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Environmental Factors Affecting the Geographical Distribution of Two Ecologically Equivalent Termite Species in Arizona

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ABSTRACT: Records of *Heterotermes aureus* (Snyder) and *Reticulitermes tibialis* Banks in the insect collecion of the University of Arizona were used to plot precisely their distributions in Arizona. Seasonal and annual mean air temperature and precipitation for each locality were plotted to illustrate environmental limits of the two species. *Heterotermes* occurs in desert and desert grasslands below 1220 m while *Reticulitermes* generally occurs in grassland, oak-piñon-juniper associations and coniferous forests above 1140 m. The distribution of *H. aureus* is limited by the lower temperatures and higher elevations in the northern part of the state, whereas *R. tibialis* is limited by the low moisture and high temperatures of the lower deserts. *Reticulitermes* may invade areas occupied by *Heterotermes* under suitable moisture and temperature conditions provided by urban and riparian situations.

Borrowing an approach from some innovative plant geographers, we have tried to explain the geographical distributions of *Heterotermes aureus* (Snyder) and *Reticulitermes tibialis* Banks in Arizona as resultants of interacting environmental parameters. The distributions of most termites are very imperfectly known from widely scattered collections, often from undocumented, parochial lists. Revisions, such as Ruelle's (1970) on *Macrotermes*, which include accurately designated localities and accompanying information on rainfall and vegetation are exceptional. The preliminary review of the termite genera in South West Africa by Coaton and Sheasby (1972) provides a basis for specific distributional analyses in the form of maps of the collecting districts, average annual rainfall, elevation and vegetation types, together with descriptions and photographs of the latter. Dealing with the termites of the western United States, Kofoid (1934) contributed one of the few discussions of the effects of climatic factors on their local occurrence and geographical distribution. In this highly speculative area, Williams (1934) stands out for having presented experimental evidence toward a partial explanation for the distribution of two species of *Reticulitermes*.

Termite colonies—indeed, perhaps the colonies of most typical social insects—have many characteristics in common with perennial plants. Colonies are generally stationary although they may grow and occupy variable territories. Dispersal is seasonal, local and usually accomplished by winged reproductive members of the colony. Large numbers of these alates may be produced, but relatively few survive to

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found new colonies. The resulting dispersion of colonies is thus dependent, as it is with plants, on a variety of factors such as predation on alates or incipient colonies, rather specific substrate and environmental requirements, and prior occupation of suitable nesting sites by the same or similar species. This provides a trial-and-error method for testing new localities as to their suitability for colonization.

A publication by Hastings *et al.* (1972) on plant distributions in the Sonoran Desert, and discussions with the late Dr. J. Rodney Hastings (Institute of Atmospheric Physics, University of Arizona) suggested that a similar approach might be used to describe the distributions of the termites in this region. Many of the approximately 40 species in the United States are now sufficiently well collected to invite analysis of environmental factors which might affect their distributions on a limited geographical basis. The large number of termite species, the diversity of climatic conditions and resulting vegetation types in Arizona combine to provide an ideal situation for this sort of ecological evaluation.

A pair of ecological equivalents, *H. aureus* and *R. tibialis,* served as subjects for a first assessment of the method. In general, *Heterotermes* is a circumtropical genus whereas *Reticulitermes* is Holarctic. Their distributions are mutually exclusive with the exception of the xeric regions of temperate Mexico and southwestern United States (Emerson, 1971).

Heterotermes aureus is the only truly Nearctic species of the genus. It occurs in the desert areas of southeastern California, southwestern Arizona, along the eastern coast of Baja California, and on the mainland of Mexico in the states of Sonora and Sinaloa. *Reticulitermes tibialis* has an extensive range through continental North Amtrica. It occurs in the inland valleys and desert areas of California, through the Great Basin and the Great Plains, northward into Montana and eastward to Indiana. It ranges throughout the southwestern deserts of the United States and extends southward to the tip of Baja California and onto the central plateau of Mexico.

On the margins of the deserts in California and Arizona, the ranges of the two species overlap, but neither intrudes far into the territory of the other. According to Kofoid (1934), in California the westward advance of *H. aureus* is checked by the lower temperature of the coastal belt, and the eastward advance of *R. tibialis* by the low humidity of the desert. We have chosen to validate his hypothesis with the data available for Arizona, the area of greatest contact between these two species in the United States.

