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Habitat Segregation Among European Tree-hole Mosquitoes

Bark-lined cavities and rot holes in deciduous trees may hold water and harbor mosquitoes specific to that habitat. In north-central France and southern Britain—where tree holes experience an even rainfall pattern throughout the year, contain a variety of mosquitoes, and lack predators—competition should be especially important.

*Mosquito species found here occupy distinct subhabitats characterized by the exposure, size, and orientation of the hole and by the pH, conductivity, and tannin–lignin content of the contained water. At the same time, each species encounters a higher density of its own species than all other species combined. Among mosquitoes, weight at pupation is both an excellent predictor of future lifetime fecundity and a highly sensitive index of food level during prior larval development. Pupae of field-collected *Anopheles plumbeus* and *Aedes geniculatus* in north-central France and southern Britain weigh less than pupae of these same species grown at field temperatures but with abundant food in the laboratory. These results indicate that, as larvae, mosquitoes in the field encounter severe resource depletion so that, regardless of the mechanism by which habitat segregation has evolved, intraspecific competition persists within segregated subhabitats.*

Ever since Malthus and Darwin, competition has been envisioned to play a pivotal role in the process of community formation. Most theory over the last 20 years has emphasized competition as the major selective force affecting the number and coexistence of species in a community. Species may coexist only if they evolve subhabitat specializations and so avoid competing for the limiting resources (Cody 1968, Cody & Diamond 1975, MacArthur & Levins 1967, Schoener 1974). Competition might well be all the more acute in restricted habitats where inhabitants are forced to deal with one another at close quarters and where outside interference is minimal.

Of the various restricted habitats, water-filled tree holes are ubiquitous to all latitudes where hardwood trees occur from the equator to the subarctic. Tree holes form when a rotting cavity penetrates into the heartwood (rot holes), when branches grow together at a crotch, or when buttress roots are completely lined with bark (pan holes, sensu Kitching 1971). When these holes contain water, they almost invariably serve as the exclusive preadult habitat for a variety of mosquitoes. In southeastern North America, predators and periodic drought reduce tree-hole mosquito populations to levels at which resources are no longer limiting and mosquitoes do not compete within or between species



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(Bradshaw & Holzapfel 1983). In northern France and southern Britain, several species are known to breed exclusively in tree holes. Individuals of two or more species may co-inhabit the same holes (Fallis & Snow 1983, Hedeon 1958, Keilin 1927, Marshall 1938, Yates 1979) at latitudes where rainfall is relatively uniform throughout the year (Bickmore & Shaw 1963, Steinhauser 1970) and the mosquitoes encounter no larval or pupal predators (Kitching 1971, Rohnert 1950).

This article addresses the following questions regarding a relatively uniform environment and in the absence of predation:

- Do European tree-hole mosquitoes exhibit habitat segregation and so encounter a higher density of their own than of other species?
- Is habitat segregation associated with specific tree-hole properties or are mosquito subcommunities patterned without regard to tree-hole types?
- Do European tree-hole mosquitoes experience resource-limited pre-adult development that indicates competition for larval resources?

Methods

Tree holes were sampled from Montpellier (43.5°N) in southern France to the Loire Valley (47.5°N) in north-central France and then in southern Britain (51.5°N) (Figure 1). The sampling period was from 21 July to 17 August 1984, when all of the European tree-hole mosquitoes should have been developing and producing pupae (Fallis & Snow 1983, Service 1968, Yates 1979). The following measurements were recorded for each hole: water temperature, height above ground, circumference of the tree at the lip of the hole, area (length times width) of the opening, angle of the opening with the horizontal plane, and whether it was a rot hole or a pan hole (Kitching 1971).

The entire content of the hole was then siphoned and its volume measured. All the mosquitoes contained therein were staged according to instar and counted. From a sample of the water, the following properties were determined: pH to the nearest 0.3 unit using pHydrion controls paper (Micro Essential Laboratory), conductivity using a Markson portable field colorimeter, and tannin–lignin content using a scaled-down Hach tannin–lignin test kit expressed as OD₆₁₀ on the Markson colorimeter after blanking with a reagent-free sample of tree-hole water. When optical density readings for full-strength tree-hole water exceeded 1.0, readings became nonlinear; consequently, darker samples were diluted, after which OD₄₆₀ or tannin–lignin content was determined from the diluted samples and then corrected for dilution. Samples of the four larval instars and all pupae of each species were preserved in 70% isopropanol. Depending upon capture date, mosquitoes remained in alcohol for three to four months. Upon arrival at the lab, individual fourth instars and pupae were dried over a desiccant, Dryerite, and weighed to the nearest 0.1 mg. Biomass of mosquitoes in each tree hole was estimated by adding actual pupal dry weights to cumulative larval dry weights extrapolated from fourth instar dry weights (methods, Bradshaw 1983).

