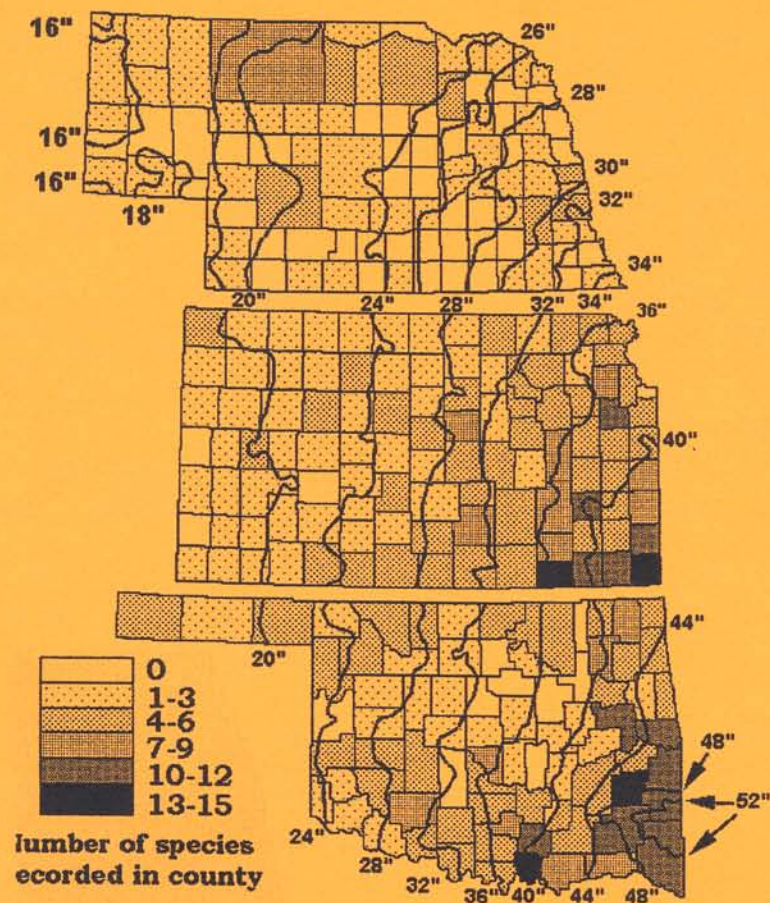


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ODONATA IN THE GREAT PLAINS STATES: PATTERNS
OF DISTRIBUTION AND DIVERSITY

Roy J. Beckemeyer p. 49-99

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ODONATA IN THE GREAT PLAINS STATES: PATTERNS OF DISTRIBUTION AND DIVERSITY¹

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This paper is dedicated to George and the late Juanda Bick, in recognition of their nearly fifty years of study of the biology and distribution of the Odonata of the Great Plains; their encouragement and generosity are greatly appreciated.

ABSTRACT: Through the March, 1999 cutoff date of this study, a total of 320 species of dragonflies and damselflies, 73% of the Nearctic fauna, had been recorded as occurring in the 13 states comprising the Great Plains of the United States. These species are listed together with the Great Plains states in which they occur and the larger biogeographic region to which they belong. A significant latitudinal gradient in species richness was found to be present in the central Great Plains, with 194 species in Texas and 55 in North Dakota. A suite of similarity and diversity measure were mapped to visually display patterns of relationships of the state faunas. This process led to the identity of four faunal groups in the central Great Plains: Texas; Kansas - Oklahoma; Nebraska - South Dakota - Colorado - Iowa; and North Dakota. In terms of

Nearctic biogeographical affinities, 43% of the Great Plains odonate fauna is of eastern origin. The large number of tropical species (42) in Texas contributes 14% of the Great Plains total. Northern transcontinental, western, southwestern, transcontinental, and central groups contribute 11%, 9%, 8%, 8%, and 7%, respectively. The Great Plains is home to major faunal boundaries and regions of overlap, many occurring in the central tier of states from Oklahoma north through North Dakota. The Bicks' 1957 assertion that the 32 to 36 inch precipitation isolines correlated with the area of overlap of eastern and western species groups in Oklahoma appears to hold true for Kansas as well.

Introduction

Knowledge of the distribution of the Odonata of the Great Plains has been accumulating very slowly and has been relatively incomplete in comparison with other regions of North America. However, recent efforts have begun to fill in the gaps, and the current availability of state species lists for all 13 of the Great Plains states and of county lists for the western and central tiers of these states has made it possible to begin looking at the overall patterns of distribution of this interesting group of insects. (The cutoff date for the data used in this analysis was March, 1999. Although additional species have been recorded for a number of states in the interim – e.g., there are now 212 species known for Texas – I believe that the patterns documented here

should provide a useful status assessment and foundation for future studies.)

Why study the Odonata of the Great Plains? This is an area where eastern and western, northern and southern faunas overlap. The Great Plains lie in the rain shadow of the Rocky Mountains, and therefore are quite arid, with a significant east-west gradient of precipitation and evaporation. This large area is also one in which there is significant latitudinal gradient, one where the winter and summer extremes are harsh and highly variable (often resulting in tenuous and short lived environments), and one where the influence of man has been widespread and far-reaching. The water resources of the prairies are under intense pressure and have rapidly changed in nature as the prairies have become populated (Batt, 1996,

¹ Bulletin of American Odonatology, 2002 6(3): 49-99

Matthews, 1988, Rabeni, 1996). The Great Plains might be looked on as a living laboratory in which Odonata at the edges of their habitat ranges are tested for adaptability and fitness.

Odonata are sensitive to the existence of adequate sites for mating, egg-laying and larval development, but adults are sufficiently vagile that they can likely search out alternative sites if required. Huggins and Moffitt (1988) have listed Kansas Odonata species and their tolerance to various pollutants and stressors. The possible utility of odonates as indicator assemblages for prairie habitats was surveyed (along with other invertebrate groups) by Arenz and Joern (1996). As Laubham and Fredrickson (1996) pointed out in their study of the vertebrates of prairie wetlands, a "...high degree of mobility is critical for species that exploit unreliable and widely spaced seasonal environment..." This is true for invertebrates as well as for vertebrates; the Great Plains may eventually have much to tell about the patterns of migration, colonization, adaptation and dispersal in the Odonata.

My immediate aim is much more modest than any of these relatively lofty goals; I wish to begin laying out patterns of distribution and diversity based on our current understanding of the Odonata fauna of the 13 states that contain the Great Plains (based on distributional data that was available through March, 1999). Hopefully this work will form a background against which more detailed studies and assessments can be made in the future. Another goal is to inspire others to fill in the gaps in our understanding of the Great Plains Odonata fauna.

After a brief discussion of methodology, a short review of the history of Odonata study in the Great Plains and a survey of the literature is given. Next patterns of beta diversity and of the gradients in the

biogeographical affinities of the odonate fauna of the Great Plains will be reviewed. These patterns will be discussed and compared with prior studies of the Odonata fauna of Kansas (Huggins, 1978, Kennedy, 1917), Oklahoma (Bick & Bick, 1957), and the Dakotas (Bick et al, 1977). Finally, the need for further study in the Great Plains will be discussed.

Materials and Methods

A list of the Odonata of the Great Plains has been assembled by reviewing the published literature together with collection records of the author and others who have made their collection data available for use. Of particular value for the state of Nebraska were the collection records of attendees at the annual collecting meeting of the Dragonfly Society of the Americas held in Valentine, Nebraska in July 1998 (see the acknowledgments section). In general, museum collections were not reviewed, though published reviews of collections were utilized. Exceptions include data extracted by the author from the University of Nebraska Natural History Museum in Lincoln on Odonata county distribution records for Nebraska, and information on Great Plains states records found in the U. S. National Museum of Natural History.

In addition to the resulting list of Odonata species occurrence by state, county occurrence lists were assembled for the states of Oklahoma, Kansas, Nebraska, and South and North Dakota. I am particularly appreciative of George H. Bick's approval for use herein of his many years worth of data on county records, including unpublished revisions (Bick, 1997a-g) to his published accounts. George and Juanda Bick spent many years collecting and studying the fauna of the Great Plains, and their work provides much of the underpinning for this analysis, particularly for Oklahoma (Bick & Bick, 1957) and the Dakotas (Bick & Hornuff, 1972, Bick et al,

1977). The work of Donald G. Huggins of the Kansas Biological Survey (Huggins et al, 1976, Huggins, 1978, 1983a) remains the source of much of our knowledge of Kansas Odonata distributions. My county distribution data for Nebraska, based on the previously mentioned collection and museum data, is in preparation for publication. These county distribution lists were assembled in support of the Dragonfly Society of the Americas' North American county dot map distribution project, which is being coordinated by Dr. T.W. Donnelly (1999a).

The two data sets, species by state for the 13 Great Plains states, and species by county for the central tier of states from Oklahoma north through North Dakota, were used together with a number of measures of similarity and diversity to quantify patterns of faunal groupings in the Great Plains. The data from these metrics were used in the form of bar graphs and maps to yield visual interpretations of the patterns.

The diversity and similarity metrics are as defined in Magurran (1988) with exceptions as noted below. The states in the central tier, Texas north through North Dakota, were used as reference states for the computation of the similarity or diversity metrics.

Four similarity metrics were used. The first was simply the fraction of species common to the reference state and to each of the other twelve states of the Great Plains. The next two metrics were Jaccard's and Sorenson's Similarity Coefficients (Magurran, 1988, Southwood, 1978). Each of these similarity measures takes a value of zero for faunas with no species in common, and a value of one for faunas with identical species lists. The final similarity metric is based on one used by B. E. Montgomery (1967) to compare odonate faunas of the north central plains. Montgomery used Preston's (1962) "Resemblance Equation"

to compute a value of the "index of resemblance" from which he then computed what he called Preston's "similarity index". Significantly similar faunas would have index values of 0.73 or greater, isolated faunas a value less than 0.73. (Montgomery's papers of 1967 and 1968 reflect the first attempt to numerically characterize the Odonata faunal similarities of various states. Because of the lack of data on distribution, he found it necessary to base his comparisons on subsets of the Odonata, usually at the family level. I compare his results with those of this study in Appendix 1.)

Two diversity measures were used. The first was a standardized form of Cody's measure (Cody, 1975, Magurran, 1988). Cody's index measures species turnover, that is, the average of the number of species lost and the number of species gained in moving along a transect. I used it to determine species turnovers in going from the reference state to each of the other states in turn (comparison states), but standardized the metric in each case by dividing the species turnover by the number of species in the reference state. The second measure used was Wilson and Shmida's index (Magurran, 1988, Wilson & Shmida, 1984), another measure of species turnover. This index is simply Cody's index standardized by the average of the number of species in the reference and comparison states. These measures both take on a value of zero if no species are gained or lost in going from the reference state to the other states, but can take on a value of greater than one when going from a state with few species to one with many species.

These six measures were used to construct a series of maps (Figures 4-9) in which shades of gray were used to indicate ranges of values of the metrics, with white indicating no similarity or maximum diversity, and black indicating total similarity or minimal diversity.

The species were also tallied as representatives of overall New World regional faunal groups: eastern, western, northern transcontinental, transcontinental, tropical, southwestern, and central. Groupings were determined using the state distribution data of Bick & Mauffray (1999) and Mauffray & Beckenbach (1999). Eastern and western groups were comprised of species which occur from the east or west coast, respectively, but do not reach completely across the country. Northern transcontinental species are those which occur from coast to coast in Canada and the northern tiers of states in the U.S. Transcontinental species are those which occur from coast to coast across the contiguous U.S. The tropical (including subtropical) species group comprises taxa that generally reach their peak numbers in Central or South America. Southwestern species are those found in northwestern Mexico and the southwestern U.S. northeast into the southern Great Plains. Finally, the central group is composed of taxa which have their peak distributions in the central part of the U.S. and which generally do not reach either coast. There is obviously an opportunity here for some circularity in the interpretation of species distribution groups, but I believe the groupings to be reasonably valid in general.

The 320 species of Odonata which were known to occur in the 13 Great Plains states: New Mexico (NM), Colorado (CO), Wyoming (WY), and Montana (MT) (the western tier), North Dakota (ND), South Dakota (SD), Nebraska (NE), Kansas (KS), Oklahoma (OK), and Texas (TX) (the central tier), and Missouri (MO), Iowa (IA), and Minnesota (MN) (the eastern tier) are listed in Appendix 1 together with the Great Plains states in which they are found and the overall regional designation assigned for this study. The Great Plains Odonata distributions in terms of these regional groups were used in the form of bar graphs and

maps to further elucidate the patterns of diversity of the Great Plains Odonata fauna. Similar data were prepared for the central tier of states from Oklahoma north through North Dakota using the county distribution data. These county record data were also used to identify areas of the Great Plains needing further collecting effort.

History of Odonata Study in the Great Plains

The first dragonfly in Linneaus' (1758) list was *Libellula quadrimaculata*, a holarctic skimmer that also occurs in the nearctic, including the northern Great Plains. The species was not recorded for the Great Plains, however, until about 135 years after its description. The first records I have found for *L. quadrimaculata* in the Great Plains were from 1893 for Wyoming (Calvert, 1893) and from 1897 for Iowa (Elrod, 1898). (While Molnar and Lavigne (1994) still show the species as widespread across Wyoming, Cruden and Gode (1998) report the species as rare to uncommon (state rarity category S3) due to habitat loss in their recent comprehensive survey of Iowa Odonata.)

In general, North American Odonata were described recently in comparison with other groups of attractive and obvious animals, e.g. the birds. The median year (i.e., the year when half the currently known species had been described) for North American birds was 1790 while that for the Odonata was 1907 (Donnelly and Beckemeyer, 1996). The watershed period for Great Plains Odonata was from 1854 to 1861, when Lt. John Pope was sent by the U.S. Army Corps of Engineers to explore Texas and New Mexico. His explorations resulted in "...no less than 21 new species of North American odonates ..." (Donnelly, 1997). Included in this list were many common Great Plains species. A number of Lt. Pope's specimens were described and listed in Herman Hagen's seminal Synopsis of

1861, in which he covered 62 North American species, 35 from the vicinity of the Pecos River in Texas. Four additional species, one each from Missouri, Minnesota, and North Dakota ("Fort Union"), and one (*Calopteryx maculata*) "... common all over the Union", brought the total number of species recorded for the Great Plains states to 39.

Calvert's catalog of 1893 included many notes on distribution across the U.S. His list adds 30 species to the Great Plains states (15 for Texas, 7 for South Dakota, 6 for Colorado, 3 for Missouri, 2 for Kansas, 1 for New Mexico, and 3 widespread species), bringing the total for the region to 69.

In 1894, Nathan Banks determined a set of specimens sent to him by F.H. Snow of Kansas University. He added 20 species to the Kansas list, 2 to Colorado, and added 7 new species to the Great Plains list, bringing it to a total of 76 species. The early part of the 20th century saw great progress being made in the study of Great Plains odonates. In 1914, E.B. Williamson reported on Texas and Oklahoma, listing 56 and 34 species, respectively. In 1917 C.H. Kennedy monographed the fauna of Kansas, analyzed their distribution, and listed 65 species for the state. This was the first paper to address the fact that the Great Plains represented a region of transition between eastern and western Odonata faunas. Williamson increased the Great Plains list by 35 species, Kennedy by another 11, bringing the total to 122 species, 38% of the current number. Additions to the list occurred episodically in the remaining years, with spurts of activity in the 30's (Oklahoma), the 50's (Oklahoma), the late 60's (Nebraska, the Dakotas), the late 70's and early 80's (Dakotas, Kansas), and again in the late 90's (Iowa, Nebraska, the western tier of states, Minnesota, and Texas). I will next review these studies, but will do so for each tier of states rather than chronologically for the entire Great Plains.

Kennedy's Kansas publication was the first attempt to summarize the odonate fauna of a Great Plains state including distribution by county. Eleven of the thirteen Great Plains states have received or are in the process of receiving such coverage to date. It is worthwhile to briefly summarize the status for each of the thirteen states and to list some of the important sources of data. I will begin with the western tier of states and progress eastward.

The states of the western tier have all received fairly recent attention, checklists with county records being available as follows: New Mexico (Evans, 1995), Colorado (Evans, 1988), Wyoming (Molnar & Lavigne, 1994), Montana (Roemhild, 1975, Miller & Gustafson, 1996). Additional data for these states published after these summaries include: New Mexico: Abbott & Stewart (1998), Daigle (1995), Donnelly (1995), Dunkle, (1975, 1995), Garrison (1994); Colorado: Barlow (1993), Evans (1995).

The states of the central tier all have some degree of coverage at the county distribution level, although many of the records are 30 or more years old. Although Johnson (1972) had covered Texas Zygoptera, the total Texas Odonata had only received sporadic attention (Dunkle, 1975, Gloyd, 1932, 1958, Harp & Harp, 1996, Tinkham, 1934, Williams, 1976, 1978, 1979a,b,c, 1982) until the recent work of Abbott (Abbott, 1999, Abbott and Stewart, 1998, Abbott et al, 1997). This excellent and comprehensive effort covers the odonate fauna of the biotic provinces of Texas and their extensions into adjacent states and Mexico. A state species list is contained in Abbott and Stewart (1998), and detailed county data may be found in Abbott's Ph.D. thesis (1999). I used Abbott & Stewart's state list in this study, but had not incorporated any county distribution data for Texas in anticipation of Abbott's then pending publication of his

dissertation data. (Abbott's thesis data has since been published (2000). See the list: **Literature on Great Plains Odonata Published After 1999** immediately following the **Literature Cited** section.)

One of the first lists for Oklahoma was Bird's 1932 publication which included 106 species. A number of species were added later in the 30's by Bird (1933) and Pritchard (1935, 1936), but the next big step in the study of Oklahoma odonates was by Bick and Bick (1957), who listed 126 species for the state. They also attempted to correlate distribution patterns with physiography and climate (see **Discussion**). Bick (1991, 1997a) has continued to track Oklahoma records, and almost all the county data used in this paper are from copies of these unpublished notes which he has quite generously made available. The state list used herein also includes species recorded by Abbott & Stewart (1998).

The most current list of species for the state of Kansas is in the checklists of Beckemeyer & Huggins (1997, 1998). County data for the state remain scattered in the literature (Allison, 1921; Beckemeyer, 1995, 1996, 1998a, 1998c; Beckemeyer & Todd, 1996; Cringan, 1978; Huggins and Harp, 1985; Kennedy, 1917) though the bulk of the records are to be found in the publications of the Kansas Biological Survey (Huggins et al, 1976; Huggins, 1978, 1983).

Until very recently, Nebraska data was limited to state lists published by Pruess (1967) and Montgomery (1967). Additional county distribution data were provided by Bick & Hornuff (1972), Moody (1967), and White (1978). Collecting accomplished in preparation for and during the 1998 Annual Meeting of the Dragonfly Society of the Americas, held in Valentine, Nebraska in July of 1998, resulted in many county records (Beckemeyer 1998f, 1999; Beckemeyer & Hummel, 1997, 1998a; Hummel, 1997, 1999a, Janovy, 1997). I

have also, with the permission and assistance of Brett Ratcliffe, Curator, collected odonate county distribution data from the University of Nebraska State Museum of Natural History collection at Lincoln.

South Dakota county data are from Bick et al (1977), Bick (1997f), and the M.S. thesis of Fresvik (1969), supplemented by Beckemeyer (1998f), Fauske (1997), Huggins (1983b), Hummel (1999a,b), Paulson et al (1999), and Provonsha & McCafferty (1997). North Dakota data are from Alby's nicely done M.S. thesis (1968), and from Bick (1997), Bick et al (1977), and Daigle (1987). Most of the county records for these northern states are those from the theses, both of which are 30 years old.

The eastern tier of states have the least documented odonate fauna of the Great Plains, though there is currently some level of activity underway in each. A list of Anisoptera by county for Minnesota was recently put together by Rith (1998) as an activity of the Minnesota Dragonfly Survey. Previous publications on Minnesota Odonata include those of Boole et al (1974), Carlson et al (1967), Hamrum et al (1965, 1971), Miller et al (1964), Whedon (1914), and Wilson (1909). There is almost no data on Zygoptera distribution available for Minnesota.

Iowa recently underwent a detailed survey by Cruden and Gode (1998), and they gathered county level distributional data. (That data had not been published when this study was accomplished, so it was not incorporated. See Cruden and Gode (2000) under the section **Literature on Great Plains Odonata Published After 1999** that follows the **Literature Cited** section.) Other information on Iowa includes the following: Bick (1997b,c), Cruden (1997), Elrod (1898), Hoffman (1924), Hummel (1999a,c), Hummel & Haman (1975, 1977),

Loudon (1933), Miller (1906), Wells (1917), Whedon (1912), Wilson (1909, 1920), and Yeager (1932).

