

STYGOBITES ARE MORE WIDE-RANGING THAN TROGLOBITES

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Stygobites are thought to be wider ranging than troglobites in the contiguous 48 United States. This assumption is confirmed by showing that stygobite species are recorded from more counties than troglobite species (Mann Whitney $U = 80189$, $Z = -6.781$, $P < 0.0001$). The properties of water flow through caves may allow greater dispersal opportunities for stygobites above the normal water table during floods and could be one reason for the larger ranges of these species.

Christman and Culver (2001) assume that stygobites, aquatic cave-dwellers, are wider ranging than their terrestrial counterparts, troglobites. Similarly, Culver *et al.* (2000) state that troglobites are confronted with different extinction risks than stygobites, because they generally have smaller range sizes. However, the assumption that troglobites have smaller range sizes is not based on data provided by Christman and Culver (2001) or Culver *et al.* (2000), nor related articles (Culver 1999; Culver *et al.* 1999; Culver *et al.* 2003). The percentage of troglobites endemic to a county in the United States is greater than for stygobites (Culver *et al.* 2000). However, this fact alone does not mean that stygobites are generally wider ranging because Culver *et al.*'s (2000) analysis does not consider range sizes of non-endemic species. Christman and Culver (2001) list the median number of counties in which both groups of cave fauna are present as three, which when taken alone, indicates a lack of range size difference between the two groups.

Using the Karst Waters Institute data from the web (<http://www.karstwaters.org> viewed online 4/27/03), I counted the number of counties in which each stygobite and troglobite species and subspecies was present in order to test whether stygobites were more widespread. I excluded interstitial species (listed as A1 species in the dataset, $N = 47$) from this analysis because they are poorly studied (this leaves 298 stygobites and 708 troglobites distributed across 538 counties). Because the distribution of stygobites and troglobites per county is similar to the range size distributions of most other organisms in being skewed right (Gaston 1998) (skewness statistic after log transformation = 1.67), I employed non-parametric Mann-Whitney U test. Stygobite species occur in more counties than troglobites (Stygobite Mean = 4, Std. Error = 0, $N = 298$, Range = 44; Troglobite Mean = 3, Std. Error = 0, $N = 708$, Range = 82: overall Mann Whitney $U = 80189$, $Z = -6.781$, $P < 0.0001$). The number of counties in which a cave-limited species is present should approximate the relative range size of that species. This analysis confirms earlier assumptions (Christman & Culver 2001; Culver *et al.* 2000) that stygobites are more wide-ranging than troglobites.

The data set used in this study contains potential biases (Christman & Culver 2001; Culver *et al.* 2000), two of which are particularly relevant to the present study: differences in our knowledge of aquatic and terrestrial taxa, and variations in county size. Certain aquatic groups have not been subject to the same level of taxonomic rigor as troglobites. However, Culver *et al.* (2000) note that the percentages of major cavernicole groups are similar to those of other well-studied temperate regions (Juberthie & Decu 1994). Furthermore, the number of species described since 1960 and the number of range extensions (as measured by additional county records) is nearly equivalent for stygobites and troglobites (Culver *et al.* 2000). One clear problem noted by Culver *et al.* (2000) involves the Edwards Aquifer (Texas), which extends under multiple counties but can only be accessed at a single spring. However, if access to this aquifer were possible in all counties, it would only reinforce the present findings by extending the known ranges of stygobites.

Similarly, Christman and Culver (2001) demonstrate that there is no correlation between the size of county and number of cave species across the US as a whole. Florida and Texas counties that contain cave species are larger than their counterparts in other states (mean area of FL and TX counties = 1837 km², $N = 65$; mean of the rest of counties = 1467 km², $N = 569$) (county area data from ERSI 2000), though the difference is not significant ($df = 632$, t statistic = -1.117, $P = 0.264$). This is important because the Florida and Texas counties contain more stygobites relative to troglobites than any other region of the country (Culver *et al.* 2003). Not only are stygobites found in more counties than troglobites in these states, the counties tend to be larger as well. Because the analysis relies on number of counties in which each species is present to reflect relative range size, the difference between the range sizes of stygobites and troglobites is likely under-represented.

Several possibilities have been put forward about why stygobites are more widespread than troglobites. Holsinger (2000) notes the tiny size of some stygobites as a trait that allows them to be unusually good dispersers. While discussing the larger numbers of endemic troglobites, Culver *et al.* (2000)

suggest that the greater degree of aquatic habitat “in the vertical extent” of caves probably indicates more connectivity between aquatic habitats in caves. Similarly, Christman and Culver (2001) state that there are more connections between aquatic habitats because caves form at or below the water table.

The climate of most caves is exceptionally stable (Poulson & White 1969). One aspect of the subterranean environment that does change is the variation in water volume, especially during floods. Unlike above ground streams, cave streams cannot overflow their banks and release flood waters across a floodplain. Instead, caves have relatively extreme increases in water depth during major flood events (White *et al.* 1995). During high water periods flooded passages should allow aquatic dispersal, while there may be no equivalent opportunity for terrestrial species to disperse. This simple characterization of added opportunities for dispersal is no different than earlier statements about the aquatic habitat being greater in extent, but it raises the possibility that the dispersal advantage stygobites have over troglobites might extend above the normal water table.

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