METHODS AND MATERIALS

Specimens in the insect collection, Department of Entomology, University of Arizona, provided locality records (29 for *H. aureus* and 67 for *R. tibialis*) for plotting their distributions on an Arizona map showing vegetation types. Relationships were next sought between these distributions and temperature and precipitation. Using extensive weather station data, J. R. Hastings (pers. comm., 1973) has developed sets of equations for calculating mean air temperature and total precipitation for each of the four seasons (December through February = winter) in various regression regions. The equations require only latitude, longitude (to nearest 0.1°) and elevation (to nearest m) for generating these data for any locality in the Sonoran and Chihuahuan deserts and adjacent areas. We have supplied the coordinates and elevation for our termite collections, and Hastings has obligingly processed the data and generated CALCOMP Plotter graphs of seasonal mean temperature vs. precipitation for all points of occurrence of each termite species. Graphs of annual mean temperature vs. total annual precipitation and latitude vs. elevation were drawn from summarized results and data input.

Results

Heterotermes is strikingly limited to desert and lower grassland areas in the S-central and southwestern parts of the state, while *Reticulitermes* occurs generally in grassland, oak-pinon-juniper associations, and coniferous forests in the remainder of the state (Fig. 1). Figure 2 shows that *H. aureus* is limited to the southern portion of the state, roughly below 34° in latitude. Near the northern limit of its range (above 33° N Lat.) it probably does not occur above 800 m. At the southern border of the state, this species may occur at elevations up to 1220 m.

Reticulitermes occurs throughout Arizona, generally above 1000 m. We suspect that its "atypical" occurrence at three locations (Yuma, Fort McDowell and Tucson) may result from a particularly favorable combination of microclimatic factors (mainly lower soil temperatures and higher soil moisture) found in urban or riparian situations.

A more striking separation of their distributions appears when mean air temperature and total precipitation for all well-documented collection sites are plotted, as in Figure 3. The extremes of these two factors, seasonal and annual, are summarized and compared in Table 1. The mean annual temperature limits for the two species overlap by only 0.5 C, although there is a maximum overlap of 1.43 C during the summer. In Arizona, *H. aureus* tolerates total annual precipitation as low as 78.6 mm (Yuma), while the comparable low for *R. tibialis* is 196.6 mm, albeit at higher latitude and elevation where temperature is lower (Canyon del Muerto, near Canyon de Chelly). For all seasons, overlap in precipitation is considerable, with *H. aureus* usually favoring the lower and *R. tibialis* the upper extremes.

Discussion

At first glance, the results of the temperature vs. precipitation plot (Fig. 3) suggest that temperature is the most critical environmental parameter limiting the distribution of these two species. However, this underemphasizes the considerable importance of moisture as a limiting factor.

Reticulitermes tibialis is much more susceptible to desiccation than *H. aureus.* Collins (1969) has shown that *R. tibialis* loses water from its body surface at a rate of 1.14 mg/cm^2/hr while *H. aureus* loses only 0.11 mg/cm^2/hr (both at 34 C, 0-4% RH). In terms of survival time during the drying, *R. tibialis* is the most desiccation-tolerant of the North American *Reticulitermes* (Collins, 1969), and has a great resistance to high temperatures (Becker, 1970). With this in mind, it would appear that the distribution of *R. tibialis* is much more dependent on moisture than that of *H. aureus.* How, then, is *R. tibialis* able to tolerate such wide variation in *precipitation* over its range in Arizona, for example?