Until quite recently, there had never been a checklist published for Missouri, even at the state level, except for that of Montgomery (1967), which was based primarily on the trip collecting report of Williamson (1932). Although Missouri should have an interesting and diverse odonate fauna because of its varied physiography, it has been noteworthy mostly because of the paucity of data on the Odonata of Missouri (see, e.g., Huggins & Harp, 1985, and Michalski, 1992). [Since this paper was originally prepared, many Missouri records have been documented through the ongoing efforts of Linden Trail of the Missouri Department of Conservation, and the knowledge of Missouri Odonata and their distribution is much improved. The present paper however reflects what was known through March of 1999, and has not incorporated the new information.]

General publications which contain information on Great Plains Odonata records include: Bick (1983), Byers (1937), Carle (1992), Cook & Daigle (1985), Donnelly & Tennessen (1994), Dunkle (1975), Garrison (1984, 1994), Johnson (1973, 1974), Kormondy (1957), Montgomery (1967, 1968), Needham & Heywood (1929), Needham & Westfall (1955), Walker (1912, 1925, 1953, 1958), Walker & Corbet (1973), and Westfall & May (1996).

Results and Discussion

SPECIES QUANTITIES BY STATE:

Appendix 1 contains a list of the 320 species of Odonata documented in the literature review as occurring in the Great Plains states. In general, Paulson & Dunkle's checklist of the Odonata of North America (1996), has been used for species names, and Garrison's New World Odonata List

(1999) as the authority for species synonymy. I should note the following choices: I have followed Garrison in placing Macromiinae as a subfamily of Corduliidae rather than according it family status, as is done by Paulson & Dunkle. However, I have followed Tennessen (1977) and Paulson & Dunkle rather than Garrison in the treatment of *Epicordulia* and *Tetragoneuria* (Corduliidae: Corduliinae) as subgenera of *Epithea* rather than as genera. Following Tennessen and Garrison, *Epithea williamsoni* is considered a synonym of *E. costalis*. *Gomphurus* (Gomphidae) is treated as a subgenus of *Gomphus* (following Garrison rather than Paulson & Dunkle). In the Coenagrionidae, I follow Westfall and May (1996) in treating the Great Plains species of *Amphiagrion* as distinct from the eastern *A. saucium* and the western *A. abbreviatum*, although specimens from the region have been listed in the literature under both species names. Finally, *Enallagma optimolocus* Miller & Ivie 1995 (Montana) is considered to be a hybrid of *E. anna* and *E. carunculatum*, following both Garrison and Paulson & Dunkle.

Figure 1 is a bar graph showing the composition of the New World (Garrison, 1998), Nearctic (used here in a restricted sense to include only that portion of North America north of the Mexican border) (Paulson & Dunkle, 1996) and Great Plains states Odonata by family. The figure shows quite well that Odonata reach their greatest diversity in the tropics: the Nearctic fauna amounts to only 24% of the New World species. The figure also shows that the odonate fauna of the Great Plains states contains a significant sample of the Nearctic fauna (73%), and that the distribution by family appears to be reasonably similar as well. The damselfly family Coenagrionidae and the dragonfly family Libellulidae, which are the largest families in their respective suborders at the world faunal level, are the largest groups in the Great Plains states fauna, comprising 50% of the species (22%

Coenagrionidae and 28% Libellulidae) The dragonfly family Gomphidae is the next largest family level taxon, contributing 20% of the Great Plains states species. For the North American fauna, the percentages for these families are 22%, 23% and 23%, respectively. I have not at this time attempted to narrow the list of species to include only those that truly occur in the Great Plains physiographic region. The present list thus includes, in addition to true Great Plains species, those additional species that might occur only in the Rocky Mountains in the western tier of states, those that may be strictly tropical or sub-tropical in distribution, reaching only into the lower Rio Grande area of Texas, or species that may be restricted to forested areas of the eastern tier of states. The county distribution data for the western tier would likely allow one to accurately eliminate the species in those states which are not found in the Great Plains physiographic area (basically the short, mid-, and tall grass prairies). However, data for Texas and the eastern tier of states satisfactory for this purpose were either not available or not yet published at the time this study was conducted. I therefore chose to put off for a future investigation a study based on county-level distribution data for those states. (I estimate that such an exercise would decrease the species list by roughly a third.) Thus I have used the somewhat artificial state boundaries to approximate the Great Plains, and this must be kept in mind as we review the results of the study.

Figure 2 contains a summary of the distribution by family and by state of the 320 odonate species that occur in the Great Plains states. It is arranged so that the first entries from left to right are for the six states of the central tier, from TX north to ND. The next four entries are for the states of the western tier from NM north through MT. The last three entries are for the states of the eastern tier from MO north through MN. There is reason to this order of presentation.

The central tier of states is most representative of the Great Plains in terms of area of the states which is included in the Great Plains physiographic region. Thus the data for those states should more accurately reflect the true fauna of the Great Plains. I also place the data for the eastern tier last, since those states are the ones with the least complete distributional information. The chart depicts the significant negative latitudinal gradient in species numbers as one travels from south to north in the central tier of states. There is by comparison a relatively slight gradient in the western tier, and basically none in the eastern tier of states. Not surprisingly, the families Libellulidae and Coenagrionidae dominate the odonate fauna of nearly all of the states, with the Gomphidae being the next largest family.

Figure 3 depicts the distribution of the larger families of Odonata in the Great Plains states by using a map with shading to indicate whether the number of species of a given family in each state is within plus or minus one, two, or three standard deviations of the average for all 13 states. A state for which the number of species is within one standard deviation from the mean is shaded medium gray, a darker shade indicating a number above the mean, lighter below the mean. A state for which the number of species is greater than one but less than two standard deviations above or below the mean, respectively, would be shaded dark gray or light gray. A state for which the number of species is between two and three standard deviations above or below the mean would be black or white, respectively.

Figure 3a shows the departure from the mean for the total number of Odonata per state. It illustrates a recurring point in nearly all the mapping to follow: the disproportionately large number of species found in Texas typically makes it appear to stand alone and apart from the other states. Texas, as a result of its size and location,

encompasses a highly diverse set of habitats, including enough that is subtropical in nature to harbor a significant number of tropical species. It is the only state where the number of species is more than two standard deviations from the average (this is also the case for Figures 3b (Libellulidae) and 3c (Coenagrionidae)).

In Fig. 3a one also sees a "trough" of low species richness at the northern end of the central tier of states. This is at least partly due to the high numbers of eastern species present in the eastern portions of the eastern tier of states. However, it also reflects a real lack of habitat diversity in the north central plains. Bick and Hornuff (1977) commented on the relatively depauperate fauna of North Dakota: "At site after site in ND, the same species were present... This rather monotonous fauna relates to the lack of habitat diversity encountered in ND." This, together with the high species richness for Texas, produces a notable south-to-north negative gradient in species richness in the central tier. This figure also shows a lesser negative gradient in moving from east to west. The line of demarcation between the above- and below-average numbers (dark and light shading) runs from south to north and tilts slightly to the east.

The combined latitudinal and east-west gradient appears again in Figures 3b, 3d and 3e. It is interesting to note that these characteristics are fairly consistent for the Anisoptera - families except for the Aeshnidae (Fig. 3f). For the Coenagrionidae (Fig. 3c), the largest family of the Zygoptera, there is a definite negative south-to-north gradient to the pattern of species numbers.

SIMILARITY AND DIVERSITY PATTERNS: DuBois (1995), in one of the few published studies of insect biodiversity in a temperate area, recommended that "...a suite of measures." be used to quantify biodiversity. I have chosen to use four

measures of community similarity and two measures of diversity. The latter are based on species richness and are thus measures of beta diversity (Magurran, 1988). The current state of knowledge of Odonata in the Great Plains does not support the use of species abundance data which would be required to assess alpha diversity. Figures 4 through 9 consist of maps with the states shaded to illustrate similarity or diversity patterns. Figure 4 is based on Texas as the reference state, Figure 5 on Oklahoma, and so on, through Figure 9, which uses North Dakota as a reference.

I am looking for recurring or consistent patterns of similarity (masses of similar shades of dark gray) or diversity (gradients of shading ranging from black to white) over the Great Plains using this central tier of states as a point of reference. In each of Figures 4 through 9 each of the six separate maps shows a different measure: a - Common species: The fraction of the reference state species common to the comparison states (similarity measure). b - Cody: A standardized form of Cody's Beta Diversity metric. c - Wilson & Shmida: Wilson & Shmida's Beta Diversity metric. d - Jaccard: Jaccard's Similarity Index. e - Sorenson: Sorenson's Similarity Index. f - Preston: Montgomery's version of Preston's Canonical Similarity Index. (Each metric is discussed in more detail in the Methods section.) Shading is in six steps from white to black, each shade of gray corresponding to an even portion of the interval from zero to one (or one to zero for the diversity measures). Black indicates nearly completely similar faunas, white nearly completely different faunas. [Note that in preparing these charts for publication, it was found necessary to use shading patterns of dots of different densities to represent the gray shading in order to facilitate reproduction of the figures.]

In looking at the set of Figures 4 through 9 as a unit, certain observations concerning

the measures can be made. First, it is notable that the Wilson-Shmida diversity index (Map c) and Sorenson similarity coefficient (Map e) have remarkably similar patterns and this similarity is consistent from figure to figure. Jaccard's similarity (Map d) generally depicts greater diversity than the other measures, again consistently from Fig. 4 through Fig. 9. Map f (Preston's similarity index) consistently tracks Jaccard's, but with diversity between that indicated by the Wilson-Shmida/Sorenson maps and the Jaccard map.

Map a (Common species) is evidently greatly influenced by the species richness of the reference state, showing great diversity when Texas (194 species) is the reference (Fig. 4), great similarity when North Dakota (55 species) is the reference (Fig. 9). Cody's measure (Map b) is almost the mirror-image of Map a, showing less diversity when Texas is the reference state, greater diversity when North Dakota is the reference. In light of these trends, I have placed greater weight on maps c, d, e, and f, in all figures, but less weight on maps a and b for Figures 4, 8, and 9 (when the reference state has very high or very low species richness).

Figure 4, using Texas as a basis of comparison, indicates some similarity between Oklahoma and Texas odonate communities, but generally the Texas fauna is pretty much separate and distinct (Texas is the only black state, Preston's index <0.73 for all states). The north-south gradient is highly visible and indicates considerable latitudinal diversity.

In Fig. 5, where Oklahoma is the reference state, the white has been mostly replaced by light gray, and there is an indication that Oklahoma and Kansas are similar (both black on maps b and e, Preston's index for Kansas >0.73), and that there might be a "southeastern" grouping of the faunas of those two states with Texas and Missouri.

Figure 6 contains only shades of gray, and a Kansas-Oklahoma (both black on maps a, b, c, e, and f, Preston's index for Oklahoma >0.73) or Kansas-Oklahoma-Missouri faunal group becomes evident when using the Kansas species list as a reference.

Figure 7, with Nebraska as a reference, shows clear evidence of a group comprising Nebraska, South Dakota, Iowa and Colorado (Nebraska and Iowa black on map a, Preston's index >0.73 for Iowa and South Dakota, Similar pattern of darkest gray for Colorado, Iowa and South Dakota on maps c, e, and f).

Figure 8, with South Dakota as a base of comparison, maintains the Nebraska-South Dakota-Colorado grouping (dark gray on maps c, e, and f, Preston's index >0.73 for Nebraska), but Wyoming replaces Iowa and Montana and North Dakota might be added (Maps c, e, and f).

Figure 9, using North Dakota as a reference, again reflects the latitudinal gradient, with a substantial amount of white appearing on the maps again. North Dakota pretty much stands alone (the only black state on maps c, d, e, and f, Preston's index <0.73), though in two of the maps there is some evidence that North Dakota, South Dakota and Wyoming might be loosely grouped together (dark gray on maps c and e).

Overall, then, it appears that one might identify the following groupings of Great Plains states Odonata faunas: 1. Texas alone. 2. A "southern Great Plains" group consisting of Kansas and Oklahoma. 3. A "northern/western Great Plains" group consisting of Nebraska, South Dakota, Colorado and Iowa. 4. North Dakota alone.

PATTERNS OF BIOGEOGRAPHIC AFFINITY: Figure 10 is a bar graph indicating the percent distribution of each state's Odonata fauna by biogeographical

affinity. The overall faunal composition for the Great Plains in total is: 42% eastern, 17% western and southwestern, 15% tropical, 11% northern transcontinental, 8% transcontinental, and 7% central.

Looking at the first six bars, which represent the six states in the central tier, we see a rapid decrease in the relative importance of southwestern and tropical species in the southern three states and a similar drop off of importance of eastern species in the northern half of the tier. These are replaced by increasing proportions of western and northern transcontinental species. We see that Texas has the only significant tropical species component, which undoubtedly accounts for its standing alone on the diversity maps. In the next four bars, the western tier states, a rapid increase in importance of northern transcontinental species offsets a similar decrease in the relative proportion of southwestern species and a slight drop off of eastern species. The eastern tier of three states, represented by the last three bars on the chart, is characterized by a large proportion of eastern species, with a growth in the significance of northern transcontinental species in comparison with transcontinental and eastern species. Iowa is the only state in this tier with any western species (6.5%), but this may be an artifact of the lack of data on Odonata occurrence in Missouri and Minnesota.

Figure 11 contains maps with the states shaded to indicate the percent of each state's fauna made up of species of that geographic affinity: a - Eastern. b - Northern transcontinental. c - Southwestern and western combined. d - Transcontinental. e - Tropical. f - Central. Figure 11a shows the sharp east-to-west drop off in the importance of eastern species, but it should be noted that even in the western tier of states, 11 to 18% of the species are still of eastern origins. This is quite different from the west-to-east drop off of western species,

which disappear completely from Minnesota and Missouri and only contribute 6.5% to Iowa's odonate fauna (Fig. 11c). Figures 11b and e show the latitudinal gradients in the northern transcontinental and tropical groups, both of which reach their extreme limits in the Kansas-Oklahoma-New Mexico-Missouri region. The transcontinental and central groups are fairly evenly-distributed over the Great Plains, as one would expect (Figures 11e, f).

INCONSISTENT SAMPLING: Figure 12 is a shaded county-level map of the central tier of states in which the shading indicates the total number of species recorded per county. Counties for which there are no records at all are white. It can be seen that there are many counties in South Dakota and Nebraska that are white; 35% and 38%, respectively, of the counties have no records. North Dakota, Kansas and Oklahoma, on the other hand, are relatively well-sampled. The fact that more sampling attention has been focused on northwestern Nebraska (Cherry County and vicinity) and southwestern South Dakota (The Black Hills area) than on other areas of those states may very well have biased the assessment of the composition and diversity of the Odonata fauna of those two states. In any event, the detailed county maps which appear in Figures 13 through 17 will reflect the unsampled counties which may obscure some faunal boundaries.

COUNTY-LEVEL DISTRIBUTION PATTERNS IN THE CENTRAL TIER:

The state-level mapping just reviewed shows that the central tier of states contain a number of faunal boundaries. Since county-level distribution data were available for them and because the central tier of states are literally the "heart" of the Great Plains, more detailed maps were constructed for the five states from Oklahoma north through North Dakota. This will hopefully help to better define the faunal boundaries. In these maps, shading is used to indicate the number

of species of a given geographic affinity that have been recorded for each county.

Figures 13, 14 and 15 illustrate the north-south boundary lines for northern-transcontinental, southwestern, and tropical groups, respectively. Figure 13 shows that Kansas and Nebraska contain the boundary for northern transcontinental species. The inadequate sampling in Nebraska and South Dakota makes it difficult to accurately locate the southern boundary of this regional fauna.

Oklahoma contains the boundary for the other two groups, though there is a trickle of southwestern species up into Kansas and Nebraska and of tropical species into Kansas. The light shading of the Oklahoma counties indicates that the primary boundary for these groups likely occurs somewhere in Texas. The county shaded medium gray in South Dakota in Figure 14 is Fall River County. Hot Brook, a small stream fed by warm springs (Provonsa & McCafferty, 1977) occurs in this county, and is a unique area where disjunct populations of the southwestern species *Brechmorhoga mendax*, *Libellula saturata* and *Argia immunda* have been found.

Figures 16 and 17 are county maps depicting the patterns of distribution of eastern and western species groups, respectively. As noted in the previous section, the eastern species still make up a substantial portion of the species totals in the western tier of states, so the boundary line does not occur in the central tier. Even so, there is a notable gradient in eastern species numbers per county in the southern states (Oklahoma and Kansas), with a quite noticeable drop in numbers of eastern species from the southeast to the north and west (Figure 16). It is also noteworthy that the Dakotas and Nebraska are characterized by fairly uniform distributions, with the gray shade (that indicates one to eight eastern species) dominating in those states. An exception is

Cherry County, Nebraska, the large county on the Nebraska-South Dakota border. Contributing factors to its higher number of species undoubtedly include its larger size, the fact that it has received a disproportionate amount of collecting attention (the 1998 meeting of the Dragonfly Society of the Americas brought almost 50 odonate collectors to the county for a week in July), and the fact that the Niobrara River serves as a unique corridor for the east-west movement of Odonata species across the state (Johnsgard, 1991).

Figure 17, which shows the pattern of distribution of western species, shows that the boundary for this geographic group does occur in the central tier of states in the south, and in the central or eastern tier of states to the north. The fact that a number of counties on the eastern borders (or one county removed from the eastern borders) of these states are shaded would lead one to believe that careful collecting effort along the western borders of the eastern tier of states might result in records of western species for those states. This is certainly true in Iowa, where 6.5% of the species were of western biogeographic affinity. Once again, the inadequate sampling of Nebraska and South Dakota counties likely obscures the eastern boundary of western species distribution in the northern portion of the central tier.

SPECIES DISTRIBUTIONS BY COUNTY IN THE CENTRAL TIER:

The patterns mapped out thus far lend insight into trends in distribution, but they also undoubtedly mask much complexity. For example, there is the possibility of north-south variations hidden in both the eastern and western regional fauna maps, as the grouping used did not differentiate, for example, between northeastern and southeastern subgroups. More importantly, the biogeographic groupings are made up of individual species, all of which have different specific distributional limits. This

can be seen in part from Figure 18, on which the counties of record have been marked for a mixed set of western and southwestern coenagrionid damselflies, most of which reach their eastern limits in the central or eastern Great Plains. We can use this map to reveal some of the detail that makes up the much simpler appearing map of Figure 17.

The coenagrionid species included in Figure 18 are made up of three species of *Enallagma*: *E. anna*, *E. clausum* and *E. praevarum*, three *Ischnura*: *I. barberi*, *I. damula* and *I. perparva*, and three *Argia*: *A. alberta*, *A. emma* and *A. immunda*.

Enallagma anna (black diamonds in Fig. 18) was described by Westfall and May (1996) as an insect of "arid western highlands". It inhabits streams and rivers. Its range extends from California and Oregon east through Arizona, Nevada, Utah, New Mexico, Colorado, Wyoming, Montana and Alberta, to Nebraska and South Dakota. It then funnels east through Iowa, Wisconsin and Illinois. In the Great Plains it appears to be restricted to a narrow band across the southern half of South Dakota and the northern 2/3 of Nebraska into Iowa. Cruden and Gode (1998) found it in streams all across Iowa, and consider the species a recent immigrant that has inhabited the state within the last 80 years. Because of the paucity and age of records from South Dakota, the species may very well be more widespread there than our records indicate. It doesn't reach its eastern limit in our region, but is restricted in its north-south range; the reason for that restriction is not obvious (but likely is tied to the nature of the streams in the area), and bears further investigation.

Enallagma clausum (gray diamonds in Fig. 18), often found in saline and alkaline waters, is a lentic species. Found from British Columbia east as far as Quebec in Canada, in the United States it ranges from

California north to Washington and east to New Mexico, Colorado, Wyoming and Montana, and Nebraska, South Dakota and Iowa. Kennedy (1917) listed it for Kansas, but the specimens of *clausum* in the Snow Entomological Museum that he worked with are all from Colorado, so Huggins removed it from the Kansas list in 1976. It has not been found in the state in the succeeding years. Cruden and Gode (1998) list it as a recent immigrant species found at 10 sites in four counties in northwestern Iowa, and it appears that the species' eastern boundary of distribution is in western Iowa. The insect appears to occur in suitable habitats pretty much across the Dakotas and Nebraska, with its southern boundary likely in Nebraska. The lack of adequate collecting in South Dakota and Nebraska again obscures better definition of the faunal boundaries for this species.

Enallagma praevarum (unfilled diamonds in Fig. 18) is primarily a pond species that has its eastern range boundary in the western part of the central tier of states, barely entering the western side of Kansas and Oklahoma. It ranges from California, Nevada, Arizona and Utah east to Texas and north to North Dakota. Westfall and May (1996) list Missouri with a question mark, but from the records available here, that appears to be an error.

