It may be that the subspecies occurs on other southwestward flowing creeks in this basin, including nearby Beaver and Grouse Creeks (Fig. 7)

Variation. All specimens (5 ♂, 1 ♀) and individuals in archived photographs (7 ♂) have the dorsum of S9 extensively yellow. All specimens have T1/T2 unfused, as in the case in archived photographs in which T1/T2 can be seen clearly (*n* = 6). Total length of *G. o. howeryi* (♂ or ♀) range from 54.0–56.8 mm, with a median of 55.0 mm (nominate, 50.8–55.1 mm, with median 53.0 mm).

Etymology. We are pleased to name this new subspecies in honor of Mark Howery, Wildlife Diversity Biologist at the Oklahoma Department of Wildlife Conservation, for his decades of dedication and important contributions to conservation of non-game wildlife in the state of Oklahoma.

We located two *G. o. ozarkensis* specimens with as much yellow on S9 as is present on Osage individuals. One, a ♂ from the Big Caney River ~2 km west of Elgin, Chautauqua County, Kansas (SEMC 1349369), is as large as *G. o. howreyi*, although the extent of yellow on S9 is right at the cutoff (i.e., ≈1.75 mm^2). It is this individual that plots within the cluster of *G. o. howeryi* on Fig. 4B. The other, a ♂ from Meramec State Park, Franklin County, Missouri (CSUC), has yellow dorsally on S9 that exceeds the cutoff (1.93 mm^2), but it is small (51.9 mm) and generally has a pattern of yellow laterally on S7 and dorsally on S8 in line with the nominate subspecies. We likewise located perhaps five photographs of *G. o. ozarkensis* with S9 as yellow, although on a photograph one cannot determine if the extent of yellow is < or > 1.75 mm^2. A tandem pair collected (CSUC) in the Wichita Mountains in southwestern Oklahoma evidently represented a vagrant record given that the species has not been seen in that range since. Both individuals were of the nominate subspecies.

That a species of dragonfly with a small geographic range and short flight season could exhibit readily discernable geographic variation is of great interest evolutionarily, particularly in light of apparent early stages of divergence in the ♀ subgenital plate. Numerous species in the Gomphidae have tiny ranges and are likely to have diverged geologically recently from their nearest relatives. An understanding of mechanisms, both geographical and ecological, that have driven speciation in the group is sorely needed.