Both of these termites are subterranean and obtain most of their

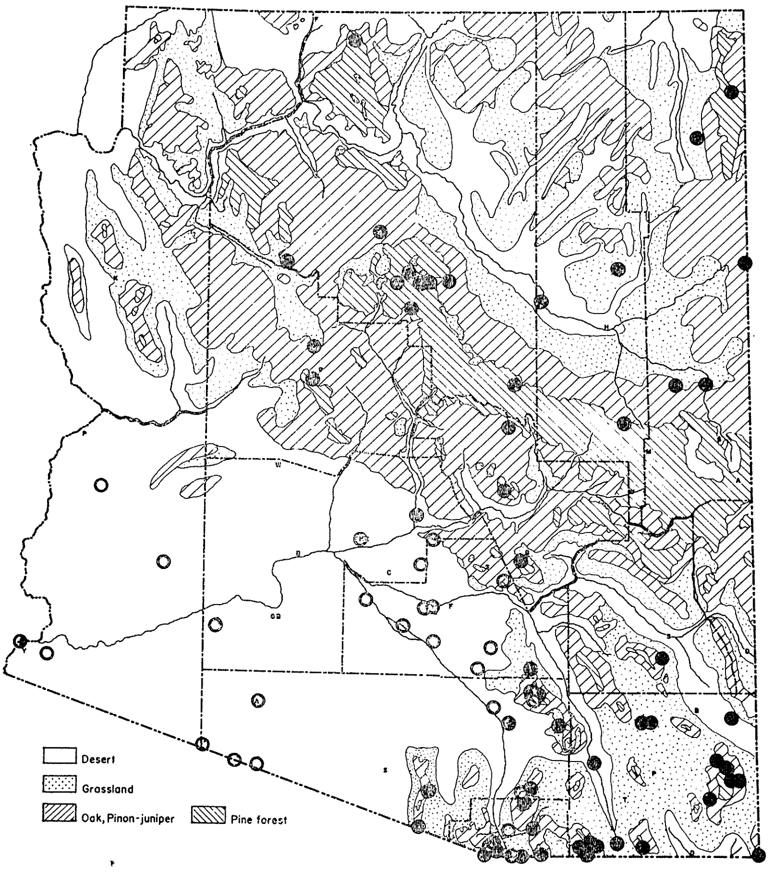

Fig. 1.—Distribution of *Heterotermes aureus* (o) and *Reticulitermes tibialis* (●) with respect to the four major vegetation types in Arizona. Half-filled circles represent overlapping collection records

water from the soil and the wood they eat. Soil receives water in one or more of four ways: from precipitation, dew, surface and subsurface drainage. Their relative importance varies according to local conditions (Williams, 1934). Precipitation in Arizona varies widely, especially from E to W, but the total amount may be less important than other factors. The amount of precipitation penetrating the soil depends mainly on slope of the land, structure of the soil, seasonal distribution of precipitation and amount and kind of cover. A steep slope obviously retains less water than level ground. Surface drainage is less from coarse, sandy soils than from fine soils. Winter rains are more effective in moistening soil because of lower evaporation associated with lower temperatures. An equivalent amount of water in the form of snow is more effective than rain because melted snow has longer to percolate into the soil. In arid regions, the small amounts of rain are more effective if they are concentrated into a few heavy, rather than several light, showers, because the latter evaporate more rapidly. Rain falling on

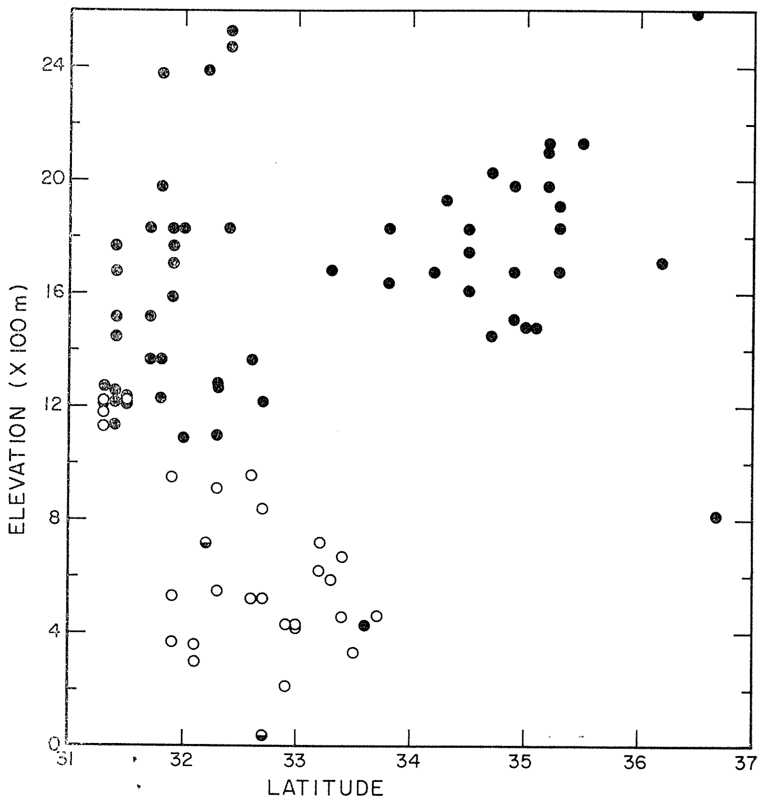

Fig. 2.—Latitude and elevation for each collection locality of *Heterotermes aureus* (o) and *Reticulitermes tibialis* (●) in Arizona

barren deserts is more subject to evaporation from sun and wind, or to loss from runoff, than rain falling on denser cover where more water finds its way into the soil.

Water which has been rather uniformly distributed during rainfall may become concentrated along certain courses by surface drainage. Of still greater importance, especially in arid regions bounded by mountains, is the fact that, by surface drainage, a generous supply of water reaches areas which receive rain only occasionally. In large