Ischnura barberi (black squares in Fig. 18) is an inhabitant of ponds and ditches in arid lands, fond of saline and alkaline environments through much of its range (Beckemeyer, 1999). A southwestern species, it ranges from California, Arizona and Utah east to Texas and north to Colorado and Nebraska. (The Nebraska records were from a salt marsh in Lancaster County. The specimens were from the 1930's, and recent efforts to collect the species were unsuccessful until quite recently – see Bedell, 2001, in the **Literature on Great Plains Odonata Published After 1999** section.) It reaches

its northeastern limits in the southern portion of our area.

Ischnura damula (gray squares in Fig. 18) is another pond species that is "... mostly found on the eastern slope of the Rockies and the Great Plains" (Westfall & May, 1996). Found from Arizona to Texas north to the Canadian prairie provinces, *damula* reaches its eastern boundary from extreme western Oklahoma and Kansas north and east through Nebraska and the Dakotas. It is another species whose distribution through the northern Great Plains is unclear because of the scattered collection data from Nebraska and south Dakota.

Ischnura perparva (unfilled squares in Fig. 18) is a species of ponds and spring runs. It is found throughout the west from California to British Columbia east to Oklahoma (I have only the state record - the county is unknown) and north to Manitoba. Both the southern and eastern boundaries appear to occur in the central tier of states.

Argia alberta (cross symbol in Fig. 18) is a creek and stream dweller often associated with spring seeps and small spring fed streams in Kansas (Huggins, 1978). It ranges from Arizona, Nevada, New Mexico and Utah east to the central tier of Great Plains states north through South Dakota. It is found across the state of Kansas and into Iowa. Cruden and Gode (1998) show it occurring in the western third of Iowa at six locations. There are no records in eastern Nebraska or south Dakota, but this may be due to inadequate collecting effort.

Argia emma (x symbol in Fig. 18) is a stream species that occurs from California to British Columbia east to Colorado, Wyoming and Montana and into Nebraska and South Dakota where its distribution is similar to that of *Enallagma anna*. It was found at one site in Iowa by Cruden and Gode (1998), in Crawford County, which is one county removed from the western

border of Iowa and roughly midway north and south. This is another species with its distribution limited on the north, south and east in our area.

Argia immunda (asterisk in Fig. 18) is a southwestern species of streams and rivers and occasionally lakes. It is found from California and Nevada east through Arizona, New Mexico, Texas, Oklahoma and Arkansas. A disjunct population occurs in the Black Hills of South Dakota. There is a single record from the extreme southeastern corner of Kansas. It reaches its northeastern limits in our area.

These patterns of individual species distributions give us some insight into the complexity hidden in each of the patterns of biogeographic affinity in Figures 13 through 17 and suggest that higher level patterns of distribution may not yield to simple explanations or interpretations. In spite of this, it is instructive to review some historical attempts at such interpretations in light of the results of this study.

PROCESS BEHIND THE PATTERNS? -

A REVIEW: Kennedy (1917) was among the first to ponder what was going on in the Great Plains. Although his assertions were based on incomplete faunal lists (his list of Kansas species in 1917 was 66 species long - today we know of 124 species), they appear to be basically sound. (He did have a good sample of the fauna. His distribution by biogeographic region was 55% eastern (49% today), 28% transcontinental (22% today) and 17% western and central (26% for western, central and southwestern today). He did not use the tropical category which today accounts for 3% of Kansas species.) The data "...showed that a pure western fauna occurred on the plains about Denver...[while]...the eastern ends of...[Oklahoma and Kansas]...had pure eastern faunas. The line between eastern and western odonate faunas occurred, then, on the plains east of Denver and west of

Topeka..." Taking note of the precipitation gradient across the state of Kansas, Kennedy postulated that western species were impeded from moving east because of his observations of the affect of several days of cold, rainy weather on western odonates: "In the mesophytic east a rainy day during the Odonata season does not seem to affect the number of dragonflies...but in the dry areas of the west rainy day will frequently kill nearly all the adults on the wing at the time."

The next study of odonate distribution in the Great Plains was by Bick and Bick (1957) for Oklahoma. They also did an assessment of biogeographic composition and, though we differ in the placement of some species and in our exact categories, a rough comparison yields (Bick and Bick/this study): eastern (52%/53%), tropical (8%/4%), western (15%/15%), transcontinental (18%/16%), central (6%/11%). They noted that 53% of the Oklahoma species were limited in an east-west direction and concluded that this was tied to the precipitation gradient:

"The western limit in Oklahoma of eastern United States species, which do not cross the state, coincided with the...32 inch rainfall line...The eastern limit of western United States species was approximately the 36 inch rainfall line...Hence the...counties ...with 32 to 36 inches of rainfall...constituted an area of overlap for eastern and western faunas."

Figure 19 maps the lines of constant precipitation over the county maps for Oklahoma, Kansas, Nebraska, South and North Dakota. (The maps were prepared by the author based on state maps that can be found on the internet at <http://www.climate-source.com>. The web-based maps were prepared and are copyrighted by Spatial Climate Analysis Service of Oregon State

University. The data are annual precipitation observations averaged over the period 1961-1990 by NOAA and other networks.) In Figures 20 through 22, I have added these precipitation isolines to the maps of Figures 16 through 18. Doing so seems to bolster the Bicks' conclusion regarding Oklahoma and to furthermore show that it holds for Kansas as well. The 32 inch line fairly well defines the boundary on Figure 20 between the very dark counties in eastern Kansas and Oklahoma and the lighter gray counties to their west. Likewise, the 36 inch line seems to track reasonably well the boundary on Fig. 21 between predominantly gray and predominantly white counties. One can also see that the position of the 32 inch line on Figure 22 fairly well marks the edge of the eastward extent of *Argia alberta* in Kansas and Oklahoma. These observations beg more questions than they answer, but they certainly provide one with some incentive to begin looking into the thermal physiology of some of the western species and how it might relate to the climatology of the southern Great Plains. Whatever the mechanism, there does appear to be some correlation between east-west species limits and precipitation.

Huggins (1978) performed the most recent assessment of Kansas odonate fauna. His biogeographic analysis can be roughly compared with that of this study (Huggins/this study): eastern (48%/49%), transcontinental (26%/22%), western (15%/12%), central (10%/14%), tropical (not used/3%). Huggins list consisted of 108 species. He looked at the proportions of eastern and western faunal elements which successfully reached across the state. He found that a greater proportion of western species were able to reach the eastern border of the state than the proportion of eastern species that reached the western border. He concluded that western species were therefore better able to tolerate mesic conditions than eastern species were to

tolerate xeric conditions. However, when one considers the number of species rather than the proportion of species that were able to cross the state, the successful eastern species outnumber the successful western species by 50%. Regardless of the numbers, however, he did make the point that many of the western species in Kansas have adapted to inhabiting springs and spring seeps, which are more stable habitats in the arid west, whereas eastern species inhabit habitats which become more scarce as one moves west.

Other factors also need to be considered in attempting to tie physiographic, climatologic or other parameters to distributional patterns. Man has had a pervasive impact on the Great Plains, and some measures of that impact are becoming available. The EPA Great Plains Atlas web site (1999) contains county level maps color coded to illustrate such factors as the number of cultivated acres per county, the number of irrigated acres per county, and the population per county. An interesting subject for future work would be to attempt to correlate odonate county distribution data with such data as these.

A number of areas requiring further work have been noted throughout this study. It seems appropriate to summarize them here:

1. Additional careful collecting and museum research is needed for the states of Nebraska, South Dakota, and Missouri for all Odonata. Particular attention should be placed in Nebraska and South Dakota on those counties which have no records at all (Fig. 12). The Minnesota Zygoptera distribution also needs to be researched.
2. A study similar to this one should be done with a restricted faunal list that includes only the true Great Plains species. This would require a county level mapping of all species to include in the list only those

which occur in the Great Plains physiographic region.

3. It is apparent that species distribution patterns that underlie the higher level patterns mapped herein are complex. An attempt needs to be made to subdivide the fauna in other ways than biogeographical. An obvious first choice might be by lentic and lotic species groups. Lentic group patterns could be correlated with drainage basins (see Hamilton et al, 1983, for an example of such an approach). Lotic group patterns might be correlated with features that impact the distribution and character of ponds and lakes, e.g. with net moisture (precipitation less evapotranspiration) with irrigation patterns, and so on.

4. The Great Plains do not stop at the Canadian border. A thorough study of diversity and distribution patterns of the Great Plains must eventually include the odonates of the prairie provinces. A problem which must then be addressed is the unit for mapping the distribution patterns, since counties as used here are no longer suitable. (Similar problems exist in doing this type of analysis in the western U.S., where counties tend to be very large in area.)

5. The apparent correlation of precipitation isolines with east-west faunal boundaries should be thought through and analyzed. One possible factor, as first postulated by Kennedy (1917) would be the impact of the thermal physiology of western odonates on their ability to tolerate mesic climates.

Our understanding of the diverse Odonata fauna of the Great Plains is advancing, but much remains to be learned. The fossils of the 27-inch wing-spanned ancestors of today's dragonflies that we find in the Permian deposits beneath the Kansas and Oklahoma prairies remind us that these incredible animals have been here longer than the prairie itself. No wonder they hold

so many secrets for us to find. The interesting and complex patterns of their distribution and diversity are among those secrets; they invite and deserve continued study and investigation.

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Appendix 1. Great Plains Odonata Species List by Biogeographic Region:

[CO = Colorado, IA = Iowa, KS = Kansas, MO = Missouri, MN = Minnesota, MT = Montana, ND = North Dakota, NE = Nebraska, NM = New Mexico, OK = Oklahoma, SD = South Dakota, TX = Texas, Wy = Wyoming]

Northern Transcontinental

Calopteryx aequabilis NE SD ND CO WY MT IA MN / *Lestes dryas* NE SD ND NM CO WY MT IA MN / *Coenagrion interrogatum* MT MN / *Coenagrion resolutum* NE SD ND CO WY MT IA / *Enallagma boreale* NE SD ND NM CO WY MT IA / *Enallagma cyathigerum* NE SD ND NM CO WY MT IA / *Enallagma ebrium* NE SD ND WY MT MO IA MN / *Enallagma hageni* NE SD ND CO WY MT MO IA MN / *Nehalennia irene* NE SD ND WY MT IA MN / *Aeshna canadensis* NE SD MT MO IA MN / *Aeshna constricta* KS NE SD ND CO WY MT MO IA MN / *Aeshna eremita* ND CO WY MT MN / *Aeshna juncea* NM CO WY MT / *Aeshna sitchensis* WY MT MN / *Aeshna subarctica* NE MT MN / *Aeshna tuberculifera* MT IA MN / *Ophiogomphus colubrinis* WY MN / *Cordulia shurtleffi* CO WY MT MN / *Epitheca canis* MN / *Epitheca spinigera* ND MT MN / *Somatochlora albicincta* MT / *Somatochlora cingulata* WY / *Somatochlora franklini* MN / *Somatochlora hudsonica* CO WY MT / *Somatochlora kennedyi* MN / *Somatochlora minor* SD CO WY MT MN / *Somatochlora walshii* MT MN / *Leucorrhinia borealis* ND CO WY MT MN / *Leucorrhinia glacialis* MT MN / *Leucorrhinia hudsonica* CO WY MT MN / *Leucorrhinia intacta* KS NE SD ND CO WY MT MO IA MN / *Leucorrhinia proxima* ND CO WY MT MN / *Libellula quadrimaculata* NE SD ND NM CO WY MT IA MN / *Sympetrum danae* SD ND NM CO WY MT MO MN / *Sympetrum internum* OK KS NE SD ND NM CO WY MT MO IA MN

Eastern

Calopteryx dimidiata TX / *Calopteryx maculata* TX OK KS NE SD CO WY MO IA MN / *Hetaerina titia* TX OK KS MO IA / *Lestes disjunctus* TX OK KS NE SD ND NM CO WY MT MO IA / *Lestes forcipatus* NE SD CO WY MT MO IA MN / *Lestes eurinus* KS MO IA / *Lestes inaequalis* TX OK MN / *Lestes rectangularis* OK KS NE ND CO IA MN / *Lestes vigilax* TX OK IA MN / *Argia apicalis* TX OK KS NE SD ND NM CO MO IA MN / *Argia bipunctulata* TX OK KS MO / *Argia fumipennis* TX OK KS NE SD NM CO WY MT MO IA MN / *Argia tibialis* TX OK KS NE MO IA MN / *Chromagrion conditum* MO / *Enallagma antennatum* OK KS NE SD ND CO WY MT IA MN / *Enallagma aspersum* TX OK KS NE MO IA / *Enallagma daeckii* TX OK / *Enallagma*

divagans TX OK KS MO / Enallagma doubledayi TX / Enallagma durum TX / Enallagma exsulans TX OK KS NE ND MO IA / Enallagma geminatum TX OK KS NE MO IA / Enallagma signatum TX OK KS NE SD MO IA MN / Enallagma traviatum TX OK KS / Enallagma vesperum TX OK KS CO IA / Ischnura kellicotti TX OK / Ischnura posita TX OK KS ND MO IA MN / Ischnura prognata TX / Ischnura verticalis TX OK KS NE SD ND NM CO WY MT MO IA MN / Nehalennia gracilis MO / Nehalennia integricolis TX OK / Telebasis byersi TX / Tachopteryx thoreyi TX OK KS MO / Aeshna clepsydra ND IA / Aeshna mutata MO / Aeshna verticalis WY IA MN / Anax longipes TX OK KS MO / Basiaeschna janata TX OK KS MO MN / Boyeria grafiana MN / Boyeria vinosa TX OK KS NE MO IA MN / Coryphaeschna ingens TX / Epiaeschna heros TX OK KS MO IA / Gomphaeschna furcillata TX / Gynacantha nervosa OK / Nasiaeschna pentacantha TX OK KS MO IA MN / Aphylla williamsoni TX / Arigomphus furcifer IA MN / Arigomphus maxwelli TX / Arigomphus villosipes MO MN / Dromogomphus spinosus TX OK KS SD MO MN / Dromogomphus spoliatus TX OK KS MO IA / Erpetogomphus designatus TX OK KS SD NM CO MT MO / Gomphus (Gomphurus) crassus MO MN / Gomphus (Gomphurus) fraternus SD MO IA MN / Gomphus (Gomphurus) hybridus TX / Gomphus (Gomphurus) lineatifrons MN / Gomphus (Gomphurus) modestus TX / Gomphus (Gomphurus) vastus TX OK KS MO IA MN / Gomphus (Gomphurus) ventricosus MO IA MN / Gomphus (Gomphus) adelphus MN / Gomphus (Gomphus) apomyius TX / Gomphus (Gomphus) descriptus IA / Gomphus (Gomphus) exilis TX MO IA MN / Gomphus (Gomphus) lividus TX NE MO MN / Gomphus (Gomphus) quadricolor MO MN / Gomphus (Gomphus) spicatus MN / Gomphus (Gomphus) viridifrons MN / Hagenius brevistylus TX OK KS MO IA MN / Lanthus parvulus MN / Ophiogomphus aspersus IA / Ophiogomphus carolus MN / Ophiogomphus howei MN / Ophiogomphus rupinulensis ND IA MN / Progomphus obscurus TX OK KS NE NM CO MO IA / Stylurgomphus albistylus OK KS MO / Stylurus amnicola KS NE MO IA MN / Stylurus laurae TX / Stylurus notatus NE IA MN / Stylurus plagiatu TX OK KS MO IA / Stylurus spiniceps MO MN / Cordulegaster erronea CO / Cordulegaster maculata TX MN / Cordulegaster obliqua TX OK KS MO MN / Didymops transversa TX OK KS MO MN / Macromia illinoensis TX OK KS SD MT MO IA MN / Macromia taeniolata TX OK KS IA / Dorocordulia libera MN / Epithea costalis TX OK KS NE NM MO / Epithea cynosura TX OK KS NE SD CO MO IA MN / Epithea princeps TX OK KS NE MO IA MN / Epithea semiaquea TX OK / Epithea spinosa OK / Helocordulia selysii TX / Helocordulia uhleri OK MO / Neurocordulia alabamensis TX / Neurocordulia molesta TX OK KS NE SD IA MN / Neurocordulia virginensis OK / Neurocordulia yamaskanensis MN / Somatochlora elongata MN / Somatochlora filosa TX MO / Somatochlora forcipata MN / Somatochlora georgiana TX / Somatochlora linearis TX OK KS MO IA / Somatochlora margarita TX / Somatochlora tenebrosa OK KS MO IA / Somatochlora williamsoni MN / Brachymesia gravida TX OK NE NM / Celithemis amanda TX / Celithemis elisa TX OK KS NE MO IA MN / Celithemis eponina TX OK KS NE NM CO MO IA MN / Celithemis fasciata TX OK KS MO / Celithemis ornata TX / Celithemis verna TX OK KS MO / Erythemis simplicicollis TX OK KS NE SD ND NM CO WY MO IA MN / Erythrodiplax berenice TX / Erythrodiplax minuscula TX OK / Erythrodiplax umbrata TX OK KS / Leucorrhinia frigida MN / Libellula auripennis TX OK MO / Libellula cyanea TX OK KS MO IA / Libellula deplanata TX OK KS MO / Libellula exusta MN / Libellula flavida TX OK KS NE MO /

Libellula incesa TX OK KS MO / Libellula julia MT MN / Libellula needhami TX / Libellula semifasciata TX OK KS MO / Libellula vibrans TX OK KS / Nannothemis bella MN / Sympetrum ambiguum TX OK KS NE MO MN / Sympetrum rubicundulum KS NE SD ND CO WY MO IA MN / Sympetrum semicinctum NM CO MN / Tramea carolina TX OK KS NE MO IA MN

Transcontinental

Hetaerina americana TX OK KS NE SD ND NM CO WY MT MO IA MN / Archilestes grandis TX OK KS NE SD NM CO WY MO IA / Lestes congener NE SD ND NM CO WY MT MO IA / Lestes unguiculatus OK KS NE SD ND CO WY MT MO IA MN / Argia moesta TX OK KS NE NM CO MO IA MN / Argia sedula TX OK KS NE NM CO MO / Argia translata TX OK KS NM MO / Enallagma basidens TX OK KS NE NM CO MO IA / Enallagma carunculatum OK KS NE SD ND NM CO WY MT IA MN / Enallagma civile TX OK KS NE SD ND NM CO WY MT MO IA MN / Enallagma dubium TX OK / Ischnura hastata TX OK KS NE NM CO MO IA / Aeshna interrupta KS NE SD ND NM CO WY MT IA MN / Aeshna umbrosa OK KS NE SD ND NM CO MT MO IA MN / Anax junius TX OK KS NE SD ND NM CO WY MT MO IA MN / Libellula luctuosa TX OK KS NE SD ND NM CO MO IA MN / Libellula lydia TX OK KS NE SD ND NM CO WY MT MO IA MN / Libellula pulchella TX OK KS NE SD ND NM CO WY MT MO IA MN / Pachydiplax longipennis TX OK KS NE SD NM CO WY MO IA MN / Pantala flavescens TX OK KS NE NM CO MT MO IA MN / Pantala hymenaea TX OK KS NE NM CO MT MO IA MN / Perithemis tenera TX OK KS NE SD NM CO MO IA MN / Sympetrum corruptum TX OK KS NE SD ND NM CO WY MT MO IA MN / Sympetrum costiferum KS NE SD ND NM CO WY MT IA MN / Sympetrum obtusum KS NE SD ND NM CO WY MT IA MN / Sympetrum vicinum TX OK KS NE ND NM CO WY MO IA MN / Tramea lacerata TX OK KS NE SD NM CO MO IA MN / Tramea onusta TX OK KS NE SD NM CO MO IA MN

Tropical

Hetaerina vulnerata NM / Lestes alacer TX OK NM / Lestes forficula TX / Lestes sigma TX OK / Neoneura aaroni TX / Neoneura amelia TX / Protoneura cara TX / Acanthagrion quadratum TX / Argia baretii TX / Argia cuprea TX / Argia hinei TX / Argia leonora TX / Argia rhoadsi TX / Argia tezpi NM / Enallagma novaehispaniae TX / Ischnura ramburii TX OK ST / Neoerythromma cultellatum TX / Telebasis salva TX OK KS NM / Aeshna psilus TX / Anax amazili TX / Aphylla angustifolia TX / Aphylla protracta TX / Erpetogomphus eutainia TX / Gomphus (Gomphurus) gonzalezi TX / Brachymesia furcata TX MO / Brachymesia herbida TX / Cannaphila insularis TX / Dythemis maya TX / Dythemis nigrescens TX / Dythemis velox TX OK KS NM / Erythemis plebeja TX / Erythemis vesiculosa TX OK KS NM / Erythrodiplax connata TX / Erythrodiplax fusca TX / Macrodiplax balteata TX NM / Macrothemis imitans TX / Macrothemis inacuta TX / Macrothemis inequinguis TX / Myathyria marcella TX / Micrathyria aequalis TX / Micrathyria didyma TX / Micrathyria hagenii TX / Orthemis ferruginea TX OK KS NM / Perithemis domitia TX / Tauriphila azteca TX / Tholymis citrina TX / Tramea calverti TX MO IA / Tramea insularis TX