As a basis for comparison with field-collected pupae, a fresh sample of *Aedes geniculatus* and *Anopheles plumbeus* was obtained from Windsor Park in November 1984. To determine the effect of instar of field collection on pupal weight in the lab, 10 first, 15 second, 50 third, and 30 fourth instars of *A. geniculatus* were reared at densities of five larvae per 100-mm petri dish. Each petri dish contained 50 mL of diluted British (Windsor Park) tree-hole water with food (equal parts by volume

of ground guinea pig chow and freeze-dried brine shrimp) provided ad libitum (i.e., as much food as could be provided every 48 hours without clouding the water or accumulating fungus) at 16.5°C and long-day photoperiod (light to dark = 18:6). To determine the effect of temperature of rearing on pupal weight in the lab, field-collected third instars of *A. geniculatus* were reared, 10 per dish, as above at 7, 12, 17, and 22°C (n = 10 larvae per temperature). To determine the effect of reduced resources on pupal weight, field-collected third instars of *A. geniculatus* were reared, 10 per dish, as above but with food provided ad libitum or 100, 50, 25, or 13 mg per dish (n = 10 larvae for ad libitum, 20 larvae at other food levels).

To determine the relationship between wet and dry weight in *A. plumbeus*, 20 third instars from Windsor Park were reared with food ad libitum at 16.5°C and long-day photoperiod (light to dark = 18:6). They were maintained in individual 15-mL chambers, because field observations indicated that they may be cannibalistic. Resultant pupae were sexed, weighed, and preserved in 70% isopropanol for four months after which time they were dried over Dryerite in a desiccator until pupal weights did not change over two weighings. Dry weight to the nearest 0.01 mg was then determined using a Mettler microgram balance. To determine the relationship between wet and dry weights in *A. geniculatus*, the pupae from experiments were sexed, weighed wet, preserved for four months in 70% isopropanol, and then dried and weighed again.

Indicators of competition relate more to the density of potential competitors than to their total abundance. Therefore, densities were compared within and among species using Lloyd's (1967) indices of mean intra- and interspecific crowding per unit resource (Hurlbert 1978, Rathcke 1976), in this case, tree-hole volume. Lloyd's indices are especially tractable for discrete habitats and are readily interpretable as the mean number of species "y" encountered per liter of tree-hole volume by the average individual of species "x." If x_i and y_i are the number of individuals of species x and y, respectively, in the i th hole and v_i is the actual volume of water in that hole, then mean interspecific crowding of x by y is given by

$$\frac{\sum \left(\frac{x_i y_i}{v_i} \right)}{\sum x_i}$$

and mean intraspecific crowding by the same formula but substituting $(x_i - 1)$ for y_i .

Routine statistical analyses followed Steel & Torrie (1980) except for canonical correlation analysis (part of the SPSS statistical package on the University of Oregon DEC 1091 computer). All analyses of variance (ANOVA) were carried out only after Bartlett's test indicated no significant heterogeneity among sample variances. Where ANOVA indicated significant differences among means, the individual means were distinguished by Duncan's new multiple range test.

Results

Tree-hole Locations

Montpellier

Despite the extremely dry conditions along the Mediterranean coast in the summer, five wet holes were located with the aid of J. A. Rioux, University of Montpellier. All holes were in pruned or pollard plane trees

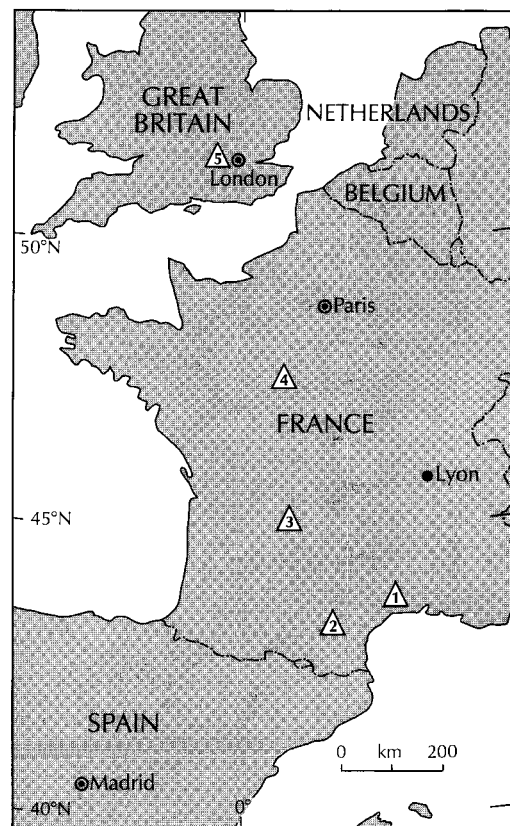


Figure 1. Collecting sites: 1, Montpellier; 2, Parc Naturel Régional du Haute Languedoc; 3, Forêt de Pompadour and Brive la Gaillarde; 4, Loire Valley; 5, Burnham Beeches, Windsor Great Park, and Silwood Park.

(*Platanus acerifolia* Willd.). Three holes contained less than 0.3 L of water and no mosquitoes. One, about 25 L in volume, contained *Orthopodomyia pulchripalpis* (Rondani), *Anopheles plumbeus* Stephens, and *Aedes berlandi* Séguy. The last hole (Figure 2) contained 38 L of water; from a 7-L subsample, the hole was estimated to be occupied by 103 *A. plumbeus*, 12 444 *O. pulchripalpis*, and no *Aedes*. Neither hole contained any *A. geniculatus*; this species occupies more ephemeral holes and is abundant in the late winter and spring (J. A. Rioux, personal communication). Physically and chemically, the large hole at Montpellier was very similar to North American holes that harbored the *Orthopodomyia*–*Anopheles*–*Toxorhynchites* subcommunity (Bradshaw & Holzapfel 1983, 1985): It was a large, permanent hole with a large opening and darkly stained, tannin- and lignin-rich, highly conductive water. However, mosquito density at Montpellier is much higher than in southeastern North America due primarily to the high density of *Orthopodomyia* (about 327/L in Montpellier versus 45/L in southeastern North America).