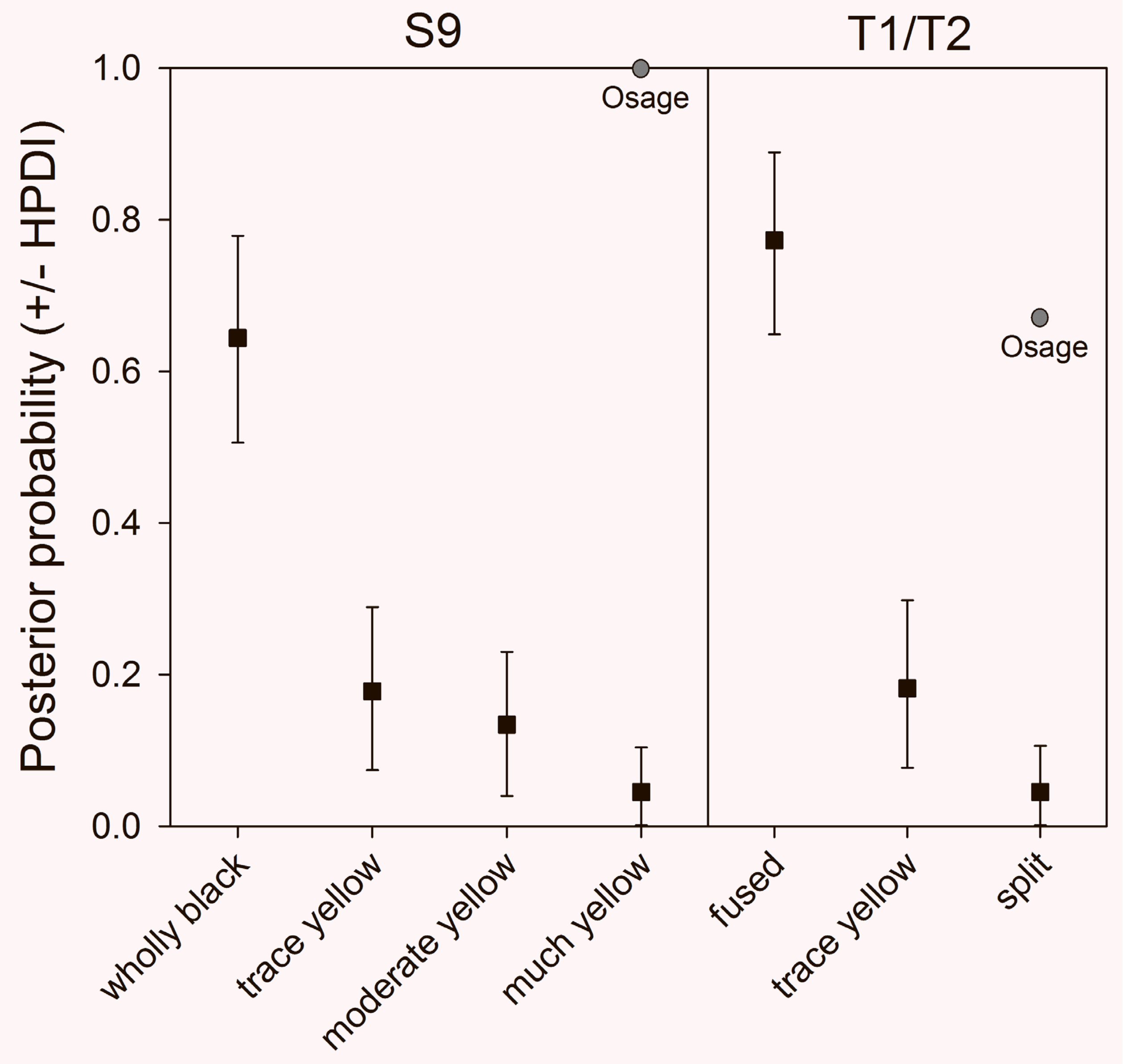

Figure 6. Posterior estimates (± highest density credible intervals) from a Bayesian multinomial model of the probabilities of occurrence of yellow dorsally on the ninth abdominal segment (S9) or of yellow bisecting the first two dark thoracic stripes (T1/T2). Data are from archived (in Odonata Central) photographs of individuals of either sex. The mean value for photographs of Osage is plotted for comparison.

Discussion

Despite its relatively small geographic distribution, we detected geographic variation in *Gomphurus ozarkensis*, both clinally with latitude and specifically with respect to an isolated population on Salt Creek in western Osage County, Oklahoma. Our initial impression that the Osage population of *G. ozarkensis* was intermediate toward *G. externus* was not supported by our data. Even so, relative to *G. ozarkensis* elsewhere in the species' four-state range, Osage individuals tended to be larger (total length averaged nearly 2 mm longer), with more yellow dorsally on S9 (especially) and S8, laterally on S7 and S8, and an unfused T1/T2, all traits of *G. externus*.