Central

Amphiagrion species OK KS NE SD ND NM CO WY MT MO IA MN / Coenagrion angulatum SD ND MT IA MN / Arigomphus cornutus NE SD ND CO WY MT IA MN /

Arigomphus lentulus TX OK KS MO / *Arigomphus submedianus* TX OK KS NE MO IA / *Gomphus* (*Gomphurus*) *externus* TX OK KS NE SD ND NM CO WY MT MO IA MN / *Gomphus* (*Gomphurus*) *ozarkensis* OK KS MO / *Gomphus* (*Gomphus*) *graslinellus* TX OK KS NE SD ND CO MT MO IA MN / *Gomphus* (*Gomphus*) *militaris* TX OK KS NE SD NM CO MO IA / *Gomphus* (*Gomphus*) *oklahomensis* TX OK / *Ophiogomphus severus* KS NE SD NM CO WY MT / *Ophiogomphus susbehcha* MN / *Ophiogomphus westfalli* KS MO / *Stylurus intricatus* TX KS NE SD NM CO WY MO IA / *Macromia pacifica* TX OK KS MO / *Epithea petechialis* TX OK KS NM CO / *Neurocordulia xanthosoma* TX OK KS NM MO / *Somatochlora ensigera* NE SD ND CO WY MT IA MN / *Somatochlora ozarkensis* OK KS MO / *Sympetrum occidentale* OK KS NE SD ND NM CO WY MT IA MN

Western

Argia alberta OK KS NE SD NM CO WY MT IA / *Argia emma* NE SD CO WY MT IA / *Argia immunda* TX OK KS SD NM / *Argia nahuana* TX OK KS NM CO / *Argia plana* TX OK KS NE SD NM CO IA / *Argia vivida* NE SD NM CO WY MT IA / *Enallagma anna* NE SD NM CO WY MT IA / *Enallagma clausum* NE SD ND NM CO WY MT IA / *Enallagma praevarum* TX OK KS NE SD ND NM CO WY MT / *Ischnura cervula* CO WY MT / *Ischnura damula* TX OK KS NE SD ND NM CO WY / *Ischnura demorsa* TX OK KS NM CO / *Ischnura denticollis* TX OK KS NM CO / *Ischnura perparva* OK KS NE SD ND NM CO WY MT / *Tanypteryx hageni* MT / *Aeshna californica* SD CO WY MT / *Aeshna multicolor* TX OK KS NE SD NM CO WY MT IA / *Aeshna palmata* NE SD NM CO WY MT IA / *Erpetogomphus compositus* TX NM / *Ophiogomphus morrisoni* WY MT / *Ophiogomphus occidentis* MT / *Cordulegaster dorsalis* CO MT / *Somatochlora semicircularis* CO WY MT / *Erythemis collocata* TX NM CO WY MT / *Libellula forensis* NE SD NM CO WY MT / *Libellula nodisticta* OK NM CO WY / *Libellula subornata* TX OK KS NE NM CO WY / *Sympetrum illotum* TX NM WY / *Sympetrum madidum* NE SD ND CO WY MT / *Sympetrum pallipes* NE SD ND NM CO WY MT

Southwestern

Argia lugens TX OK SD NM CO W / *Argia munda* TX NM / *Argia tonto* NM / *Hesperagrion heterodoxum* TX NM CO / *Ischnura barberi* TX OK KS NE NM CO / *Aeshna dugesi* TX NM TR / *Aeshna persephone* NM CO / *Anax walsinghamsi* TX NM / *Oplonaeschna armata* NM / *Erpetogomphus crotalinus* NM / *Erpetogomphus heterodon* TX NM / *Erpetogomphus lampropeltis* TX NM / *Ophiogomphus arizonicus* NM / *Phyllogomphoides albrighti* TX NM / *Phyllogomphoides stigmatus* TX OK NM / *Progomphus borealis* TX NM CO / *Macromia annulata* TX OK NM / *Brechmorhoga mendax* TX OK KS SD NM / *Dythemis fugax* TX OK KS NM / *Erythrodiplax funerea* TX / *Libellula commanche* TX OK KS NM CO / *Libellula composita* TX KS NM WY MT / *Libellula croceipennis* TX OK NM / *Libellula saturata* TX OK KS SD NM CO WY MT / *Paltotemis lineatipes* TX NM / *Pseudoleon superbus* TX NM

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Appendix 1:

COMPARISON OF MONTGOMERY'S (1967, 1968) AND THIS STUDY'S RESULTS USING PRESTON'S SIMILARITY INDEX: Montgomery (1967, 1968) was the first and, until now, the only student of Odonata to attempt to compare the odonate faunas of the states in the central United States. His 1967 paper focused on the north-central region of the U.S., and the 1968 paper the western U.S.

As odonate distributions were even less well known 30 years ago, Montgomery used family or suborder level taxa for comparisons. In his 1967 paper, he used the Coenagrionidae. In 1968 he used Anisoptera and three families: Libellulidae, Aeshnidae, and Gomphidae. In the latter paper, he also based some of his faunal comparisons on combinations of states. For example, he grouped the Kansas and Nebraska faunas together into unit, and did the same with the Texas and Oklahoma faunas.

Table 1 compares values of Preston's similarity index computed in this study with those of Montgomery. The values are of course not directly comparable, but are interesting in their similarity in some cases. Note especially the data from this study for Kansas Odonata as compared with Montgomery's Kansas Coenagrionidae data, as

well as the same comparisons for North Dakota and Missouri.

Figure 23 contains maps that show the value of Preston's similarity index using Texas and Oklahoma as bases for comparison. The states missing from the maps are those for which Montgomery lacked data and for which he did not compute an index value. The outlines of those states were removed to differentiate them from states with a low index value, which would be unshaded outlines. The patterns of shading in the various maps are generally similar, though no specific conclusions are obvious.

Figure 24 contains similar data using Kansas and Nebraska as bases of comparison. Once again the general shading patterns show similar trends, but are again somewhat inconclusive.

Figure 25 contains maps comparing this study and Montgomery's 1967 paper, for which he used the Coenagrionidae as a basis of comparison. The Nebraska data (b and e in Fig. 25) lead to different conclusions, the Odonata data indicating similarity between Nebraska and South Dakota and Nebraska and Iowa faunas, and the Coenagrionidae data showing similarity between Nebraska and Kansas faunas. Note the similarity, however, in shading. The shades of gray between the maps (a and d, b and e, c and f) are much more in agreement than any of those in Figures 23 or 24.

The general failure of these values to present a coherent pattern leads me to conclude that such assessments should be based on as complete and consistent an

understanding of the fauna as possible, and that, as DuBois (1995) recommended, "...a suite of measures..." should be used to assess faunal diversity.

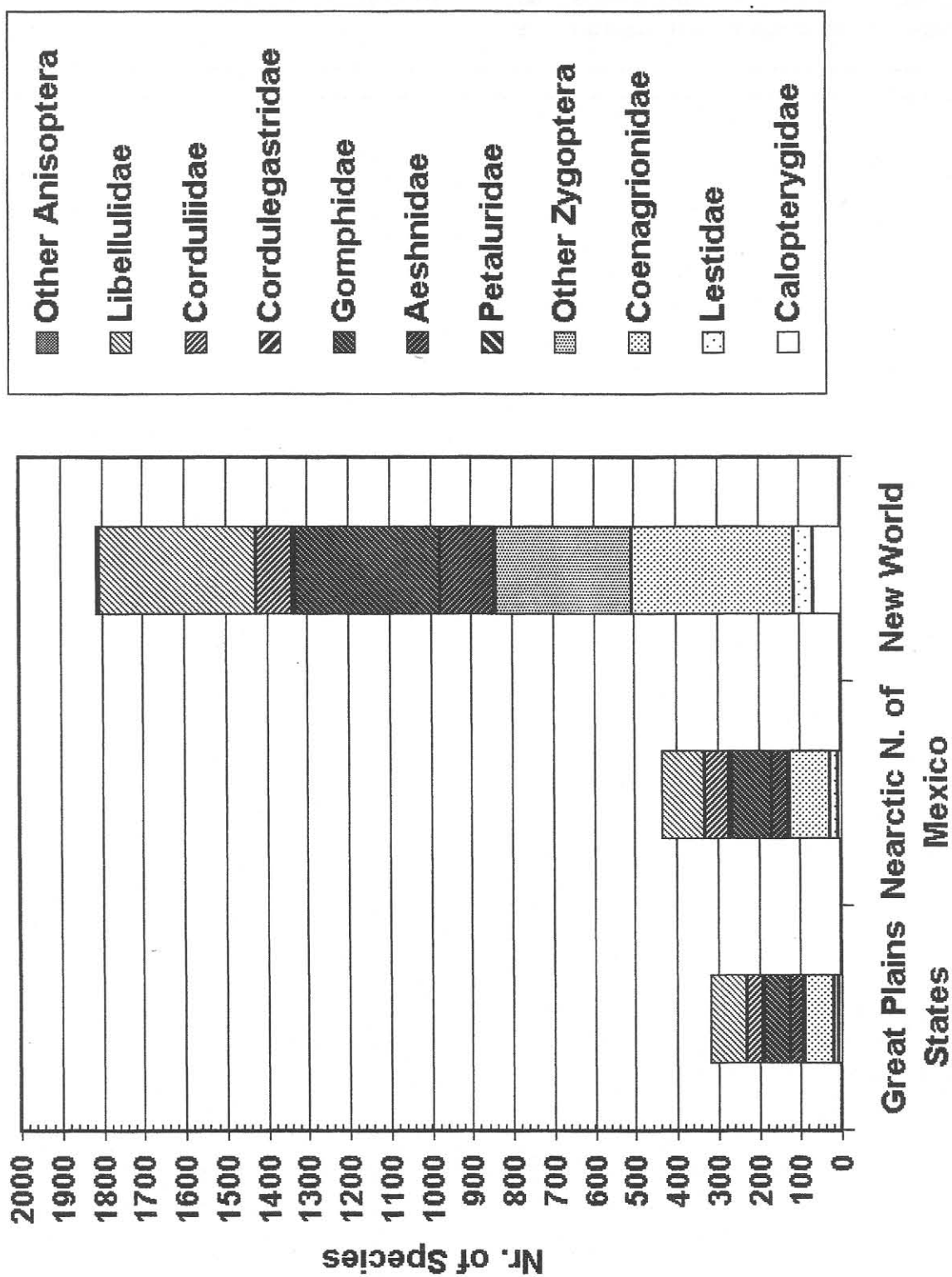


Figure 1. Odonata faunal composition by family for the New World, the Nearctic (north of Mexico), and the Great Plains states.

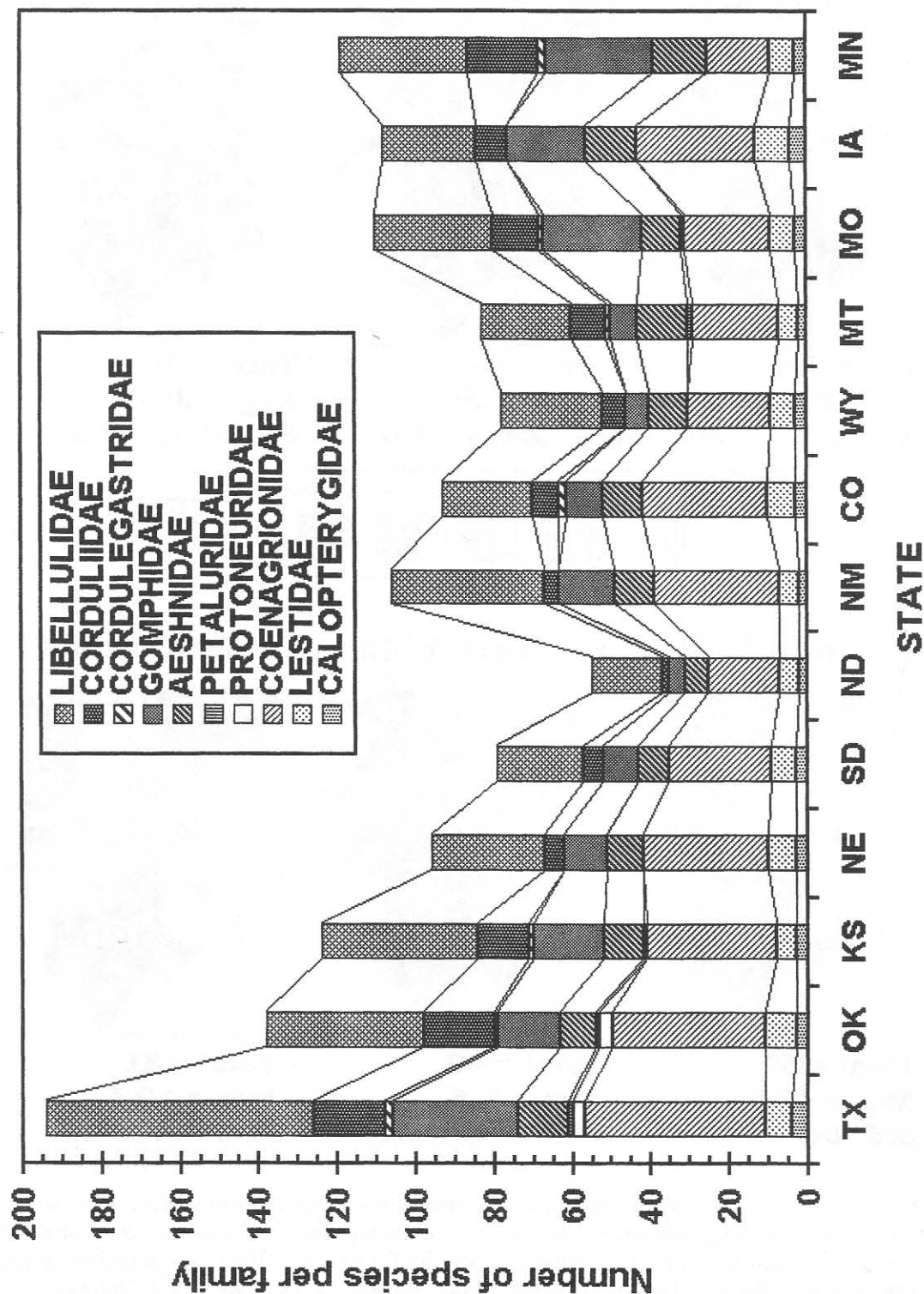


Figure 2. Odonata faunal composition by family for the 13 Great Plains states. The first 6 bars are the central tier states, the next 4 bars the western tier, and the last 3 bars the eastern tier. Each group is arranged from south (left) to north (right) to allow visualization of latitudinal gradients.

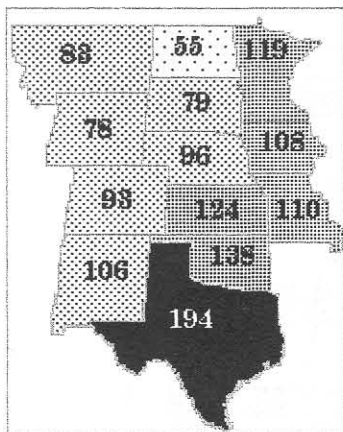
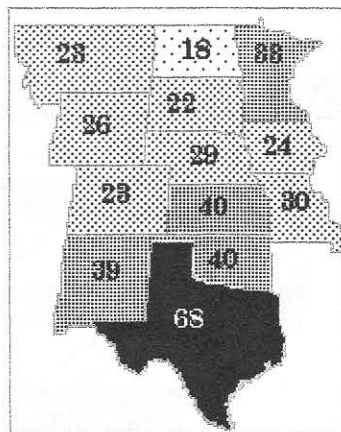
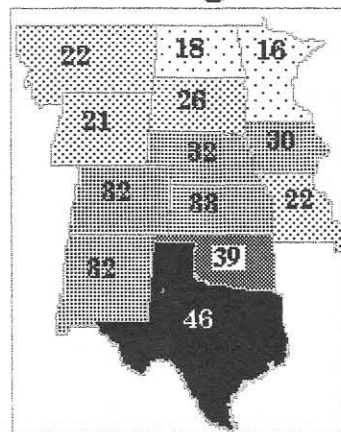
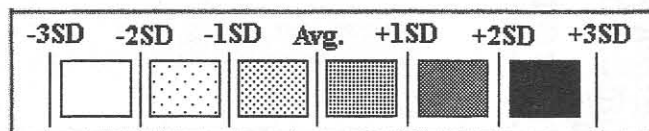
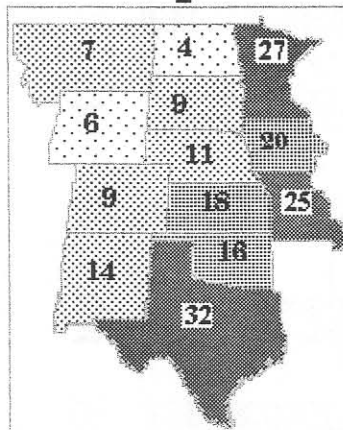
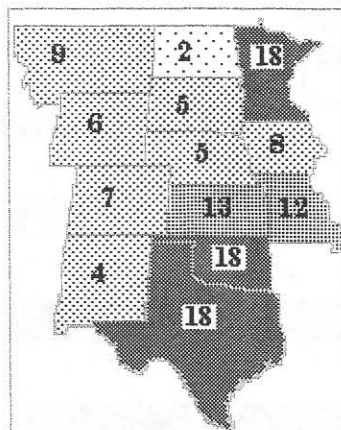
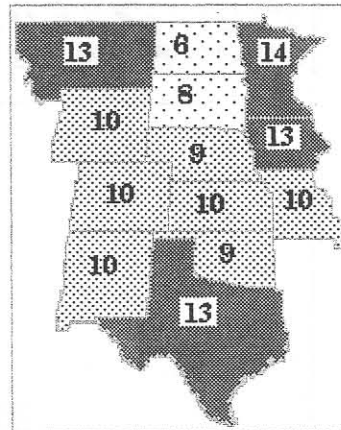
a - Odonata**Total = 320****Avg. = 106.4****Std. Dev. = 34.4****b - Libellulidae****Total = 89****Avg. = 31.9****Std. Dev. = 13.0****c - Coenagrionidae****Total = 70****Avg. = 28.4****Std. Dev. = 8.6****KEY****d - Gomphidae****Total = 62****Avg. = 15.2****Std. Dev. = 8.8****e - Corduliidae****Total = 40****Avg. = 9.6****Std. Dev. = 5.7****f - Aeshnidae****Total = 31****Avg. = 10.4****Std. Dev. = 2.3**

Figure 3. Maps showing the number of Odonata species and the number of species in the larger family groups by state. Shading indicates departure from the average for all 13 states in terms of standard deviations. For each group, the total number of species for the Great Plains states and the average and standard deviation for the 13 states are listed below each map. a. Odonata. b. Libellulidae. c. Coenagrionidae. d. Gomphidae. e. Corduliidae. f. Aeshnidae.