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Figure 2. A large (38 L) tree hole near Montpellier, France, with darkly stained water; a characteristic habitat of *Orthopodomyia pulchripalpis*.

Southern and Central France

The search for tree holes continued northward and concentrated in two areas, the Parc Naturel Régional du Haute Languedoc south of Castres (43.5°N, 2.5°E) and the Forêt de Pompadour south of Limoges (45.5°N, 1.5°E). Despite several days of searching, only one wet tree hole was found. Both localities and many intermediate woodlots either had been consistently and recently logged or contained primarily smaller, younger trees. The one hole that was located was in a beech tree (*Fagus sylvatica* L.) in the woods surrounding an old manor house near Brive la Gaillarde (45.2°N, 1.5°E). This 1.3-L rot hole was occupied by both *A. geniculatus* (175) and *A. plumbeus* (19) in darkly stained, tannin- and lignin-rich, highly conductive water.

Loire Valley

In the Loire Valley, the forests illustrated on the topographic maps of the area and those suggested by local naturalists were searched. Again, small trees or stump sprouts were found. However, in the communal forests near Blois (48.5°N, 1.5°E), a stand of more mature trees was located; it consisted mainly of oak (*Quercus petraea* [Mattuschka] Liebl.), beech, and maple (*Acer campestre* L.). The beech trees contained a variety of holes. Of the 24 wet holes, 22 harbored mosquitoes, all *A. geniculatus* and *A. plumbeus* except for one *O. pulchripalpis* pupa.

Britain

In southern England (51.5°N, 0.5°W) several substantial stands of hardwoods were located. Burnham Beeches north of Slough contained primarily beech trees of mixed ages including 300-year-old and older pollard beeches with large central cavities. However, of the 50 pollard beeches inspected, the central wells were either dry or filled to the rim with detritus. Trees of more intermediate age yielded eight holes, six of which harbored mosquitoes. Windsor Great Park and Silwood Park near Ascot contained many mature hardwood trees which contained 20 wet holes (17 beech, 1 oak *Q. petraea*, 1 horse chestnut *Aesculus hippocastaneum* L., and 1 tree of heaven *Ailanthus altissima* [Mill]). All of the wet holes without mosquitoes were in beech trees. Holes at all three localities harbored *A. plumbeus*, *A. geniculatus*, and/or *Culex torrentium* Martini.

The holes in Britain and the Loire Valley were sufficiently similar in

their physical, chemical, and faunal attributes, and in climatic zone (Steinhauser 1970) that they were lumped into a single data set. Of the 54 combined wet holes, 29 were rot holes (Figure 3) and 25 were pan holes. The latter included 21 buttress holes (Figure 4) and four crotch holes, all in beech trees. Thus, holes in these two general areas were located primarily in beech trees, were evenly divided between rot and buttress holes, and had a mosquito occupancy rate of about 85%.

Habitat Segregation

Of the four species encountered in north-central France and southern Britain, *O. pulchripalpis* was represented by a single pupa while *A. geniculatus*, *A. plumbeus*, and *C. torrentium* were abundant. Among the latter three species, mean intraspecific crowding (Figure 5) ranged from 60.0 to 144.4/L; by contrast, interspecific crowding ranged from 0.7 to 23.9/L. Of all mosquitoes found, intraspecific encounters ranged from 60 to 97%. These results show that tree-hole mosquitoes in north-central France and southern Britain experience higher densities of their own than of other species.

In order to determine if habitat segregation was occurring among the three principal European species, the relationships between mosquito subcommunities and particular tree-hole properties were studied. From the 54 tree holes, number ($r = 0.029$) or biomass ($r = -0.021$) of all mosquitoes combined did not correlate significantly with tree-hole volume. Likewise, volume was not a significant predictor of number or biomass of the individual species: *A. geniculatus* ($r_{\text{num}} = -0.064$; $r_{\text{bm}} = -0.020$), *A. plumbeus* ($r_{\text{num}} = 0.024$; $r_{\text{bm}} = -0.023$), *C. torrentium* ($r_{\text{num}} = 0.37$; $r_{\text{bm}} = 0.015$).

Numbers of individuals can be misleading because the presence of a few pupae represents more biomass, as well as developmental success, than a much larger number of first instars. Consequently, to look at the association among mosquito species and the physical and chemical attributes of tree holes they occupy, biomass was corrected for volume as the measure of each species. Linear correlations among tree-hole attributes and mosquito biomasses yielded an unwieldy correlation matrix and exhibited many confusing intercorrelations among both dependent (mosquitoes) and independent (tree-hole attributes) variables.

Canonical correlation analysis allows extraction of features that mosquito subcommunities have in common and correlation of them with the corresponding tree-hole attributes that distinguish this subcommunity. Canonical correlation analysis derives a linear combination from each of the sets of variables (mosquitoes or tree-hole attributes) in such a way that the correlation between the two linear combinations is maximized. Out of the residual variation in both sets, canonical correlation next derives a pair of factors that are again maximally correlated but subject to the restriction that they must be uncorrelated with the first pair of factors. This procedure is repeated until no more significant canonical correlations can be derived.