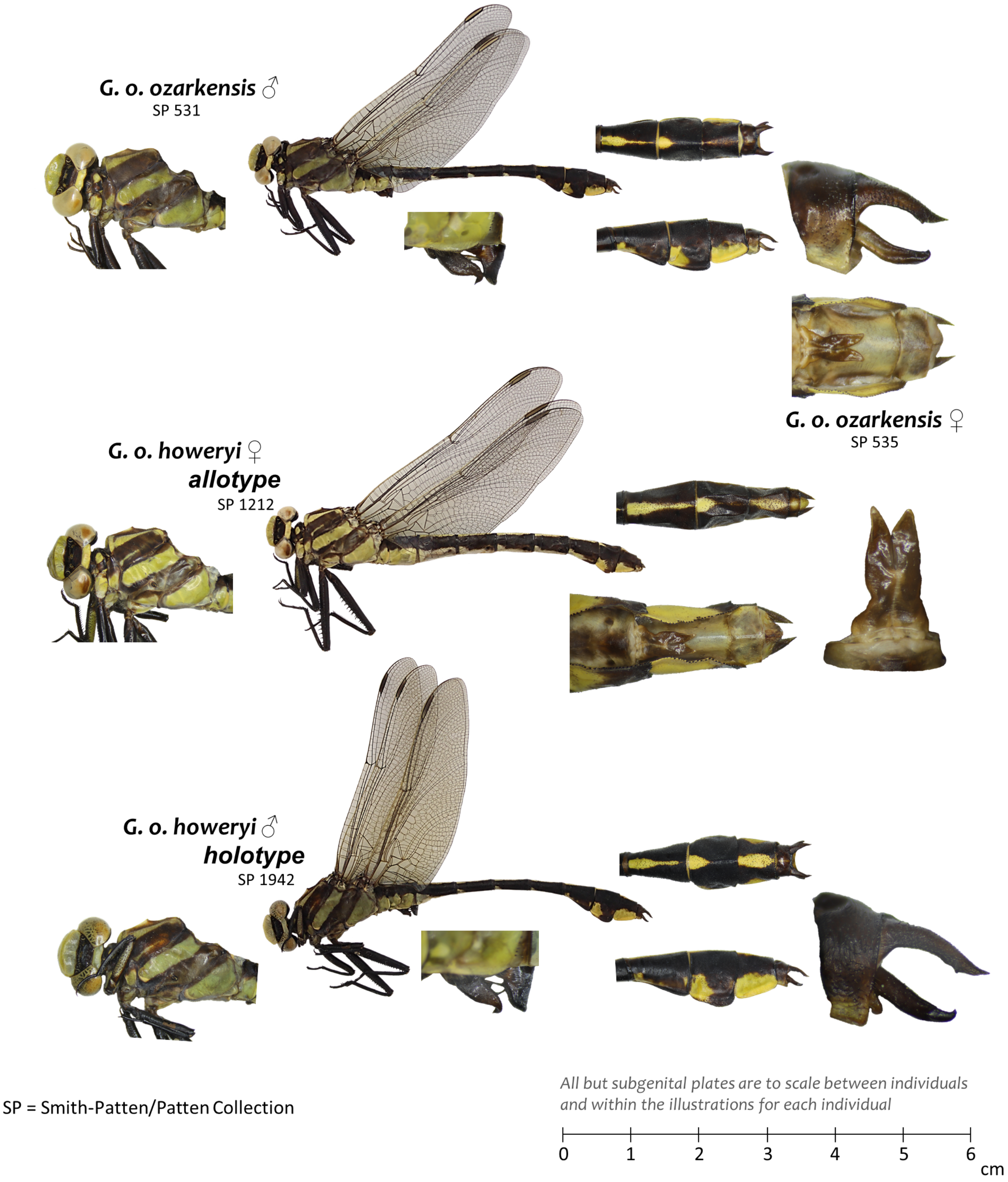

Figure 7. Comparison of nominate *Gomphurus ozarkensis* to *G. o. howeryi* subsp. nov. All like images (e.g., thoraces, cerci, overall body) are to scale between individual specimens.

We further considered whether the Osage population constituted an undescribed species, although our examination and analysis of specimens suggested that it is diagnosable as *G. ozarkensis*. Critically, no aspect of ♂ cerci or epiprocts differed appreciably, and the hamules are nearly identical, although it may be that hamules of Osage individuals have slightly longer curved tips (we could not quantify this trait, but if a difference exists it is on the order of <1 mm).