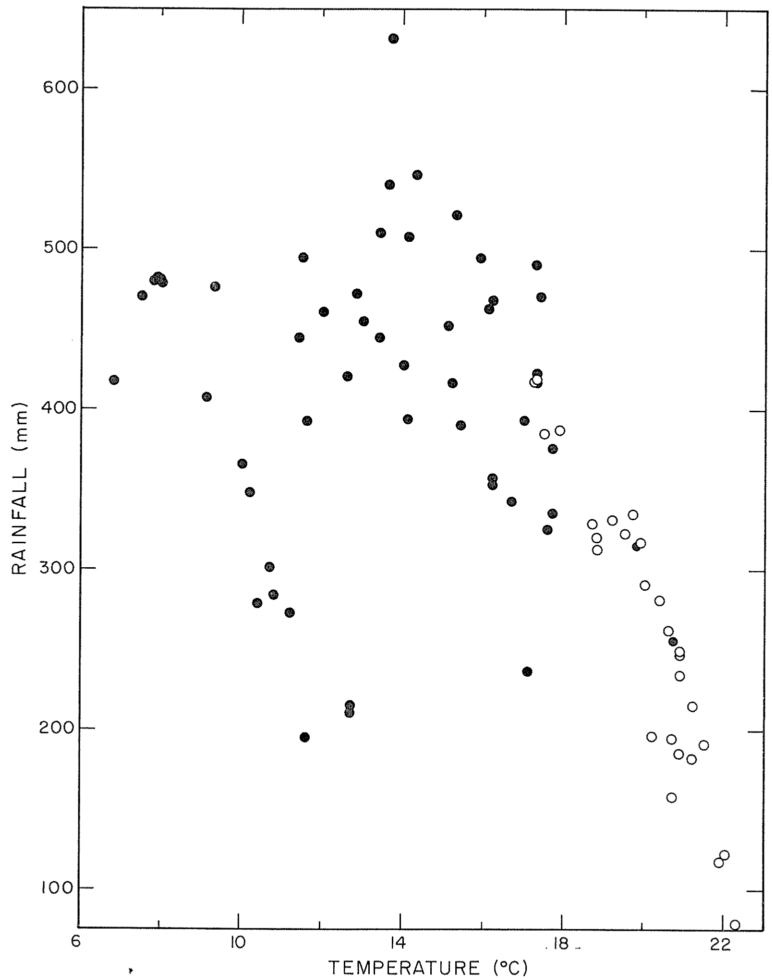

Fig. 3.—Mean annual temperature and total precipitation for each collection locality of *Heterotermes aureus* (o) and *Reticulitermes tibialis* (●) in Arizona

desert washes, subsoil drainage forms a constant source of water, even during the hot, dry summer months. Water distributed by subsoil drainage may be available to subterranean termites.

The weather parameters considered in our presentation are macroclimatic and do not reflect the variation in the microclimate where the termites were actually collected. What they do emphasize, however, is the inseparability of temperature and precipitation as factors limiting the local occurrence and geographic distributions of termites. *H. aureus* occupies areas of rather high temperature and is apparently limited by low rather than high temperature (Fig. 3). It also seems to be sufficiently desiccation-tolerant (Collins, 1969) that it may inhabit some of the hottest and driest desert areas of Arizona.

On the other hand, *R. tibialis* is nearly as high-temperature tolerant as *H. aureus* (Becker, 1970; Haverty, 1974) but requires more moisture because of its more permeable cuticle (Collins, 1969). It typically occurs in areas of lower annual temperatures and somewhat higher rainfall or where the winter precipitation is likely to be in the form of snow, conditions insuring a higher soil moisture content. Therefore, wherever it invades desert habitats, it does so only where suitable moisture conditions prevail.

The results of our analysis corroborate the observations of previous authors. The distributions of these two species in Arizona are closely paralleled by conditions in southern California where Kofoid (1934) found that the westward advance of *H. aureus* is limited by the lower temperatures of the coastal belt, while eastward progress of *R. tibialis* is limited not only by the low moisture but also by the high temperatures of the lower deserts. *Reticulitermes* may invade the areas occupied by *Heterotermes* under suitable moisture and temperature condi-

TABLE 1.—Long-term seasonal and yearly extremes of environmental parameters at documented collection sites of *Reticulitermes tibialis* and *Heterotermes aureus* in Arizona. Data for Yuma, Ft. McDowell and Tucson omitted, since these sites probably present combinations of microclimatic factors favorable to both species

Limits of	Collection site data for *R. tibialis*		*H. aureus*	
$\bar{X}$ Temperature C	Low	High	Low	High
winter	—2.74	10.13	9.42	13.09
spring	5.01	17.15	16.21	21.27
summer	16.89	26.97	25.54	31.93
autumn	8.02	18.49	17.65	23.28
annual	6.80	17.71	17.21	22.37
Total precipitation mm				
winter	36.8	175.3	24.6	103.6
spring	25.1	87.7	7.7	51.8
summer	70.3	273.5	21.6	218.6
autumn	52.3	129.0	20.3	77.3
annual	196.6	631.8	78.6	418.7

tions provided by urban and riparian situations. Our study substantiates Emerson's (1955) earlier conclusion that temperature and moisture are the major physical factors limiting the dispersal, and hence the distribution patterns, of termites.

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