Canonical correlation of mosquito biomass with physical and chemical properties of the combined tree holes in north-central France (Blois) and southern Britain resulted in two significant canonical variates (Figure 6). The first canonical variate was negatively correlated with biomass of *Aedes* and *Culex* but not significantly correlated with *Anopheles* biomass. The first canonical variate is thus a measure of *Aedes*-*Culex* co-occurrence independently of *Anopheles*. This same variate was negatively correlated with circumference of the tree and area of the tree-hole opening and positively correlated with angle of the opening and dark-



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Figure 3. A smaller (1.3 L) rot hole near Brive la Gaillarde, France, with darkly stained water; a characteristic habitat of *Anopheles plumbeus* and *Aedes geniculatus*.

ness (OD_{460}) of the water. The second canonical variate was negatively correlated with *Aedes* and *Anopheles* biomass but positively correlated with *Culex* biomass. This variate was positively correlated with circumference of the tree and negatively correlated with angle of the opening, and conductivity and pH of the water.

Resource-dependent Development

At the time of each tree-hole census in Europe, the temperature of the water was taken. The time of measurement spanned early morning to late afternoon with the latter times predominating. In general, daytime tree-hole temperature was lower in Britain than in France: In Britain it ranged from 13 to 17°C (mean, 13.5°) and in northern France it ranged from 15 to 17°C (mean, 16.2°).

To establish laboratory weights for comparison with field weights, *A.*



Figure 4. A pan (buttress) hole near Windsor, England, with clear water; a characteristic habitat of *Aedes geniculatus* and *Culex torrentium*. The scale shows 1-cm black and white bars.

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geniculatus and *A. plumbeus* were reared at 17°C from field-caught third instars to the pupal stage, preserved in isopropanol for four months, dried, and weighed. Since lab pupal weights were determined at the highest temperature observed in the field at the warmest time of the year and from pupae preserved as long or longer than field-collected pupae, lab-reared pupae should, if anything, be biased toward lighter pupae. Nonetheless, to account for other sources of variation in pupal weight, three comparisons were made in *A. geniculatus*: effect of instar at which the larvae were collected in the field and started on lab conditions; effect of rearing temperature on field-collected third instars; and effect of reduced resources on field-collected third instars.

Figure 7 shows the results of these control experiments. Males were consistently lighter than females. Consequently, the effects of treatments were compared separately for each sex. Stage of capture had a significant effect on male pupal weight (ANOVA: $F_{3,58} = 4.32, p < 0.01$) but not female pupal weight (ANOVA: $F_{3,40} = 2.21, p > 0.05$) (Figure 7A). Among the males, pupal weight increased with stage of field collection but third instars did not produce significantly heavier pupae than second or fourth instars ($p > 0.05$). Rearing temperature of field-caught third instars (Figure 7B) had a significant effect on females (ANOVA:

$F_{3,11} = 6.69, p < 0.01$) but not males (ANOVA: $F_{3,18} = 2.46, p > 0.05$). Among the females, pupae reared at 22°C were lighter than at 7 or 17°C ($p < 0.01$) but pupae reared at 7, 12, or 17°C did not differ from one another ($p > 0.05$). Food level did have a significant and substantial effect on the weights (Figure 7C) and on pupation success (Figure 7D) of both males (ANOVA: $F_{2,28} = 66.73, p < 0.001$) and females (ANOVA: $F_{2,10} = 22.71, p < 0.001$). In both cases, pupal weight declined consistently with lower food levels.

For both *A. geniculatus* and *A. plumbeus*, fresh wet weight was closely correlated with dry weight after four months' preservation in isopropanol (Figure 8). Analysis of covariance for regressions of male and female pupae revealed homogeneity of regression coefficients (*Aedes*: $F_{1,48} = 0.38, p > 0.05$; *Anopheles*: $F_{1,6} = 1.77, p > 0.05$) and no significant differences between adjusted means (*Aedes*: $F_{1,49} = 0.12, p > 0.05$;