Another possibility is infraspecific differentiation—the Osage population constitutes a previously unrecognized subspecies. We do not know if the population represents an evolutionary divergent lineage (an "incipient species"), a demand made by some (e.g., Braby *et al*. 2012), even though the incipient species criterion was expressly not a part of the original conceptualization of subspecies (Patten 2015). Moreover, in light of how subspecies evolve, determination of lineages would require access to more than neutral genetic markers (Patten & Remsen 2017). Setting aside the lineage argument, it remains that subspecies can and have been rigorously (statistically) defined in terms of the "75% rule," a rule that emphasizes diagnosablitiy over differences in means (Patten & Unitt 2002). In short, 75% of individuals from one population of interest must differ from 99% of individuals from the other, and *vice versa*.

Our data suggest that the population is taxonomically diagnosable chiefly on the basis of the extent of yellow on the dorsum of S9 and overall size.

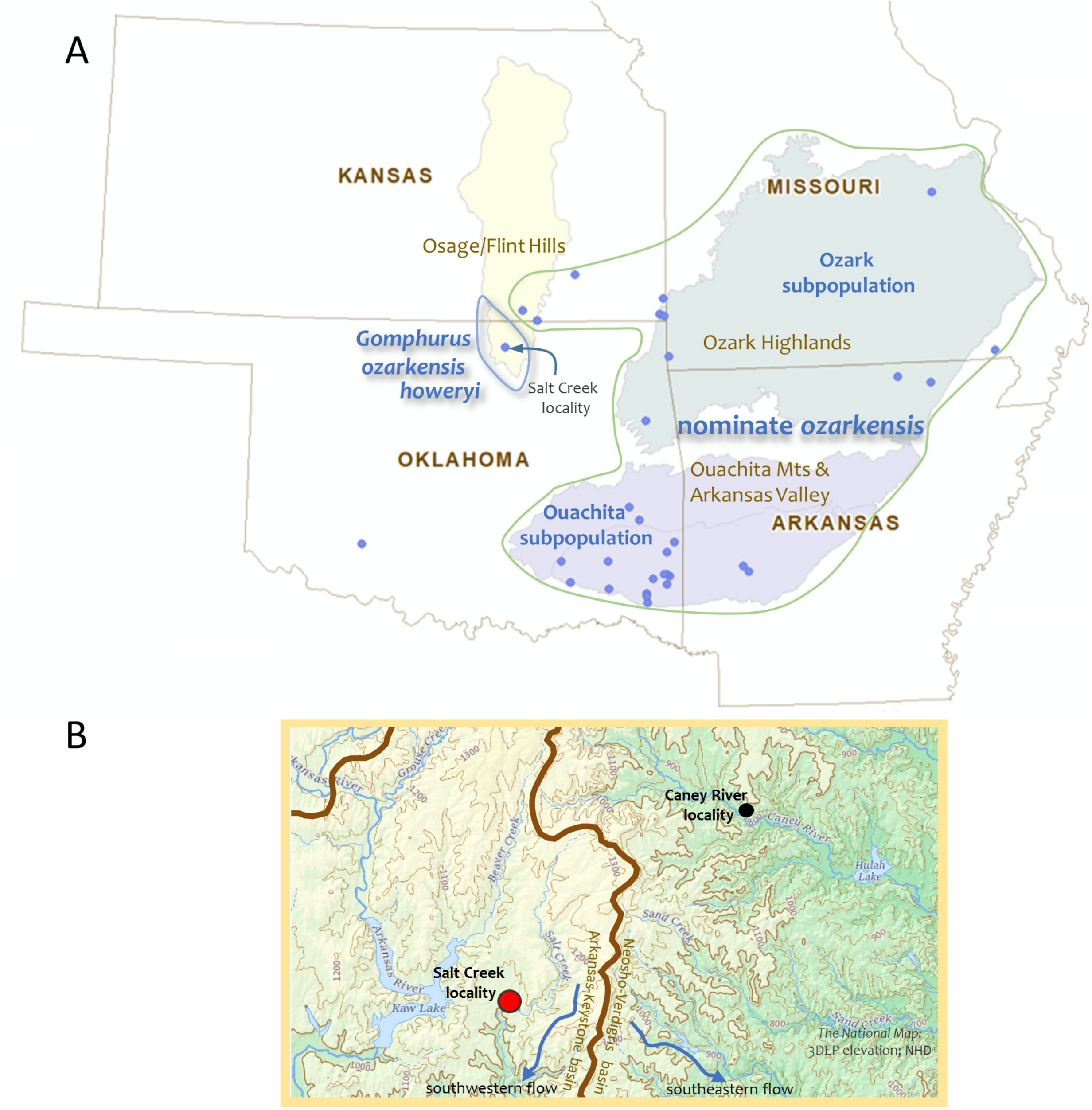

Figure 8. A, Geographical range of nominate *Gomphurus o. ozarkensis* and *G. o. howeryi* subsp. nov. **B,** In the Osage Hills, distance between localities of known occurrence is not great (~48 km), but topographic relief is: the highest elevation along a straight line between the two nearest is 382 m, and the highest point in the area is 413 m. This physiographic break coincides with watershed sub-regions, basins, and sub-basins (HUC-4, 6, 8, respectively). Away from Salt Creek, the single (one of several taken) specimen that matched *G. o. howeryi* is from the Caney River site.

Acknowledgments

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References

Battin T. 1992. Geographic variation analysis among populations: the case of *Platycnemis pennipes* (Pallas, 1771) (Insecta: Odonata: Zygoptera) in the Aegean. *Journal of Biogeography* 19: 391–400.