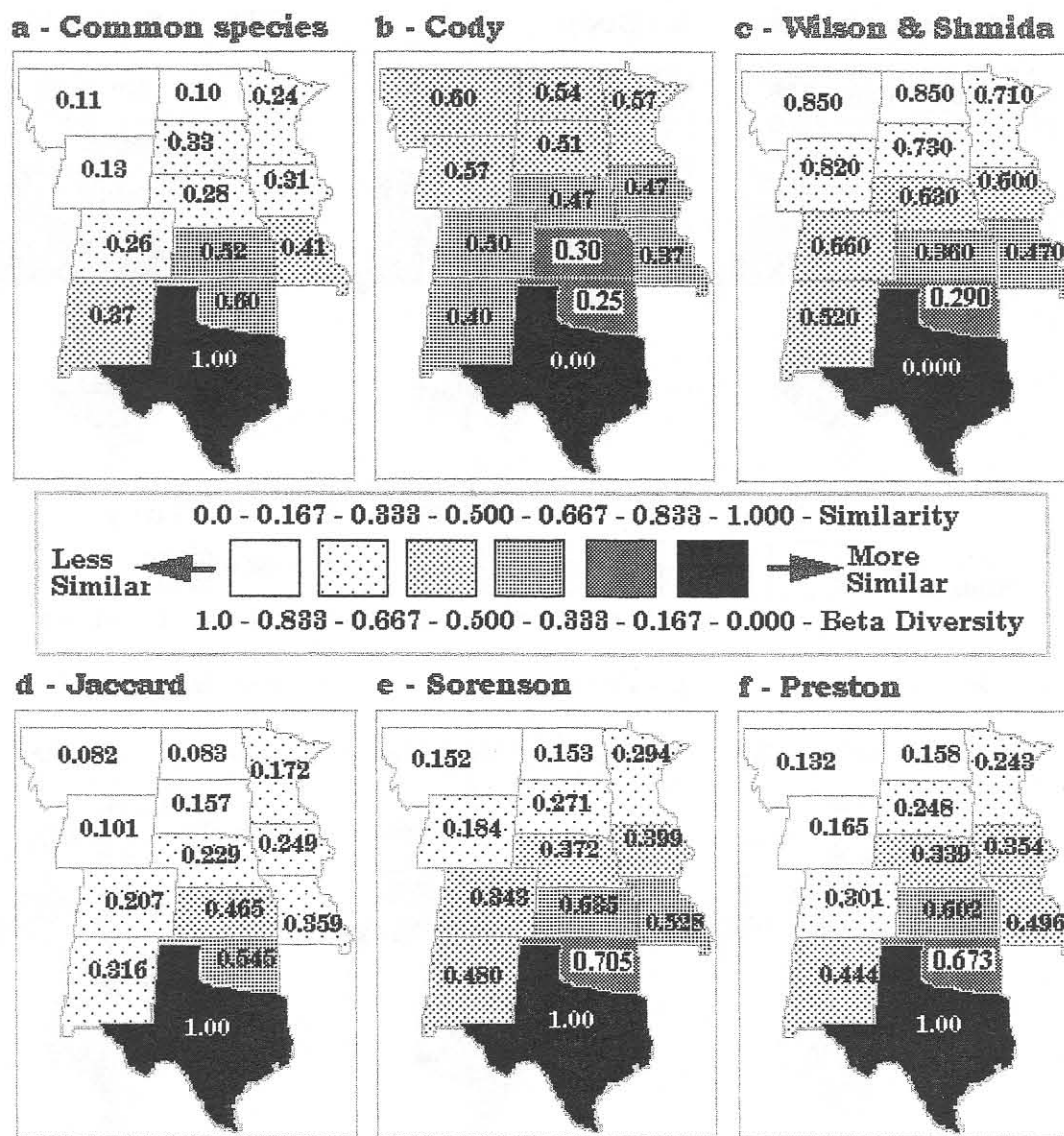


Figure 4. Maps showing measures of species similarity and diversity for the Great Plains states using Texas as a basis of comparison. a. Fraction of species common to Texas. b. Cody's Beta Diversity measure standardized by the number of species in Texas. c. The Wilson-Shmida Beta Diversity Measure. d. Jaccard's Similarity Index. e. Sorenson's Similarity Index. f. Montgomery's form of Preston's Similarity Index.

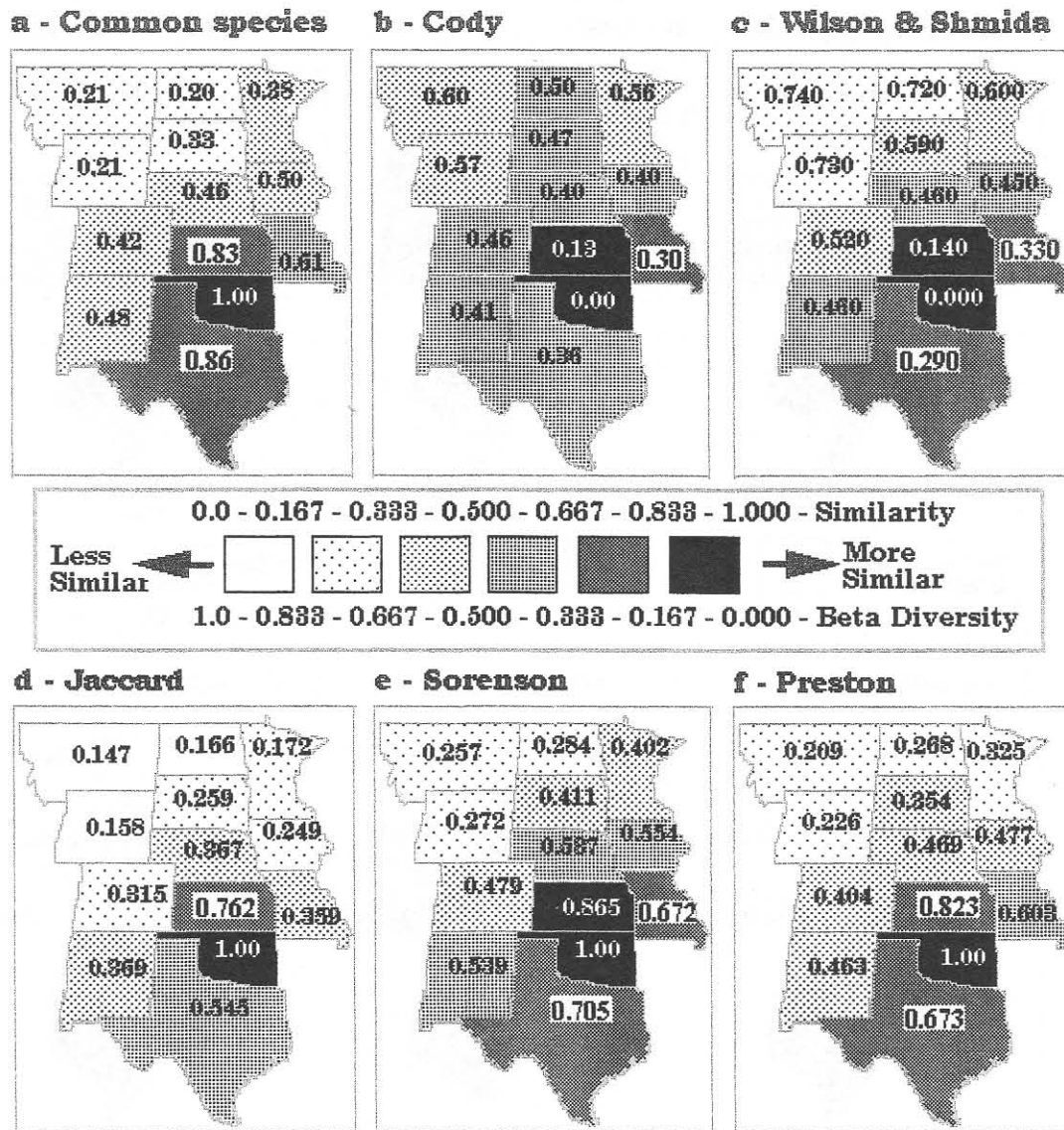


Figure 5. Maps showing measures of species similarity and diversity for the Great Plains states using Oklahoma as a basis of comparison. a. Fraction of species common to Oklahoma. b. Cody's Beta Diversity measure standardized by the number of species in Oklahoma. c. The Wilson-Shmida Beta Diversity Measure. d. Jaccard's Similarity Index. e. Sorenson's Similarity Index. f. Montgomery's form of Preston's Similarity Index.

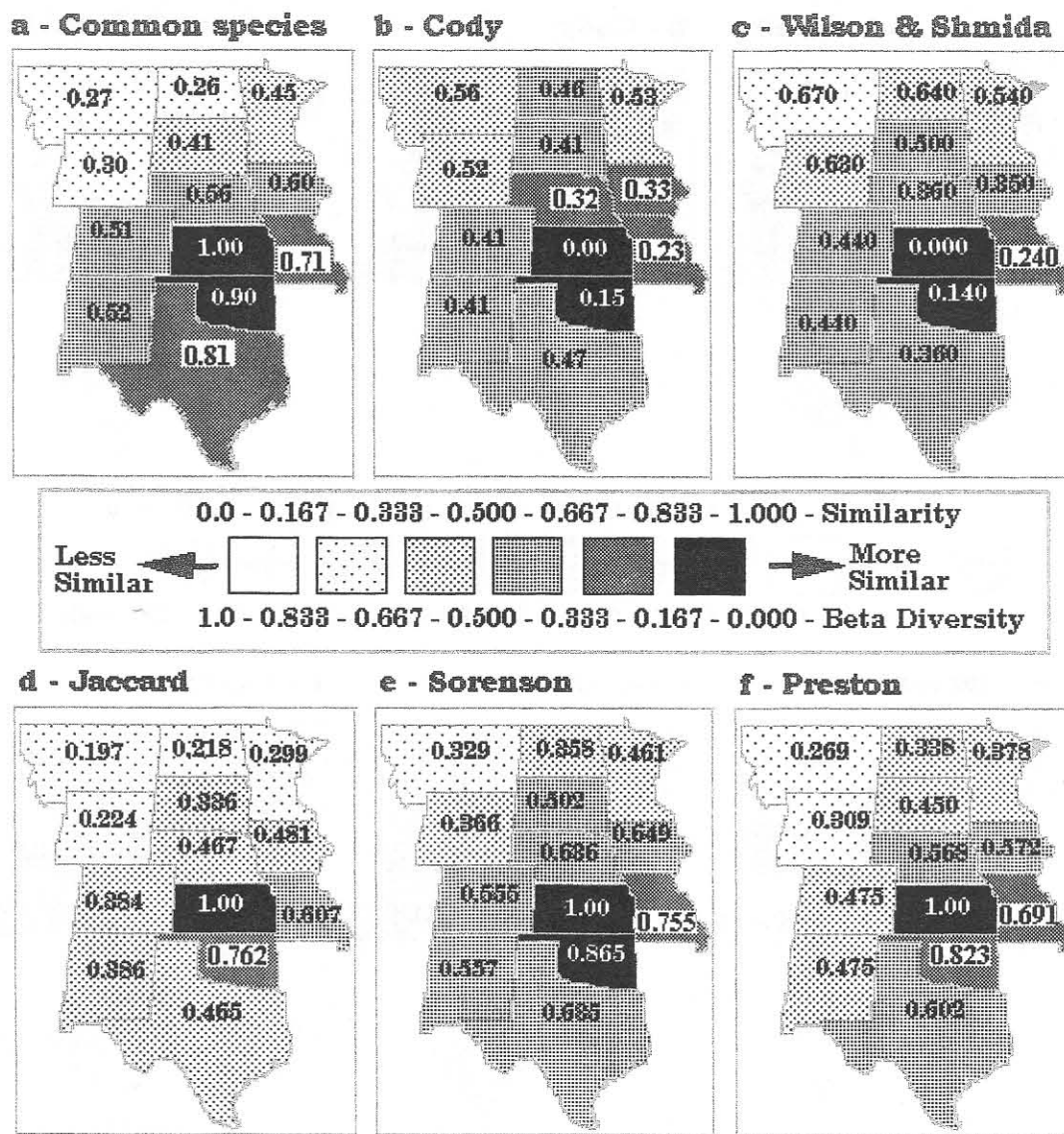


Figure 6. Maps showing measures of species similarity and diversity for the Great Plains states using Kansas as a basis of comparison. a. Fraction of species common to Kansas. b. Cody's Beta Diversity measure standardized by the number of species in Kansas. c. The Wilson-Shmida Beta Diversity Measure. d. Jaccard's Similarity Index. e. Sorenson's Similarity Index. f. Montgomery's form of Preston's Similarity Index.

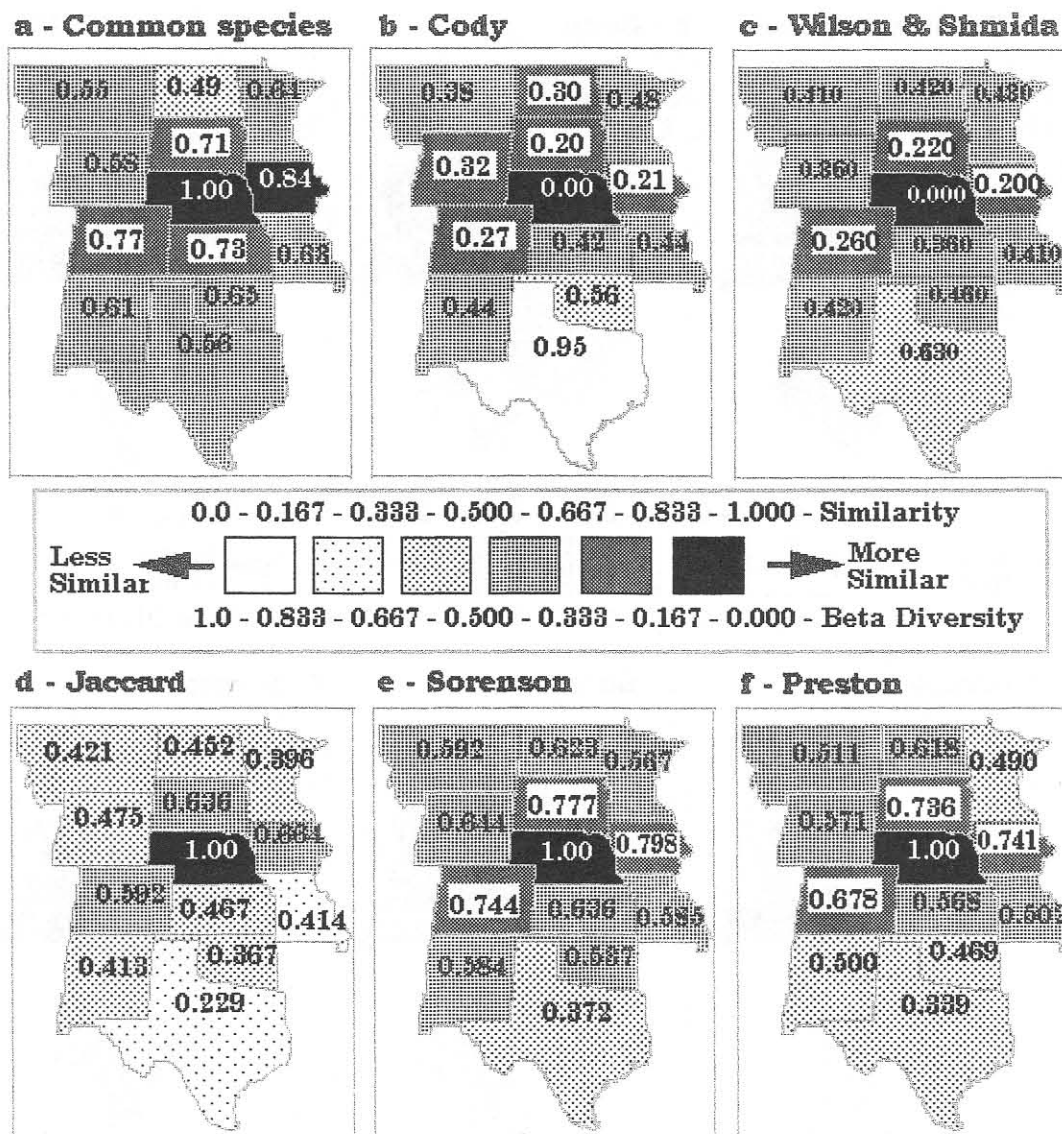


Figure 7. Maps showing measures of species similarity and diversity for the Great Plains states using Nebraska as a basis of comparison. a. Fraction of species common to Nebraska. b. Cody's Beta Diversity measure standardized by the number of species in Nebraska. c. The Wilson-Shmida Beta Diversity Measure. d. Jaccard's Similarity Index. e. Sorenson's Similarity Index. f. Montgomery's form of Preston's Similarity Index.

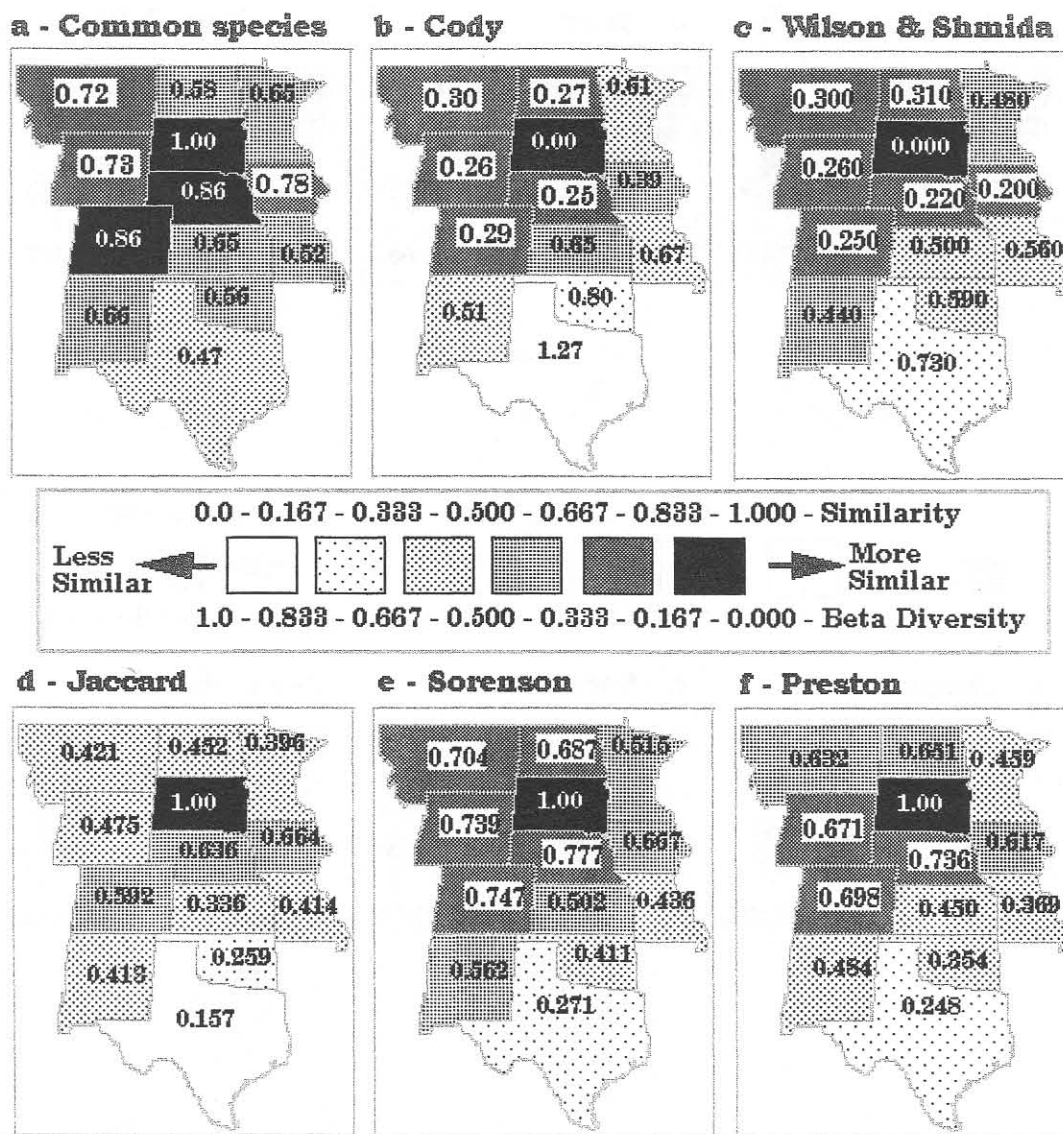


Figure 8. Maps showing measures of species similarity and diversity for the Great Plains states using South Dakota as a basis of comparison. a. Fraction of species common to South Dakota. b. Cody's Beta Diversity measure standardized by the number of species in South Dakota. c. The Wilson-Shmida Beta Diversity Measure. d. Jaccard's Similarity Index. e. Sorenson's Similarity Index. f. Montgomery's form of Preston's Similarity Index.