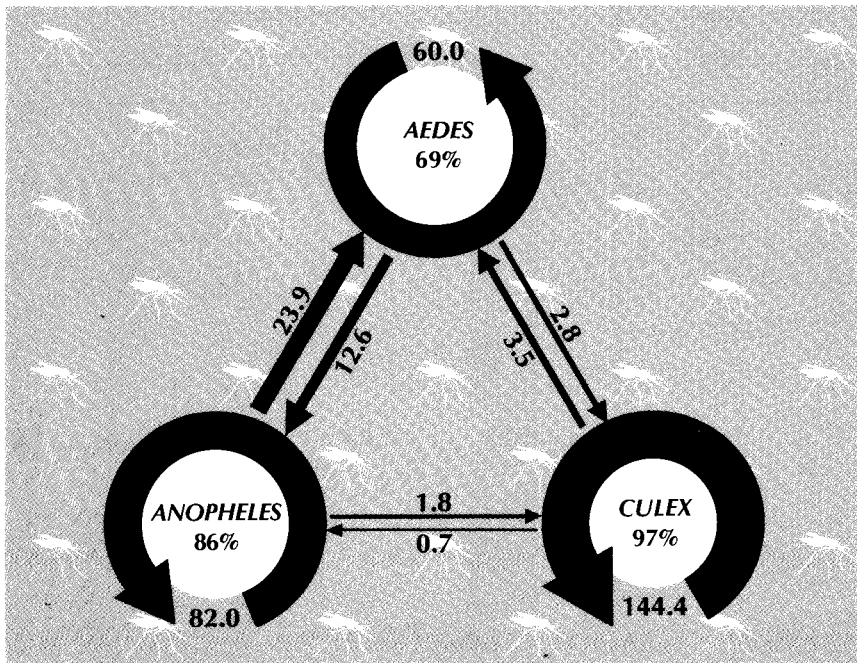


Figure 5. Mean intra- and interspecific encounter per liter of tree-hole mosquitoes near Blois, France, and southern Britain combined. The number on the straight arrow indicates the mean crowding by the distant species on the species the arrow points to. Thickness of lines reflects relative values. For circular arrows the number between point and end indicates intraspecific crowding. The percentage is the proportion of individuals of a species encountered by members of its own species.

Anopheles: $F_{1,7} = 0.11, p > 0.05$). Consequently, the combined regression equations were used to estimate equivalent fresh wet weight of field-collected pupae:

fresh wet weight of *Aedes* = $0.61 + 6.33(\text{preserved dry weight})$

fresh wet weight of *Anopheles* = $0.83 + 4.64(\text{preserved dry weight})$

Figure 9 shows that for both *A. geniculatus* and *A. plumbeus*, pupae reared at 17°C on full rations in the lab were generally heavier than those collected from nature. Among field-collected *A. geniculatus*, 61% of male and 81% of female weights fell below the 95% confidence limits of respective lab-reared pupae. Further, some of the field-collected pupae of both sexes were lighter than the most nutritionally deprived individuals in the laboratory (Figure 7C). Among field-collected *A. plumbeus*, 44% of male and 77% of female weights fell below the 95% confidence limits of respective lab-reared pupae.

Discussion

Of the three species normally considered to be tree-hole dwellers, two were regularly encountered, *A. geniculatus* and *A. plumbeus*, while the

third, *O. pulchripalpis*, was found abundant only near Montpellier, France. *O. pulchripalpis* is usually found in large holes with brown water of high pH (Beattie & Howland 1929, Cambournac 1938, Fallis & Snow 1983, Macan & Tutin 1932, Shannon & Hadjinicolaou 1937). The tree hole at Montpellier had the largest volume, highest pH, and high intermediate optical density (OD_{460}) when compared with holes encountered in north-central France or southern Britain. Most of the trees encountered throughout this region were younger, smaller trees. Stands of predominantly mixed ages were infrequently encountered. These ob-