https://doi.org/10.2307/2845567

Bick G. H. 1983. Odonata at risk in conterminous United States and Canada. *Odonatologica* 12: 209–226.

Bick G. H. 2003. At-risk Odonata of [the] conterminous United States. *Bulletin of American Odonatology* 7: 41–56.

Braby M. F., Eastwood R. & Murray N. 2012. The subspecies concept in butterflies: Has its application in taxonomy and conservation biology outlived its usefulness? *Biological Journal of the Linnean Society* 106: 699–716.
https://doi.org/10.1111/j.1095-8312.2012.01909.x

Catling P. M. & Hughes M. 2008. Variation in Canadian *Gomphus fraternus* (Odonata: Gomphidae) in relation to the recognition of subspecies *manitobanus*. *Canadian Entomologist* 140: 327–337.
https://doi.org/10.4039/n07-036

Chown S. L. & Gaston K. J. 2010. Body size variation in insects: A macroecological perspective. *Biological Reviews* 85: 139–169.
https://doi.org/10.1111/j.1469-185X.2009.00097.x

Donnelly T. W. 1987. Structural variation of *Ophiogomphus mainensis*: Description of a new subspecies and relationship to sibling species (Odonata: Gomphidae). *Proceedings of the Entomological Society of Washington* 89: 205–214.

Gillham N. W. 1956. Geographic variation and the subspecies concept in butterflies. *Systematic Zoology* 5: 110–120.
https://doi.org/10.2307/2411573

Hawkins B. A. & DeVries P. J. 1996. Altitudinal gradients in the body sizes of Costa Rican butterflies. *Acta Oecologica* 173: 185–194.

Hubbell T. H. 1956. Some aspects of geographic variation in insects. *Annual Review of Entomology* 1: 71–88.
https://doi.org/10.1146/annurev.en.01.010156.000443

Kenner R. D. 2000. *Somatochlora kennedy* (Odonata: Corduliidae): A new species for British Columbia, with notes on geographic variation in size and wing venation. *Journal of the Entomological Society of British Columbia* 97: 47–50.

Kosterin O. E. 2014. Notes on infraspecific variation of some Gomphidae (Odonata) species in Cambodia. *International Dragonfly Fund Report* 68: 1–16.