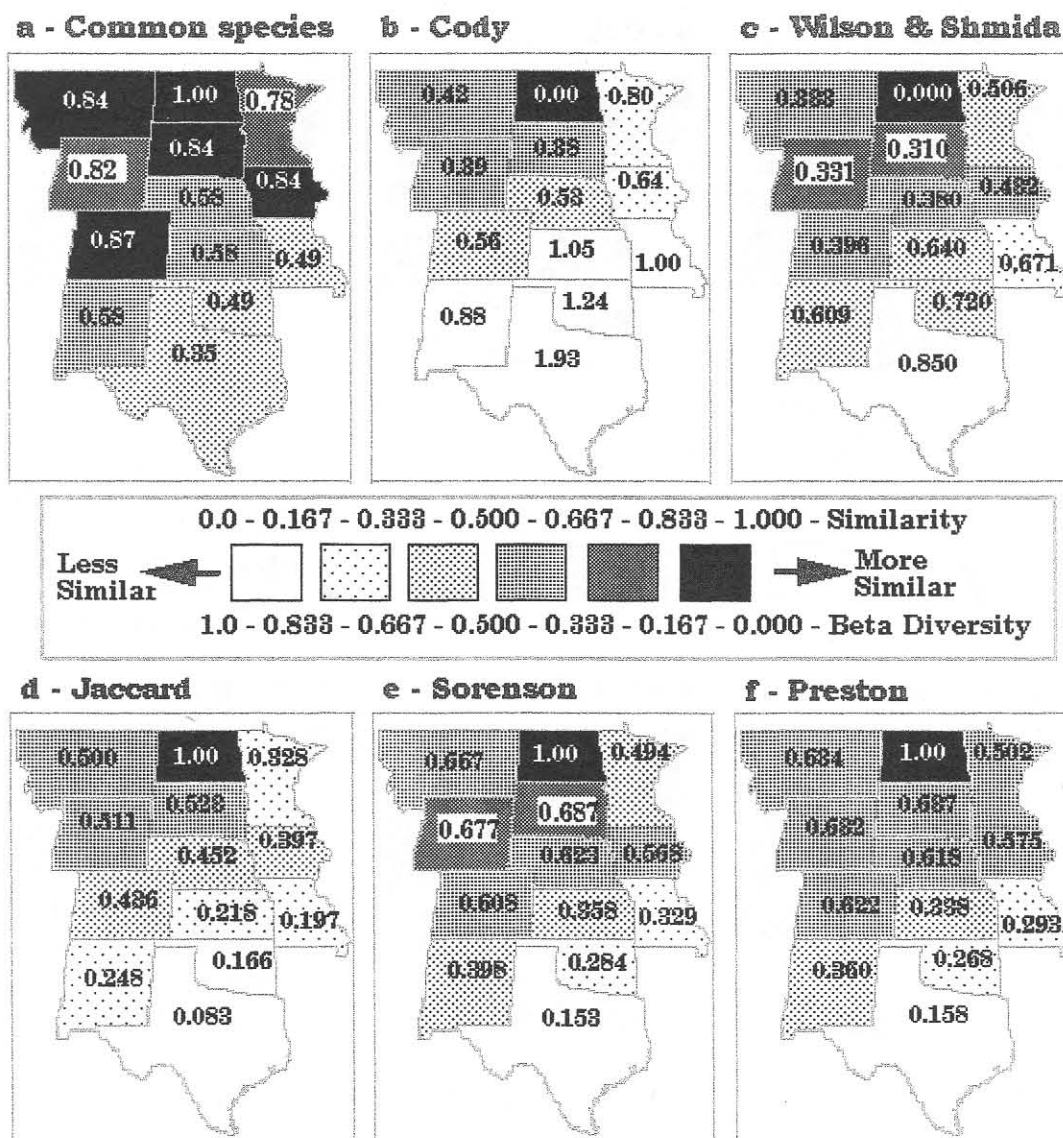


Figure 9. Maps showing measures of species similarity and diversity for the Great Plains states using North Dakota as a basis of comparison. a. Fraction of species common to North Dakota. b. Cody's Beta Diversity measure standardized by the number of species in North Dakota. c. The Wilson-Shmida Beta Diversity Measure. d. Jaccard's Similarity Index. e. Sorenson's Similarity Index. f. Montgomery's form of Preston's Similarity Index.

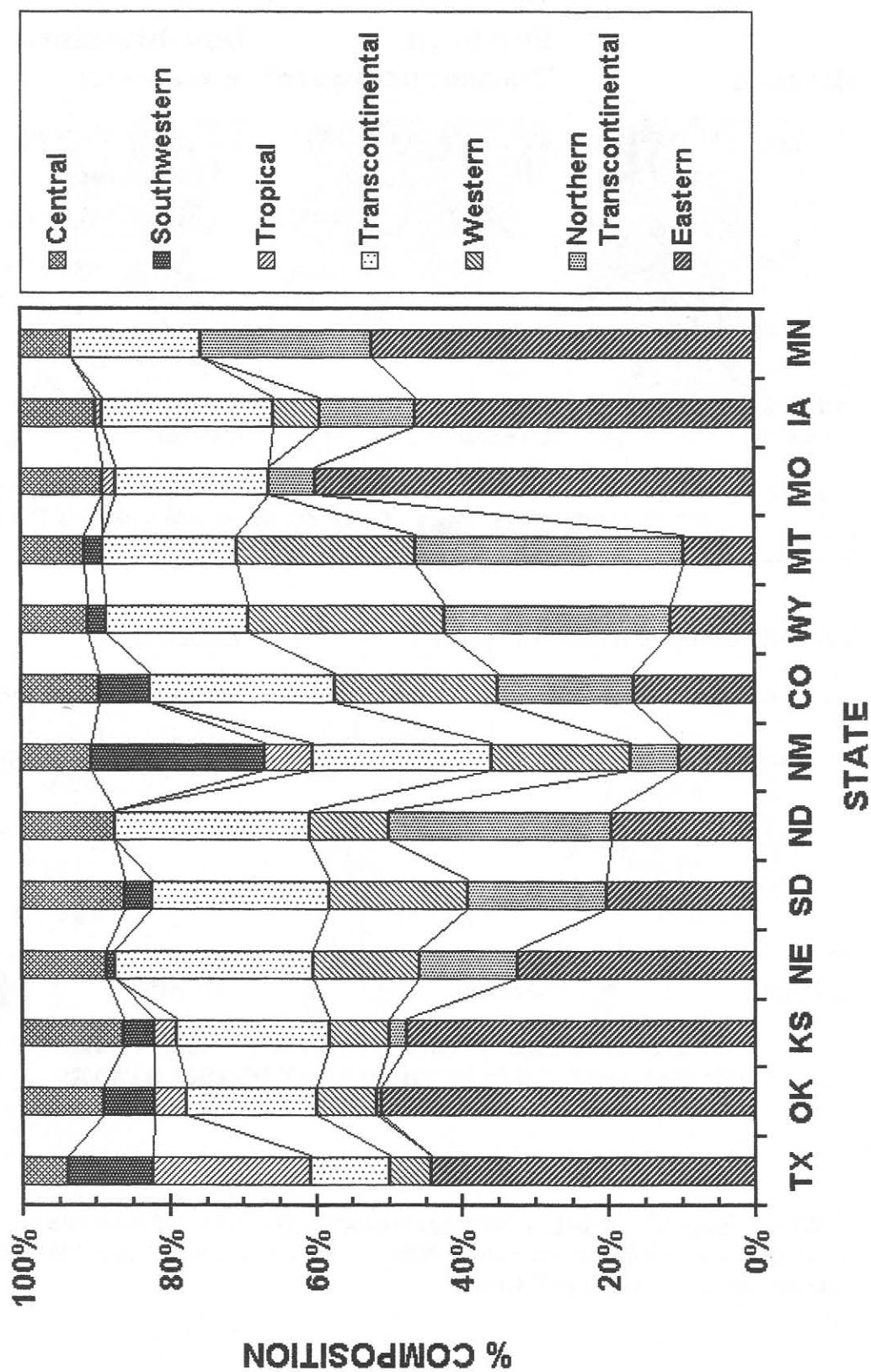


Figure 10. Percent composition of the Odonata fauna of the Great Plains states by biogeographic affinity.

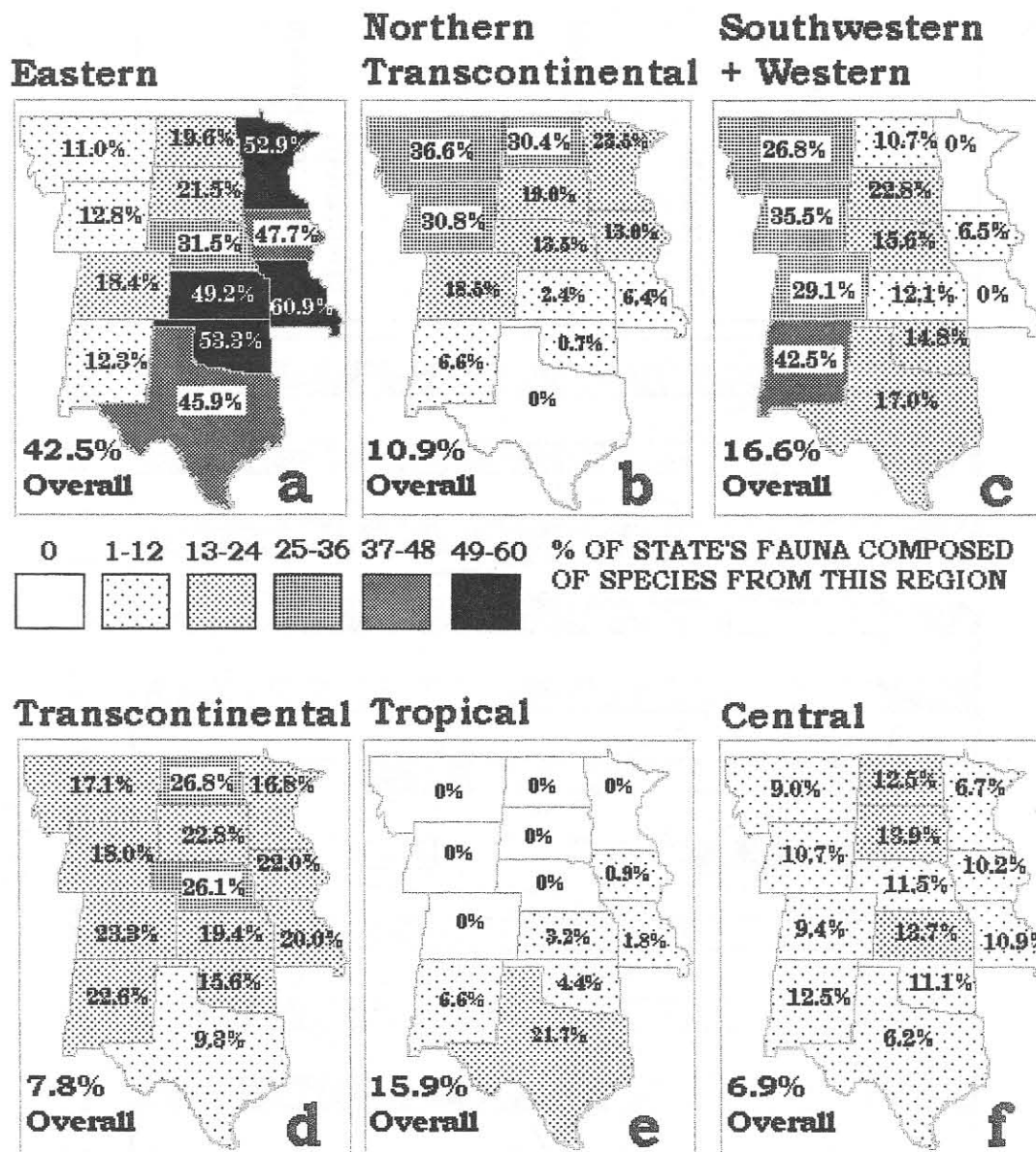
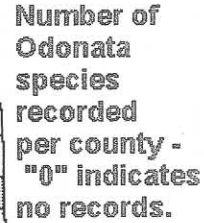


Figure 11. Maps showing the percentage composition of state Odonata faunas by biogeographical affinity. a. Eastern. b. Northern Transcontinental. c. Southwestern. d. Transcontinental. e. tropical. f. Central.



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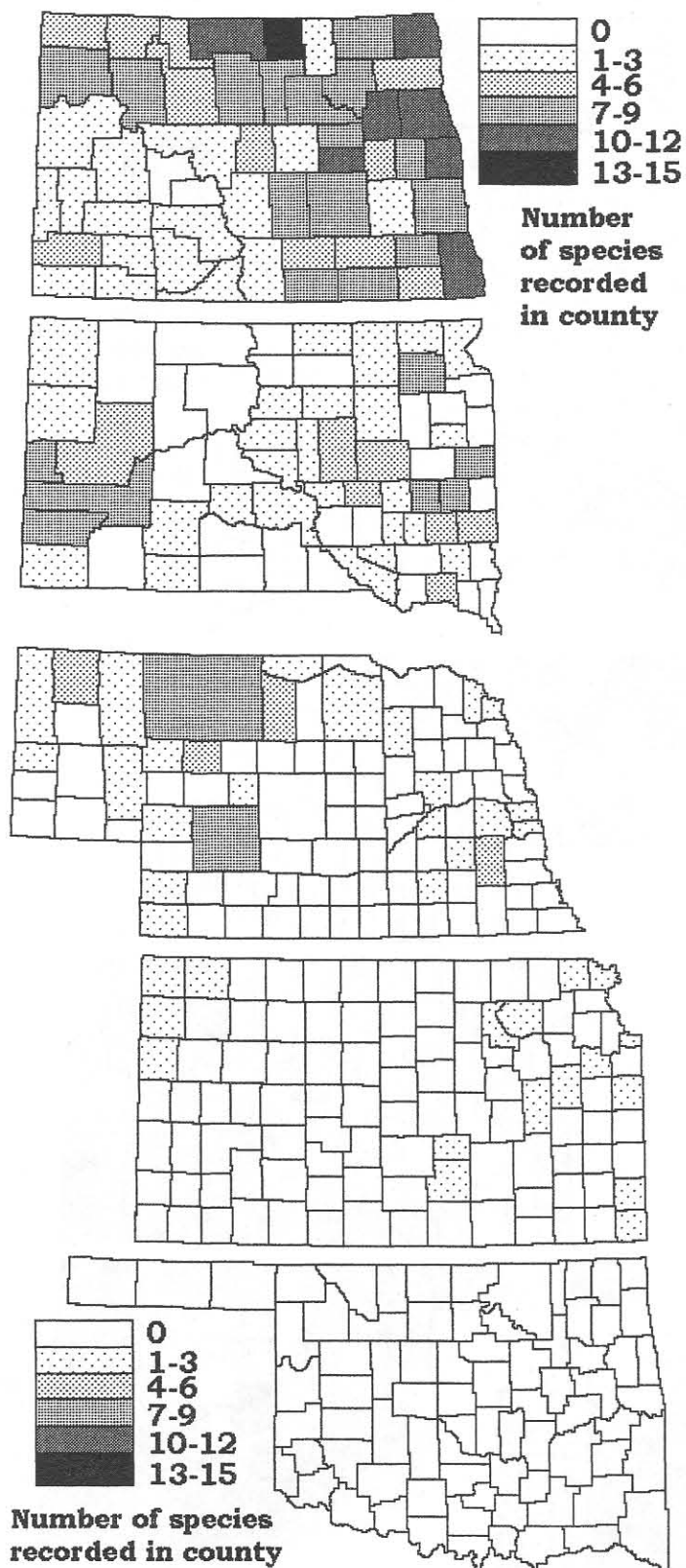


Figure 13. Map showing the number of species of the northern transcontinental biogeographic group recorded per county in the central tier of Great Plains states from Oklahoma north through North Dakota.

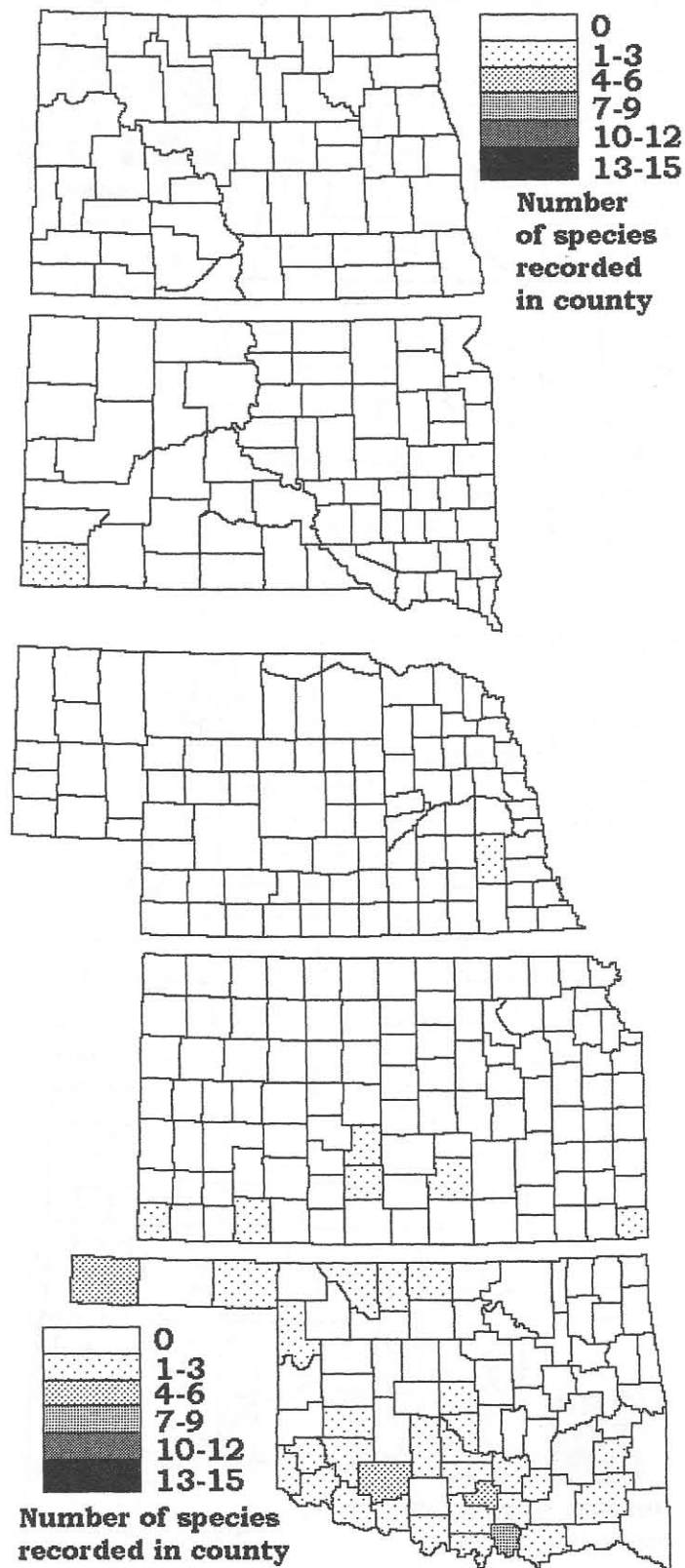


Figure 14. Map showing the number of species of the southwestern biogeographic group recorded per county in the central tier of Great Plains states from Oklahoma north through North Dakota.

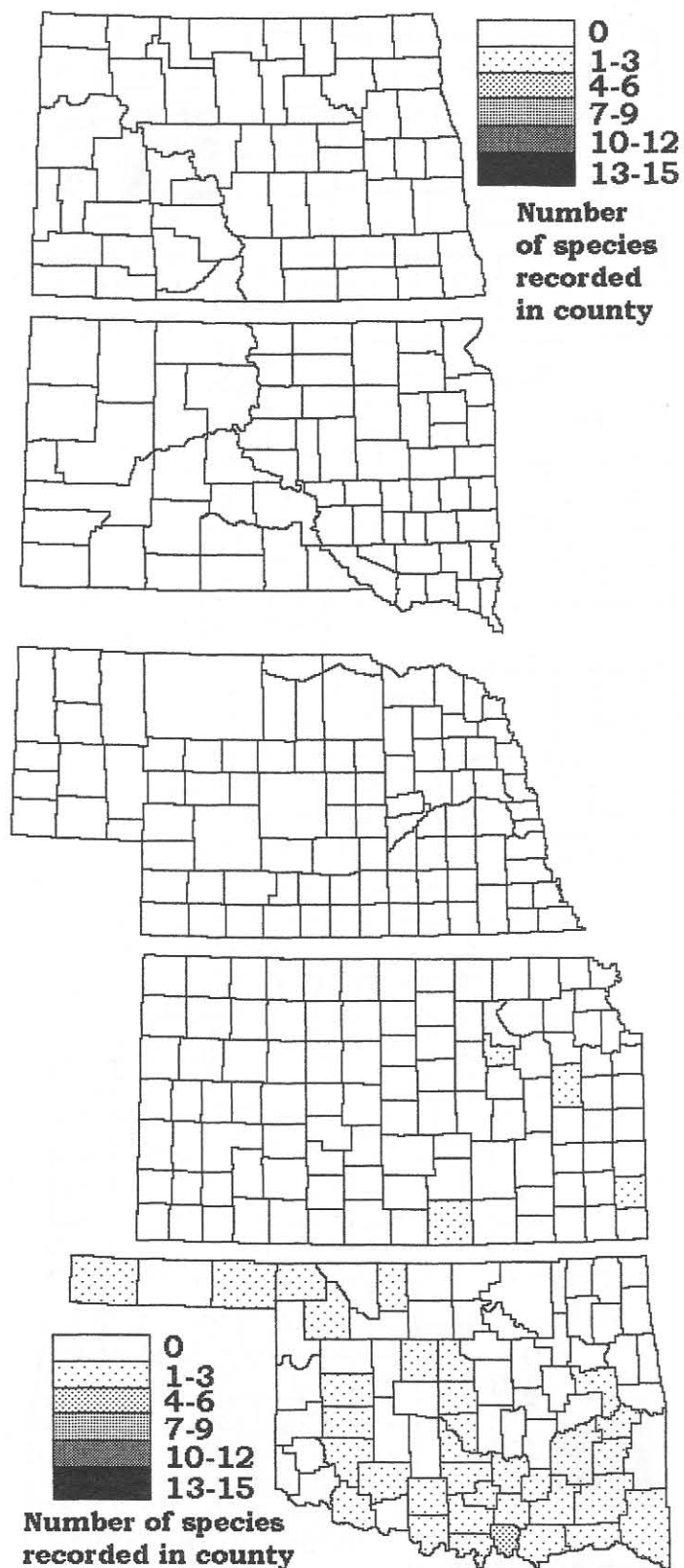


Figure 15. Map showing the number of species of the tropical biogeographic group recorded per county in the central tier of Great Plains states from Oklahoma north through North Dakota.