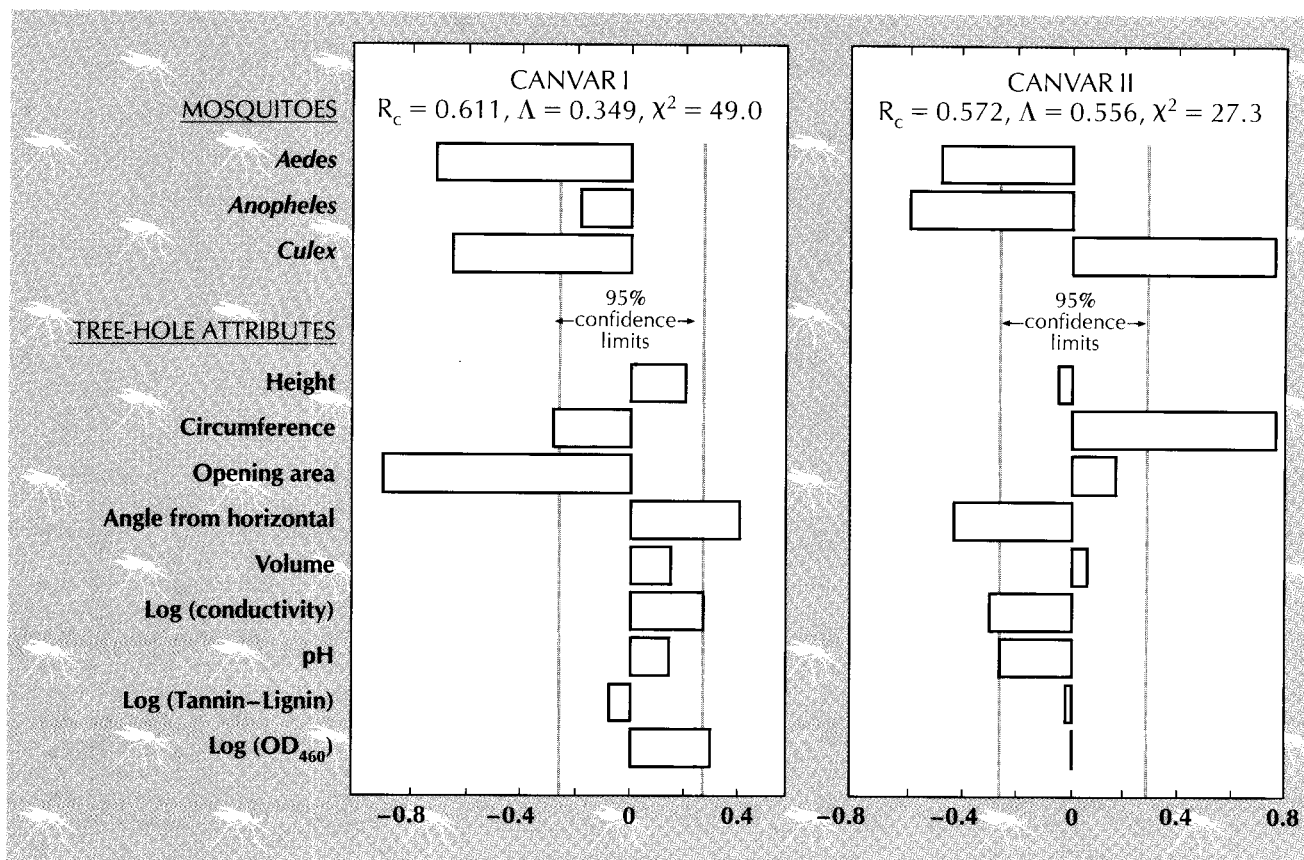


Figure 6. Canonical correlation between mosquitoes (top) and physical and chemical attributes of tree holes (bottom). The bar graphs plot the correlation coefficients between the first (Canvar I) or second (Canvar II) canonical variate and the original variables. The gray lines indicate the 95% confidence limits, so correlations, negative or positive, that lie outside these lines are significant ($p < 0.05$). Statistics provided are the canonical correlation coefficient (R_c), Wilk's lambda (Λ), and chi squared (χ^2) to test the significance of the correlation.

servations reflect those of Zauner (1981:4) who concluded that the European forests are artificially young:

Generally, they are not more than 150 years old, for, at that age, they have already attained the limit of economic marketability and are cut. It is otherwise among trees in sylviculture in gardens and parks and along roads and lanes which are not exploited. These trees may be planted but, as they are not intended for the production of wood, they have a chance to grow old. It is in such places that one finds 500-year-old beech and linden trees and oaks attaining a millennium.

Indeed, virtually all of the trees in which past investigators and the authors found *O. pulchripalpis* were located in parks or along roadways. The authors therefore believe that the infrequency with which *O. pulchripalpis* is encountered is due, not to its intrinsic scarcity, but to the low incidence of appropriate tree holes. The scarcity of appropriate tree holes is a direct consequence of human forest management practices.

Culex torrentium has not usually been considered a tree-hole mosquito; yet, if a *Culex* is found in tree holes, it is almost always *C. torrentium* and not its sibling species, *C. pipiens* L. (J. K. Waage, personal communication). Since *C. torrentium* was found in six of the 54 wet

holes, the authors consider it more than an incidental occupant of tree holes and have included it in the analyses of species interactions. All of the holes inhabited by *C. torrentium* extended well out from the trunk of the tree; much of their large surface area was exposed to the open, and they contained the clearest water (Figure 4). These qualitative observations are substantiated by the correlations between the first canonical variate and the physical and chemical properties of tree holes (Figure 6). Despite the abundance of *C. torrentium* in holes where they were found, no pupae of this species were found. Either the holes were sampled prior to their normal pupation time or tree holes represent a "dead end" habitat for *C. torrentium*. Buttress holes of the sort they frequent are superficially similar to small groundwater pools normally inhabited by *C. pipiens* (Marshall 1938). The occurrence of *C. torrentium* in tree holes could represent female response to conflicting oviposition cues as well as

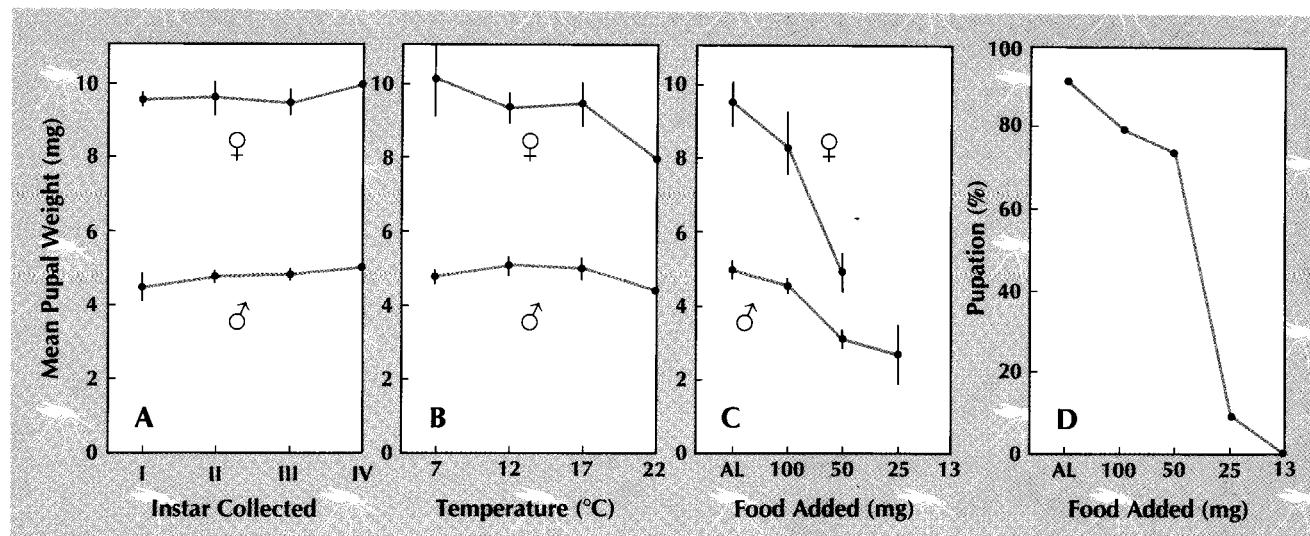


Figure 7. Control experiments in the laboratory to test the effects of various rearing conditions on developmental success and pupal weights: **A**, effect of instar of collection on pupal weight at 16.5°C; **B**, effect of rearing temperature on pupal weight; **C**, **D**, effect of food level on pupal weight and on percentage pupation (AL = ad libitum).

to adaptive exploitation of an extreme tree-hole habitat.