Kruschke J. K. 2013. Bayesian estimation supersedes the *t* test. *Journal of Experimental Psychology: General* 142: 573–603.
https://doi.org/10.1037/a0029146

McCauley S. J. 2010. Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). *Ecological Entomology* 35: 377–385.
https://doi.org/10.1111/j.1365-2311.2010.01191.x

Páll-Gergely B., Asami T. & Sólymos P. 2019. Subspecies description rates are higher in morphologically complex land snails. *Zoological Scripta* 48:in press.
https://doi.org/10.1111/zsc.12319

Patten M. A. 2015. Subspecies and the philosophy of science. *Auk: Ornithological Advances* 132: 481–485.
https://doi.org/10.1642/AUK-15-1.1

Patten M. A. & Remsen J. V., Jr. 2017. Complementary roles of phenotype and genotype in subspecies delimitation. *Journal of Heredity* 108: 462–464.
https://doi.org/10.1093/jhered/esx013

Patten M. A. & Smith-Patten B. D. 2013. Odonata species of special concern for Oklahoma, USA. *International Journal of Odonatology* 16: 327–350.
https://doi.org/10.1080/13887890.2013.868328

Patten M. A. & Unitt P. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk* 119: 26–35.

https://doi.org/10.2307/4090009

Pérez-Valencia L. I. & Moya-Raygoza G. 2015. Body size variation of *Diaphorina citri* (Hemiptera: Psyllidae) through an elevation gradient. *Annals of the Entomological Society of America* 108: 800–806. https://doi.org/10.1093/aesa/sav072

Phillimore A. B., Orme D. L., Davies R. G., Hadfield J. D., Reed W. J., Gaston K. J., Freckleton R. P. & Owens I. P. F. 2007. Biogeographical basis of recent phenotypic divergence among birds: A global study of subspecies richness. *Evolution* 61: 942–957. https://doi.org/10.1111/j.1558-5646.2007.00068.x

Plummer M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*.

Rapoport E. H. 1969. Gloger's rule and pigmentation of Collembola. *Evolution* 23: 622–626. https://doi.org/10.1111/j.1558-5646.1969.tb03545.x

Sagedhi S., Adriaens D. & Dumont H. 2009. Geometric morphometric analysis of wing shape variation in ten European populations of *Calopteryx splendens* (Harris, 1782) (Zygoptera: Odonata). *Odonatologica* 38: 343–360.

Sawilowsky S. S. 2009. New effect size rules of thumb. *Journal of Modern Applied Statistical Methods* 8: 597–599. https://doi.org/10.22237/jmasm/1257035100

Shelomi M. 2012. Where are we now? Bergmann's rule *sensu lato* in insects. *American Naturalist* 180: 511–519. https://doi.org/10.1086/667595

Skalski J. R., Townsend R. L., McDonald L. L., Kern J. W. & Millspaugh J. J. 2008. Type I errors linked to faulty statistical analyses of endangered subspecies classifications. *Journal of Agricultural, Biological, and Environmental Statistics* 13: 199–220. https://doi.org/10.1198/108571108X310771

Smith-Patten B. D. & Patten M. A. 2017. Update on the Oklahoma Odonata Project: Anisopterans. *Argia* 29(1): 1–10.

Stewart S. S. & Vodopich D. S. 2018. Environmental effects on wing shape and wing size of *Argia sedula* (Odonata: Coenagrionidae). *International Journal of Odonatology* 21: 189–203. https://doi.org/10.1080/13887890.2018.1523752

Stewart W. E. 1982. An analysis of geographic variation of the adults of the Australian genus *Diphlebia* Selys (Odonata: Amphipterygidae). *Australian Journal of Zoology* 30: 433–460. https://doi.org/10.1071/ZO9820435

Susanke G. R. & Harp G. L. 1991. Selected biological aspects of *Gomphurus ozarkensis* (Westfall) (Anisoptera: Gomphidae). *Advances in Odonatology* 5: 143–151.

Venables W. N. & Ripley B. D. 2002. *Modern Applied Statistics with S*, 4th edn. Springer, New York. https://doi.org/10.1007/978-0-387-21706-2

Westfall M. J., Jr. 1975. A new species of *Gomphus* from Arkansas (Odonata: Gomphidae). *Florida Entomologist* 58: 92–95. https://doi.org/10.2307/3493387