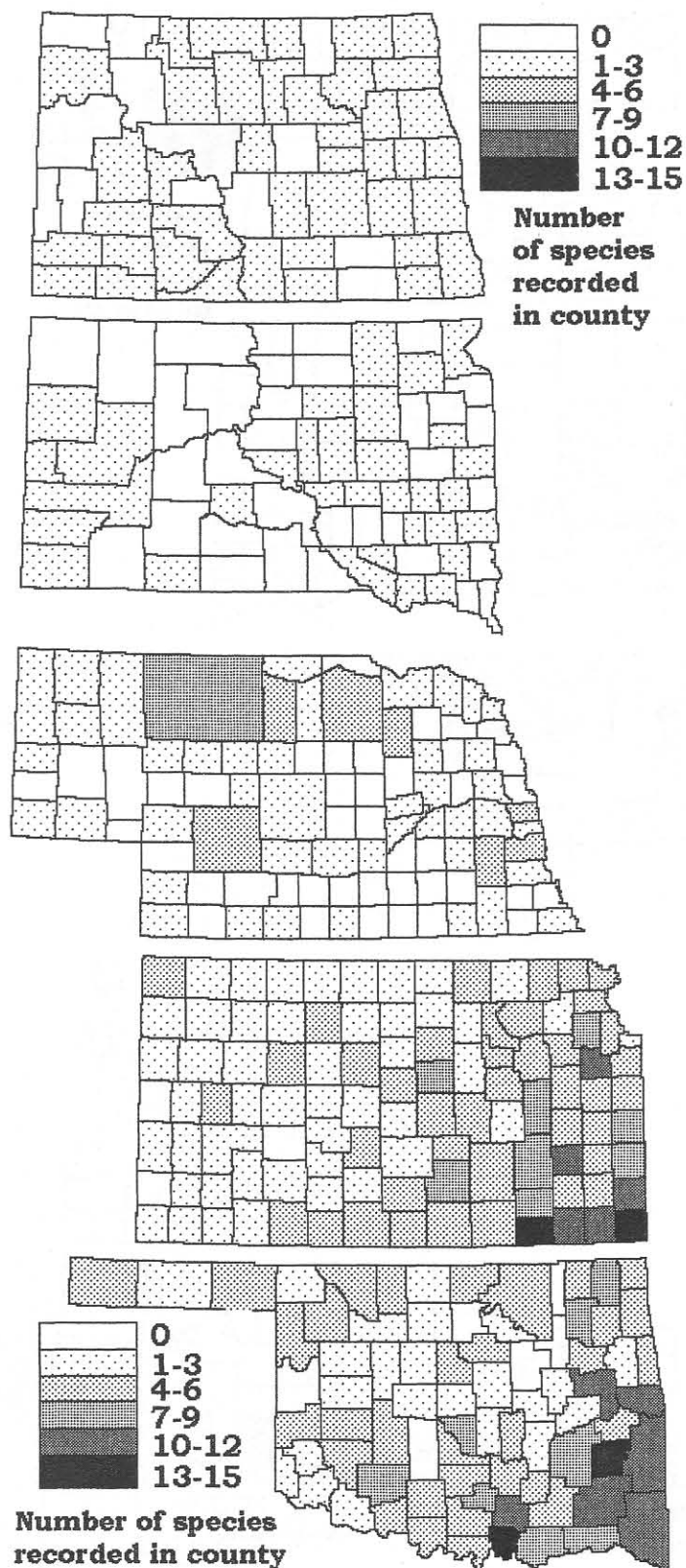


Figure 16. Map showing the number of species of the eastern biogeographic group recorded per county in the central tier of Great Plains states from Oklahoma north through North Dakota.

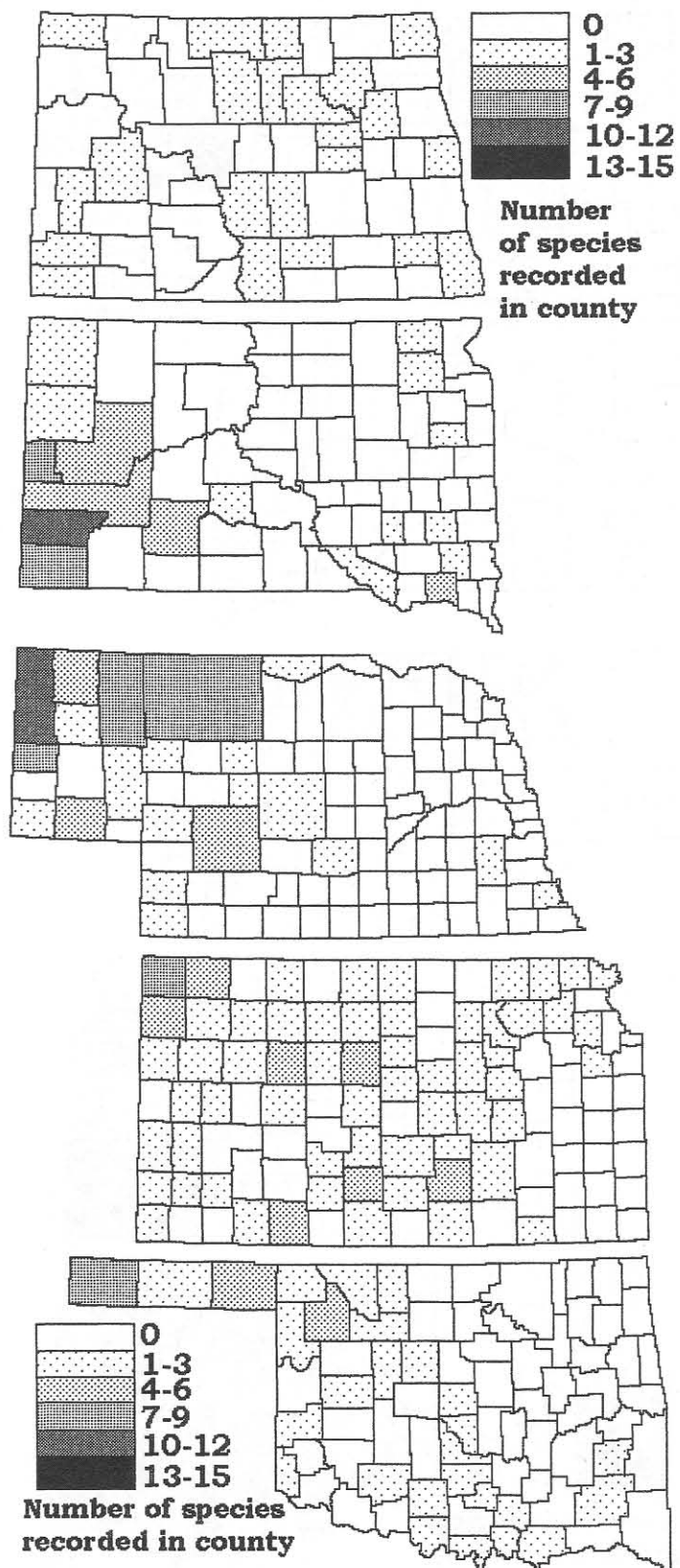


Figure 17. Map showing the number of species of the western biogeographic group recorded per county in the central tier of Great Plains states from Oklahoma north through North Dakota.

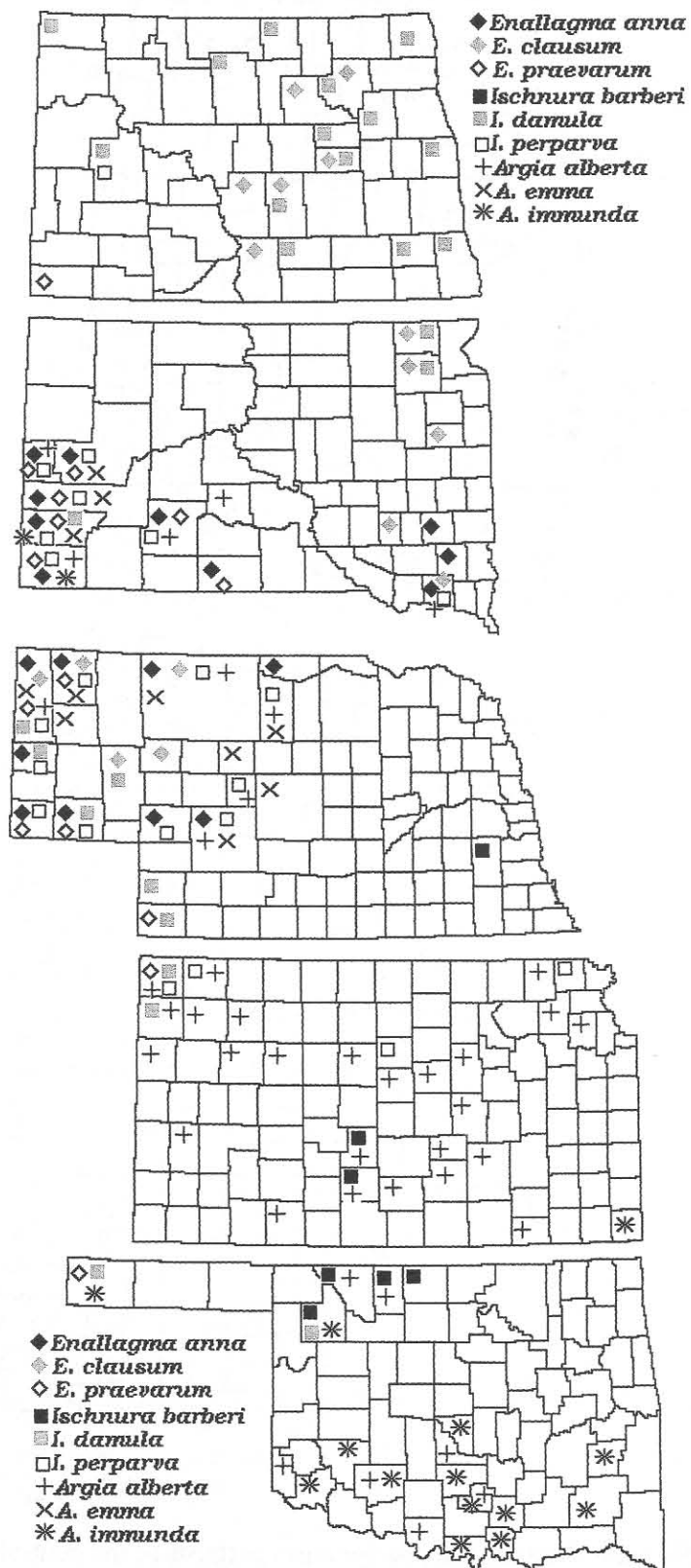


Figure 18. Map showing the county distribution of selected western and southwestern Coenagrionidae in the central tier of Great Plains states from Oklahoma north through North Dakota.

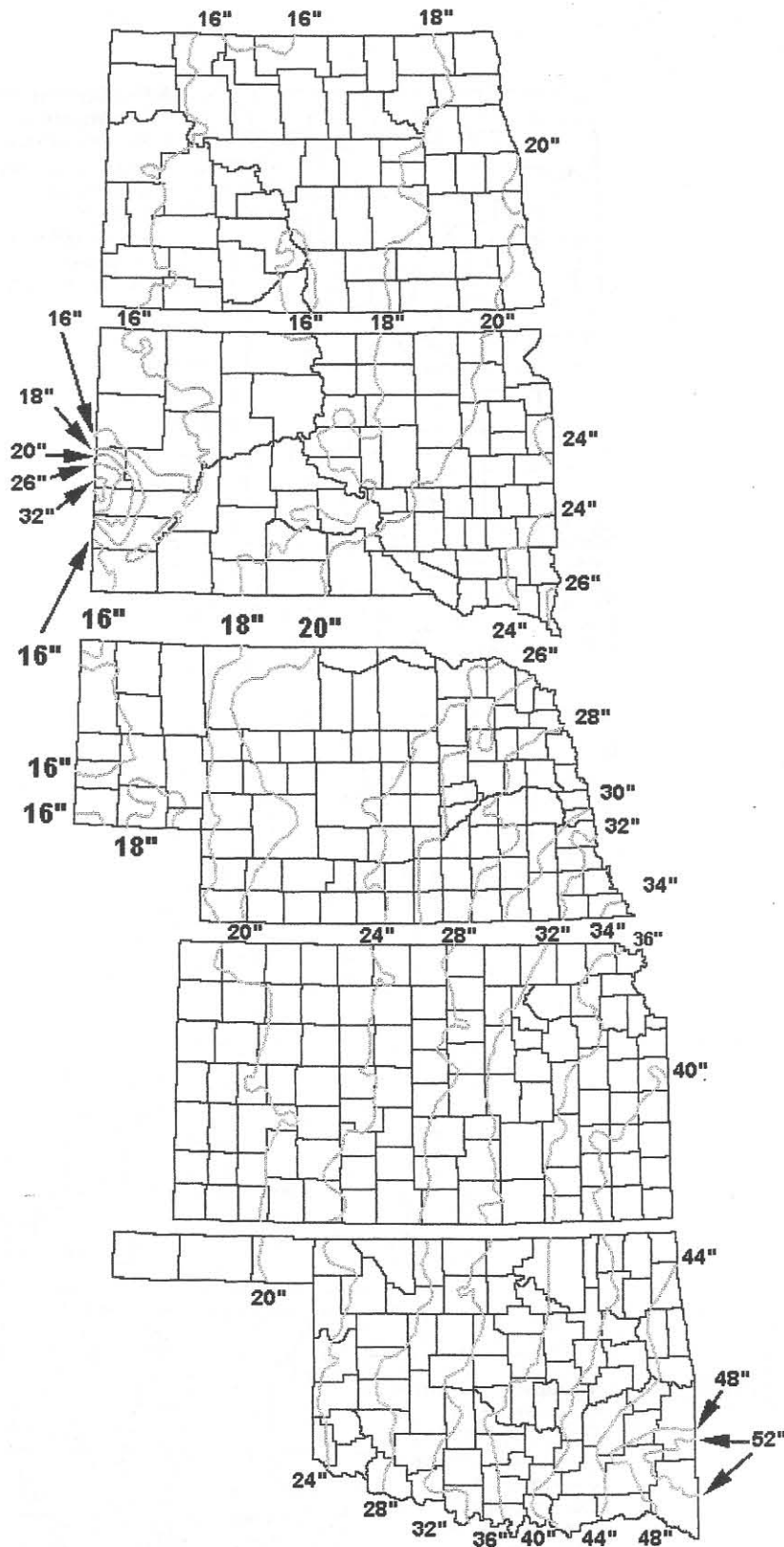


Figure 19. Map showing the precipitation patterns in the central tier of Great Plains states from Oklahoma north through North Dakota. Average annual precipitation 1961-1990.

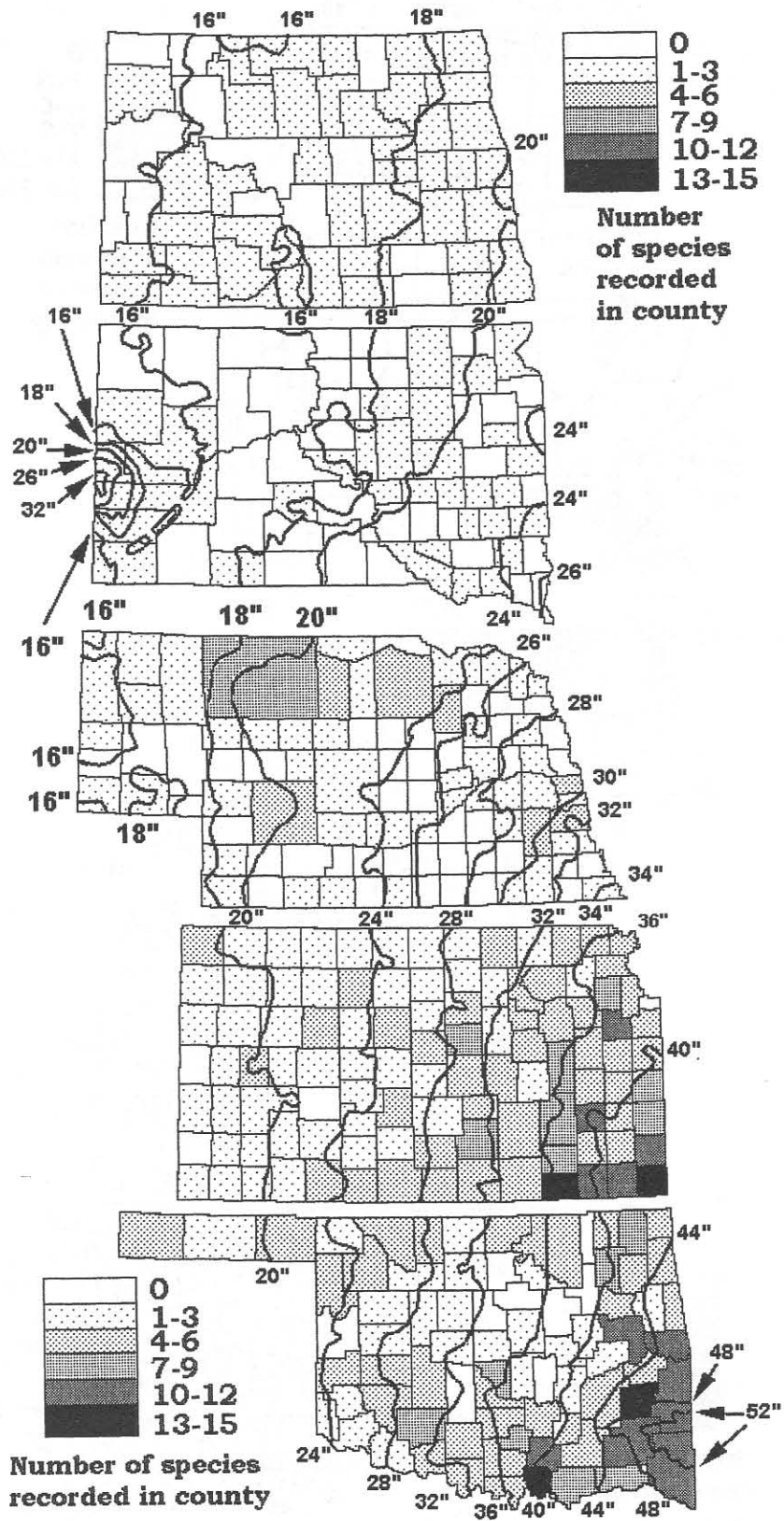


Figure 20. Data of Figure 16 (numbers species of eastern biogeographic group per county) with overlay of precipitation isolines from Figure 19.

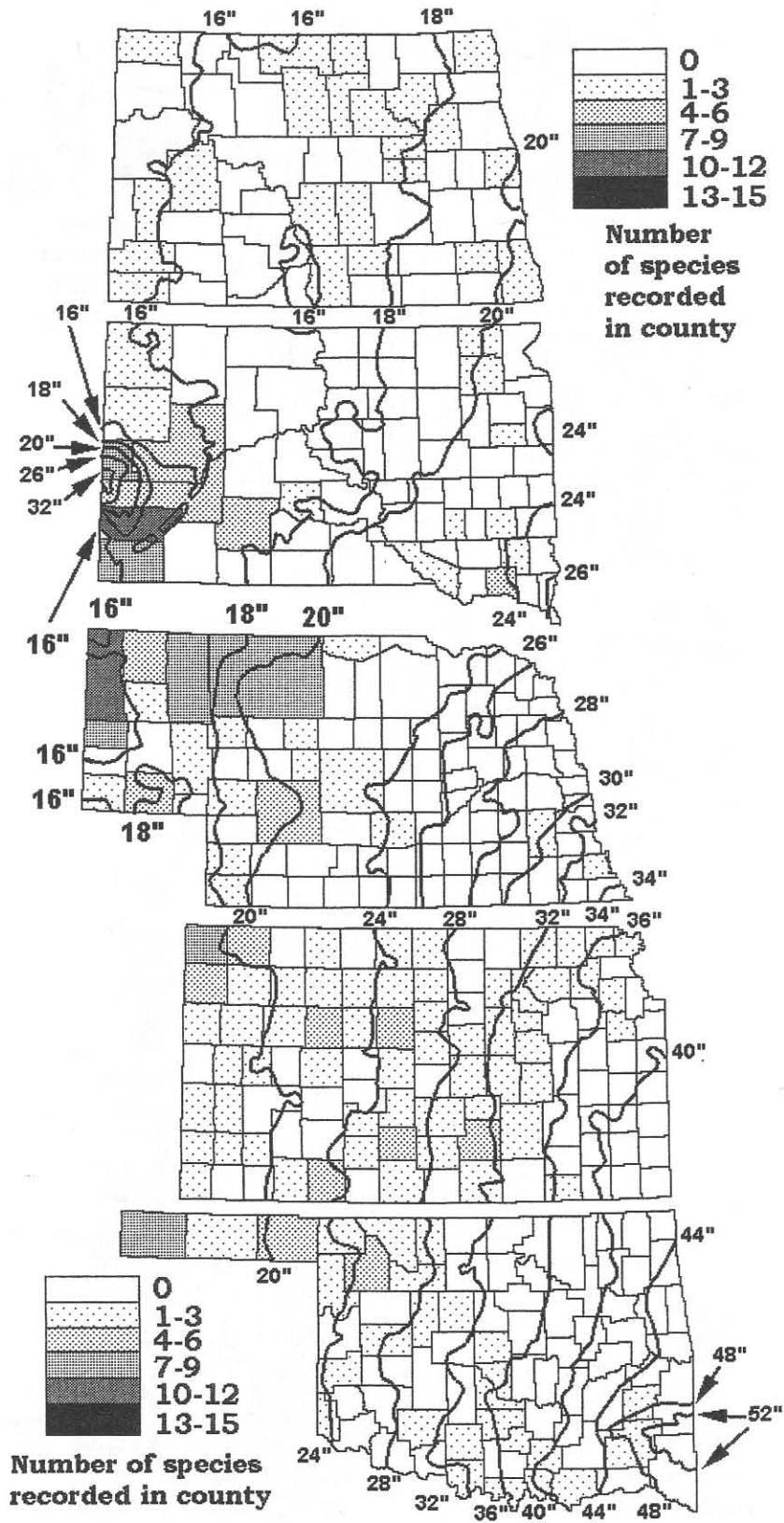


Figure 21. Data of Figure 17 (numbers species of western biogeographic group per county) with overlay of precipitation isolines from Figure 19.