The correlation of mosquitoes and physical and chemical properties of tree holes with the second canonical variate (Figure 6) indicates that *A. geniculatus* and *A. plumbeus* are found without *C. torrentium* in holes that have vertical openings, hold water with high conductivity and pH, and occur in narrow trees; that is, rot holes (Figure 3) as opposed to buttress holes (Figure 4). Thus the two subcommunities are included among the holes sampled. The first subcommunity contains *A. geniculatus* and *C. torrentium* and is found primarily in large exposed buttress holes with clear water. The second subcommunity contains *A. geniculatus* and *A. plumbeus* and is found in rot holes and more cryptic buttress and crotch holes with more dissolved salts in the water. The literature cited above indicates a third subcommunity which contains *O. pulchripalpis* as well as *A. geniculatus* and *A. plumbeus*. This subcommunity is found in the largest rot holes (Figure 2) with the darkest water and highest level of dissolved salts and pH and, by implication from the authors' work in North America (unpublished), the most permanently wet of the holes. In the extreme situation along the Mediterranean coast, *A. geniculatus* is less frequent in the third subcommunity and tends to be replaced by *A. berlandi*. The borders of these subcommunities seem indistinct; the subcommunities occur in a continuum of tree-hole types, with mosquito species segregated along this continuum.

The question still remains as to the factors selecting for or maintaining the habitat segregation observed in northern France and southern Brit-

ain. Among mosquitoes, scarce resources leading to density-dependent constraints to growth and development result in slower development, lighter pupae, and increased preadult mortality. The factors most sensitive to resource deprivation are rate of development and pupal weight. Information derived from single censuses cannot be used to calculate developmental rate directly, but pupae are a direct, sensitive indication of resources available to developing larvae at a given temperature. Where food level and temperature have both been varied, food level is the most important predictor of pupal or adult weight (Nayar 1969). The authors therefore sought to compare pupal weights of field-collected individuals reared in the laboratory with abundant food and at field temperatures. A high degree of overlap in the weights of lab and field pupae would then indicate high resource levels in nature, while lighter field than lab pupae would indicate resource-limited development.

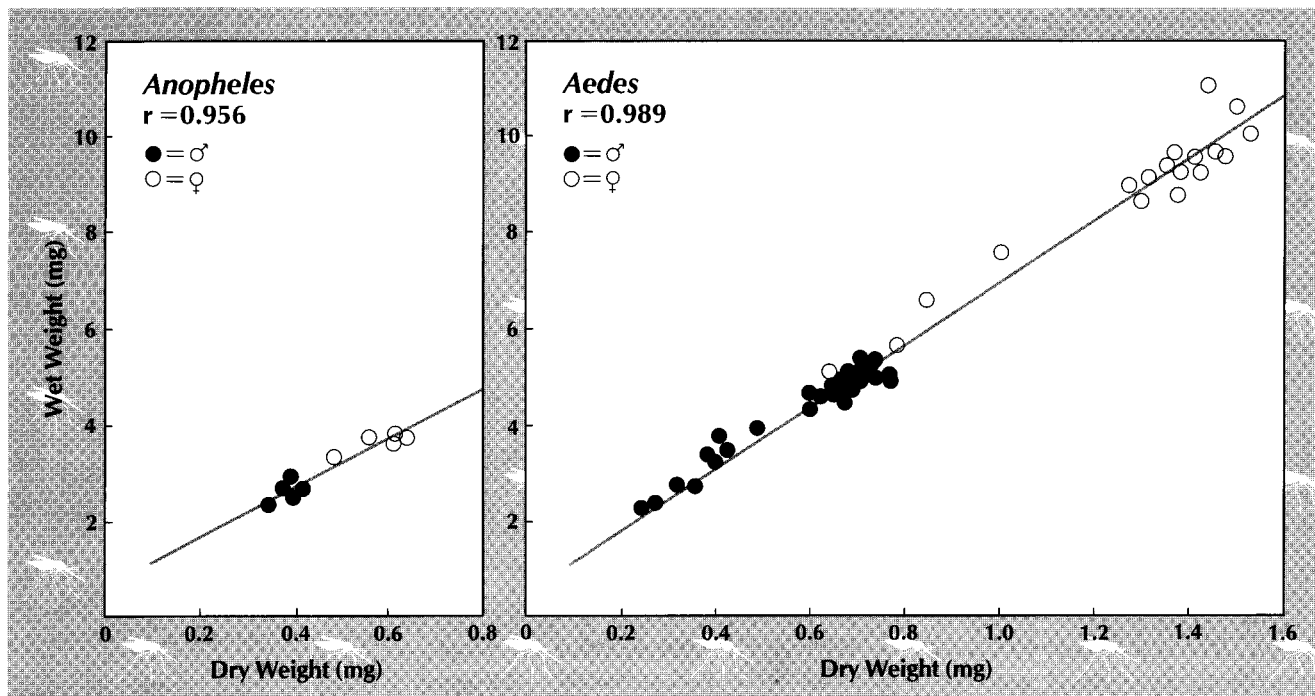


Figure 8. Correlation of original wet weights with dry weights of pupae preserved in 70% isopropanol for four months.