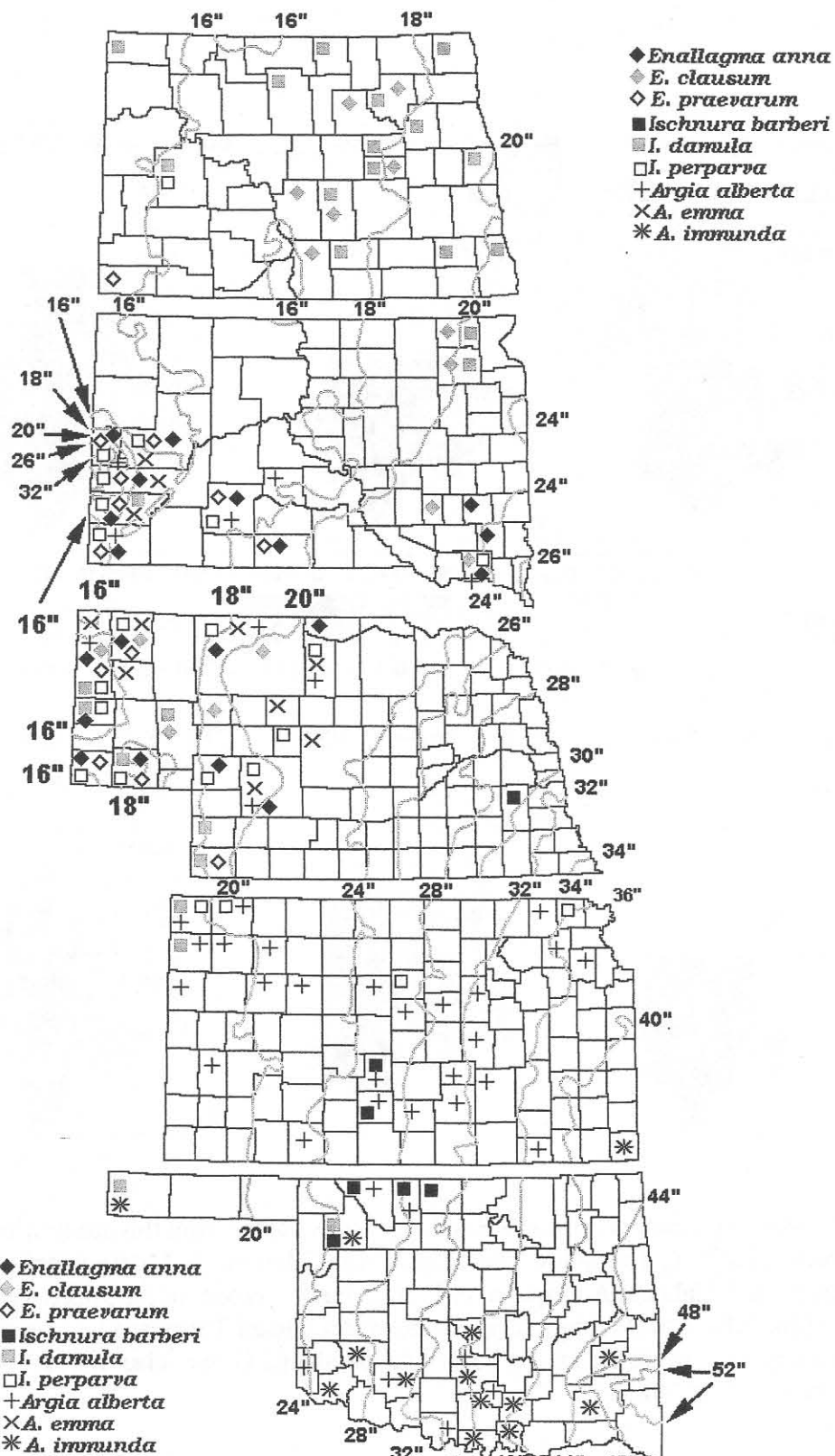


Figure 22. Data of Figure 18 (distribution by county of selected western and southwestern Coenagrionidae) with overlay of precipitation isolines from Figure 19.

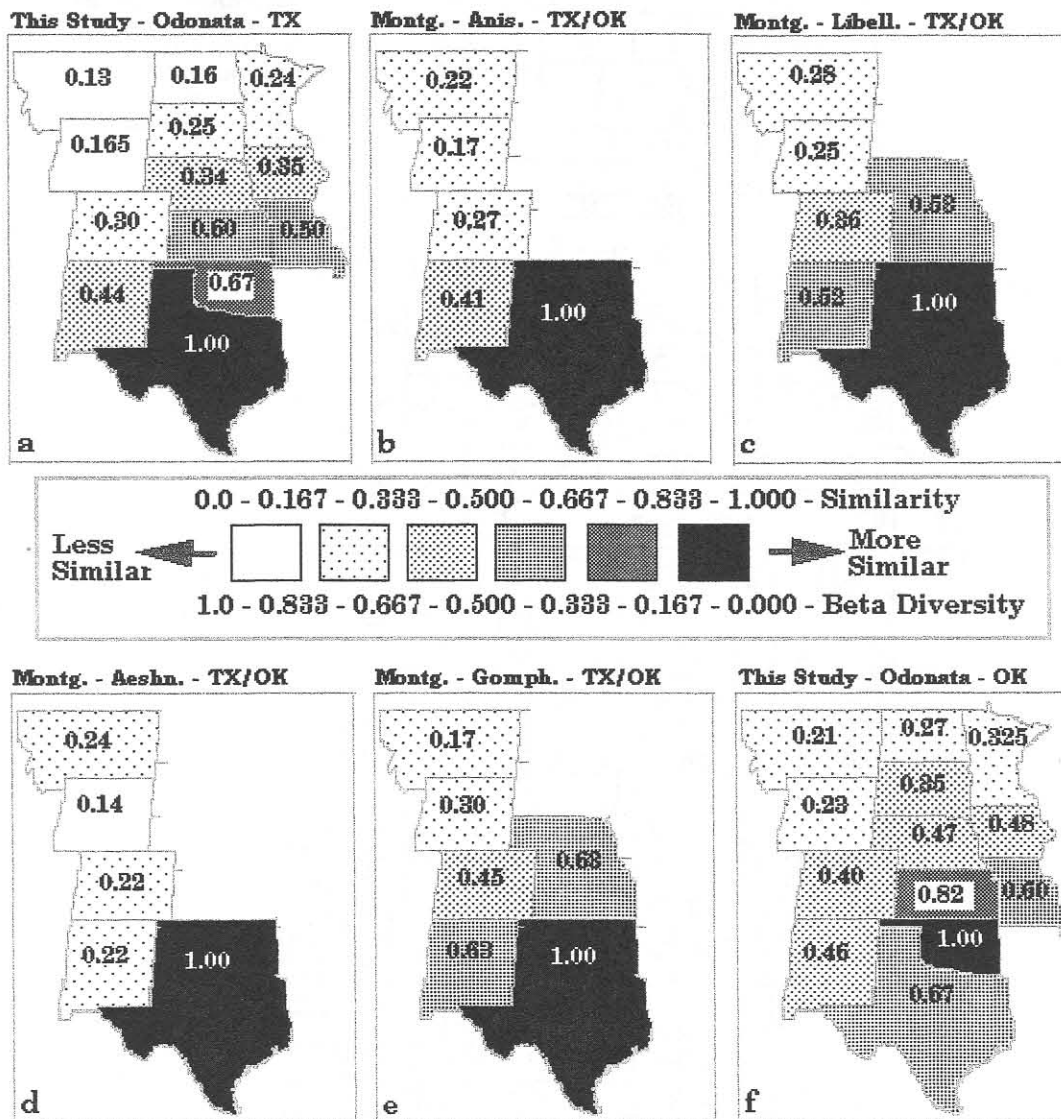


Figure 23. Maps comparing Preston's Similarity Index values from this study with those of Montgomery (1967). a. This study – based on Texas Odonata. b. Montgomery – based on the joined Texas and Oklahoma Anisoptera. c. Montgomery – based on the joined Texas and Oklahoma Libellulidae. d. Montgomery – based on the joined Texas and Oklahoma Aeshnidae. e. Montgomery – based on the joined Texas and Oklahoma Gomphidae. f. This study – based on Oklahoma Coenagrionidae.

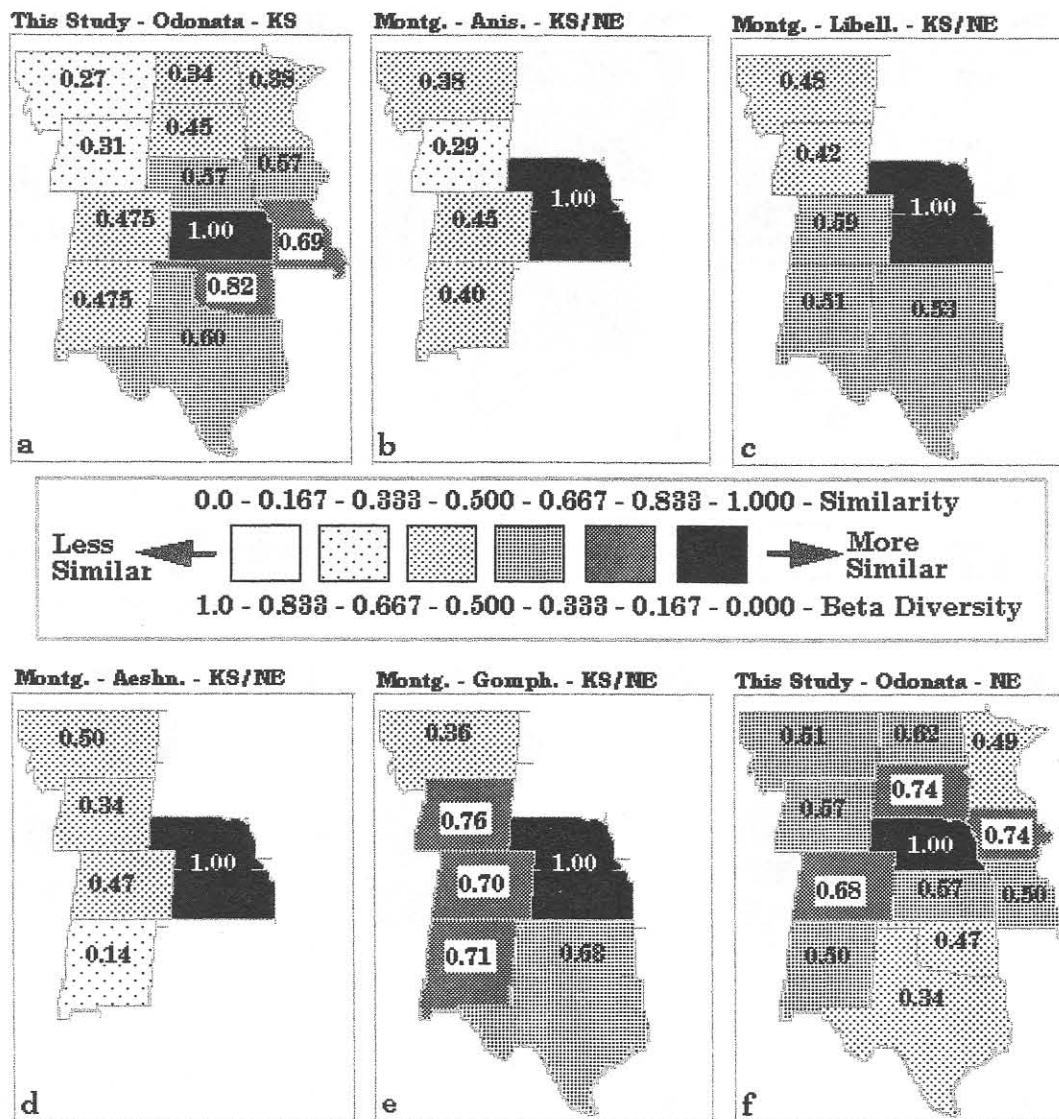


Figure 24. Maps comparing Preston's Similarity Index values from this study with those of Montgomery (1967). a. This study – based on Kansas Odonata. b. Montgomery – based on the joined Kansas and Nebraska Anisoptera. c. Montgomery – based on the joined Kansas and Nebraska Libellulidae. d. Montgomery – based on the joined Kansas and Nebraska. e. Montgomery – based on the joined Kansas and Nebraska Gomphidae. f. This study – based on Nebraska Coenagrionidae.

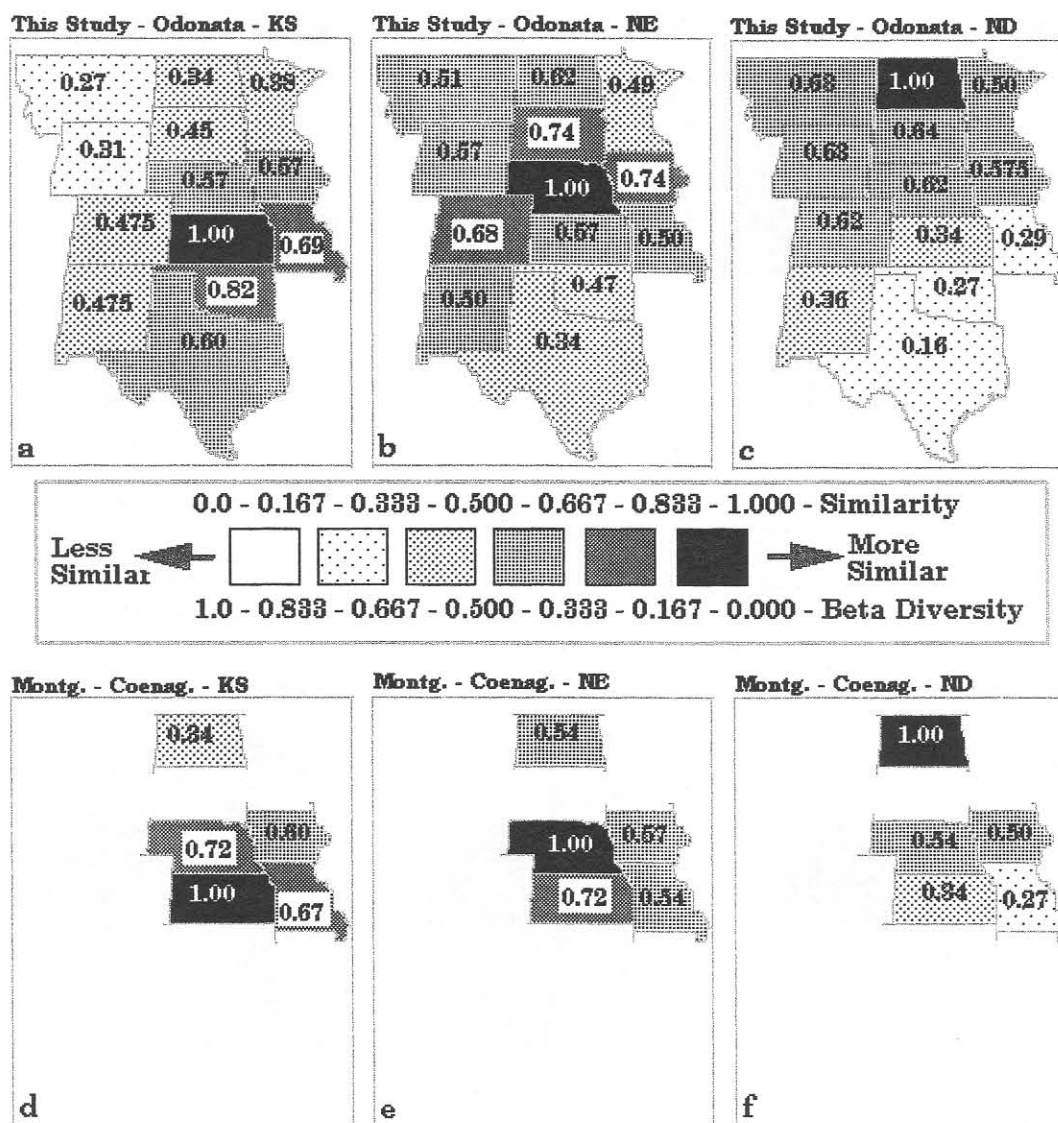


Figure 25. Maps comparing Preston's Similarity Index values from this study with those of Montgomery (1967). a. This study – based on Kansas Odonata. b. This study – based on Nebraska Odonata. c. This study – based on North Dakota Odonata. d. Montgomery – based on Kansas Coenagrionidae. e. Montgomery – based on Nebraska Coenagrionidae. f. Montgomery – based on North Dakota Coenagrionidae.

	NM	CO	WY	MT	TX	TX/OK	OK	KS	KS/NE	NE	SD	ND	MO	IA	MN
TX Odonata	0.44	0.30	0.165	0.13	1.00		0.67	0.60		0.34	0.25	0.16	0.50	0.35	0.24
OK/TX	0.41	0.27	0.17	0.22		1.00									
Anisoptera															
OK/TX	0.52	0.36	0.25	0.28		1.00			0.53						
Libellulidae															
OK/TX	0.22	0.22	0.14	0.24		1.00									
Aeshnidae															
OK/TX	0.63	0.45	0.30	0.17		1.00			0.63						
Gomphidae															
OK Odonata	0.46	0.40	0.23	0.21	0.67		1.00	0.82		0.47	0.35	0.27	0.60	0.48	0.33
KS Odonata	0.475	0.475	0.31	0.27	0.60		0.82	1.00		0.57	0.45	0.34	0.69	0.57	0.38
KS								1.00		0.72		0.34	0.67	0.60	
Coenagrionidae															
KS/NE	0.40	0.45	0.29	0.38					1.00						
Anisoptera															
KS/NE	0.51	0.59	0.42	0.48		0.53			1.00						
Libellulidae															
KS/NE	0.14	0.47	0.34	0.50					1.00						
Aeshnidae															
KS/NE	0.71	0.70	0.76	0.36		0.63			1.00						
Gomphidae															
NE Odonata	0.50	0.68	0.57	0.51	0.34		0.47	0.57		1.00	0.74	0.62	0.50	0.74	0.49
NE								0.72		1.00		0.54	0.54	0.57	
Coenagrionidae															
SD Odonata	0.48	0.70	0.67	0.63	0.25		0.35	0.45		0.74	1.00	0.65	0.37	0.62	0.46
ND Odonata	0.36	0.62	0.63	0.63	0.16		0.27	0.34		0.62	0.64	1.00	0.29	0.575	0.50
ND								0.34		0.54		1.00	0.27	0.50	
Coenagrionidae															
MO Odonata					0.495		0.60	0.69		0.50	0.37	0.29	1.00		
MO								0.66		0.54		0.27	1.00	0.72	
Coenagrionidae															
IA Odonata					0.35		0.48	0.57		0.74	0.62	0.575		1.00	
IA								0.60		0.57		0.50	0.72	1.00	
Coenagrionidae															
MN Odonata					0.24		0.325	0.38		0.50	0.46	0.59			1.00

Table 1. Comparison of Preston Similarity values of Montgomery (1967, 1968) with those of this study (shaded entries).