Results of these experiments (Figure 7) show that the stage at which larvae were captured had a slight effect on weight of male pupae only; temperatures within the range observed in northern France and southern Britain (13 to 17°C) had no effect on either male or female pupal weight; and food level had a profound effect on pupation success and pupal weight of both sexes. Therefore the weight used as the basis for comparison with pupae caught in the field was that of pupae captured as first through third instars and reared at 17°C on full rations.

Field-collected pupae generally weigh less than would be expected of the same species reared in the laboratory (Figure 9). This observation argues strongly that these mosquitoes are competing for limiting resources; but, the higher incidence of intraspecific relative to interspecific encounter (Figure 5) indicates that the mosquitoes are competing mainly among members of their own species rather than with others. However tempting it may be to ascribe the above patterns of habitat segregation to adaptive niche shifts as the result of ancestral competition, these patterns may also have arisen as the result of ancestral opportunism (Bradshaw & Holzapfel 1985). The degree to which interspecific competitive exclusion contributes to the observed pattern of tree-hole usage will then

only be resolved by manipulation of populations in the field.

These interactions are important considerations for mosquito control. *Aedes*, *Anopheles*, and *Culex* are genera known for their ability to transmit some of the most noxious and persistent of human diseases. Spraying adults or introducing a larval predator may actually relieve competition for resources, resulting in the emergence of larger, more fecund, long-lived adults than were present before control measures were implemented. Thus, indiscriminate control practices might have little net effect by balancing out natural density-dependent population regulation, or might have an adverse effect by relieving density-dependent constraints. Alternate control practices might include habitat reduction or the introduction of larval competitors. In the latter case, it would be imperative to assess in advance the extent to which habitat segregation would reinforce or negate the consequences of a putative competitor.

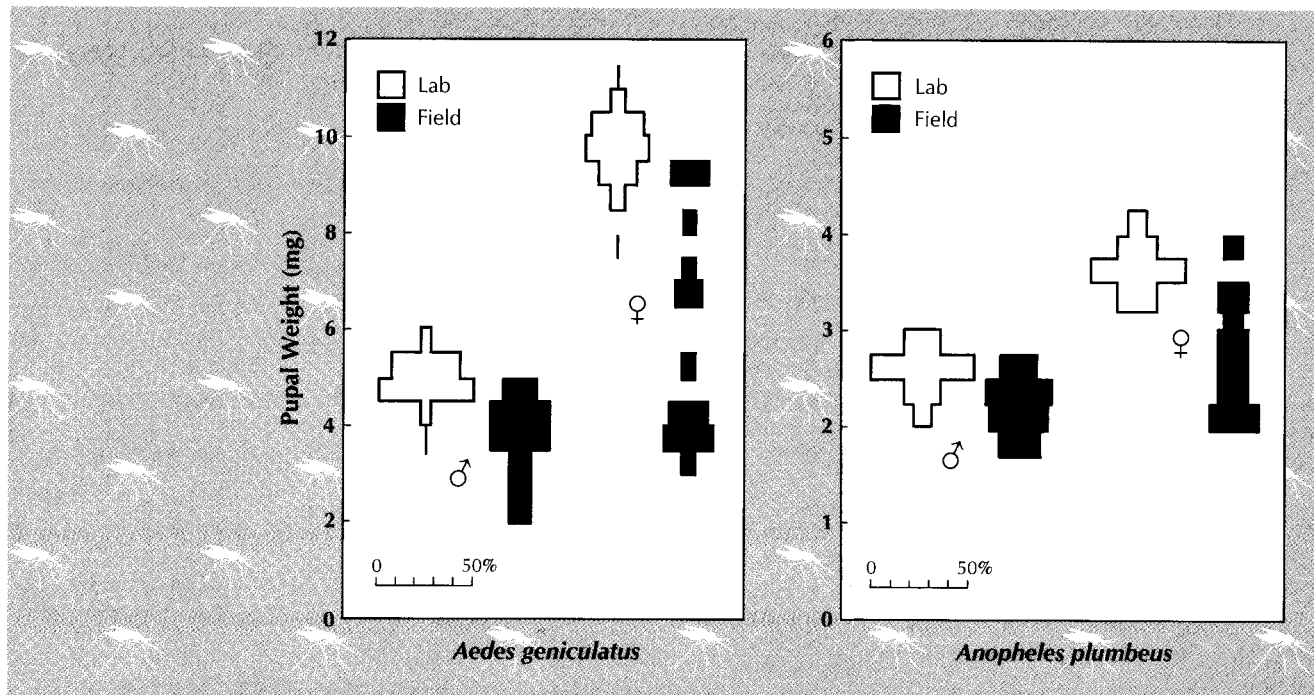


Figure 9. Frequency distributions of wet weight of lab-reared and field-collected pupae. The area within each category (female, field; female, lab; male, field; male, lab) totals 100%; the 0-to-50% scale applies to each.

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