# EVOLUTIONARY PATTERNS OF ALTERED BEHAVIOR AND SUSCEPTIBILITY IN PARASITIZED HOSTS

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*Abstract.*—Adaptation is the usual context for interpreting parasite-host interactions. For example, altered host behavior is often interpreted as a parasite adaptation, because in some cases it enhances parasite transmission. Resistance to parasites also has obvious adaptive value for hosts. However, it is difficult to evaluate the adaptive significance of host-parasite interactions without considering the historical context in which these traits have evolved and if they can be predicted by host (or parasite) phylogeny. We examined the influence of host phylogeny on patterns of altered behavior and resistance to parasitism in a cockroach-acanthocephalan system. A consensus cladogram for cockroach subfamilies was produced from the morphological data of McKittrick. We used this cladogram to predict patterns of altered host behavior in seven cockroach host species. Each species was experimentally infected with a single species of acanthocephalan, *Moniliformis moniliformis,* a parasite that is transmitted when cockroaches are eaten by rodent final hosts. Activity patterns, substrate choices, and responses to light were measured for control and infected animals. These data were recoded into a behavioral matrix of discrete characters. We determined the most parsimonious distribution of the behavioral characters on the tree obtained from McKittrick's data. We then measured the concordance between the behavioral data and the cockroach cladogram with the consistency index (CI). We compared the observed CI to the expected value based on a randomization of observed character states. For three different models of evolutionary character change, there was no evidence of strong concordance (significantly large CI) between altered host behavior and host relationships. Parsimony analysis of the interior nodes of the phylogenetic reconstruction suggested that unaltered behavior was the ancestral state for most host behaviors. We also compared host phylogeny to a data set on the susceptibility of 29 cockroach species to infection with *M. moniliformis.* At the species level, there was a significant concordance between susceptibility and host phylogeny. This pattern was consistent with the finding that susceptibility of species varied significantly among different subfamilies. However, at the subfamily level, susceptibility was not strongly concordant with phylogeny. We predict that, given enough time, resistance should be lost in subfamilies that are currently resistant to parasitism. In spite of the potential importance of phylogeny in the evolution of behavior and susceptibility, we found little evidence for phylogenetic effects in this system. We conclude that changes in the behavioral responses of hosts to parasites and, to a lesser extent, changes in susceptibility are more frequent than cockroach speciation events in different cockroach lineages. This finding strengthens the assertion that at least some of the altered behaviors are adaptive for host and/or parasite.

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The outcomes of parasite-host interactions are often interpreted as adaptive for host and/or parasite (e.g., Toft et al. 1991; Lafferty 1992). For instance, behavioral alterations are ubiquitous among parasitized hosts. Animals with parasites are known to differ from unparasitized conspecifics in their choices of microhabits, thermal regimes, and diet items. Their social status, competitive ability, and attractiveness to mates often varies from that of uninfected animals (see Moore and Gotelli 1990, for review). Despite the breadth of such effects on animal behavior, the evolutionary context is poorly understood. Behavioral changes are often assumed to benefit the parasite by enhancing transmission (Rennie 1992), and in a few cases, the occurrence of altered behavior and increased predation has been demonstrated in the same host-parasite association (e.g., Moore 1983). Enhanced parasite transmission has not been demonstrated in the majority of cases of altered behavior, however (Moore and Gotelli 1990), and other explanations for altered behavior include kin-selected host suicide (Smith Trail 1980), host defense (Hart 1988; Horton and Moore 1993), and prolonged host survival (Baudoin 1975). Dawkins (1982) argued that host behavior is a "shared phenotype" that represents a compromise between conflicting host and parasite strategies. Regardless, the beneficiary of parasite-induced behavioral alterations is not always obvious.

Resistance to parasitism has also been examined in an adaptive framework, and its cost and life-history implications have been thoroughly investigated in a snail-trematode association (Minchella 1985). Indeed, one way to avoid behavioral alterations associated with parasitism is to avoid parasitism altogether. The evolutionary basis for host specificity—why some parasites are narrowly restricted in their use of hosts, whereas others are more catholic—is a central, unresolved question in the study of host-parasite interactions (e.g., Combes 1991). Likewise, the ability of a host species to resist some invaders and not others is poorly understood, despite its importance to public health considerations.

Explaining phenomena in terms of adaptation can be a powerful tool for both prediction and clarification (Williams and Nesse 1991). Adaptive explanations nonetheless need to be contrasted with alternative explanations for a trait (Gould and Lewontin 1979). We need to elucidate the pattern of altered host behavior that might be expected in the absence of any host or parasite adaptation.

Phylogeny provides us with such a pattern. The fact that all species are related to one another, some more closely than others, is another powerful predictive tool. Even in the ab-

sence of adaptation, we expect closely related species to exhibit similar traits (Harvey and Pagel 1991), including similar responses to parasites. The likelihood of a trait being available for natural selection may be strongly influenced by the history of the taxon, especially if the trait is not easily lost or acquired. In fact, in the absence of strong selection, the distribution of the trait may largely reflect phylogeny. Such a distribution can be considered an evolutionary null hypothesis (Kochmer and Handel 1986; Gittleman and Kot 1990).

In the event of a concordance between phylogeny and the distribution of the trait, adaptation cannot be ruled out definitively as an explanation for the distribution: the trait may be currently adaptive in a way that is coincident with a phylogenetic pattern, or it may have been adaptive in an ancestor and is now shared by descendants of that ancestor (Coddington 1988). By comparing altered behaviors and susceptibility of a group of related host species to host phylogeny, however, we can evaluate the importance of history in producing these patterns (Brooks and McClennan 1991). If the traits reflect a strong phylogenetic component, adaptive explanations for the traits may need to be deemphasized, particularly if the selective regimes are very different for extant taxa.

This historical perspective is often lacking in many studies that purport to be of evolutionary significance, including the study of parasite effects on hosts. The test of the null hypothesis of phylogenetic influence on these and other phenomena requires data collected from related hosts under comparable conditions and some independent estimate of the phylogenetic relationships among these hosts.

We looked for phylogenetic patterns of altered host behavior in an acanthocephalan parasite-cockroach host system. The ability to alter intermediate host behavior is widespread in the phylum Acanthocephala (Moore 1984), where the alterations usually involve responses to specific environmental stimuli rather than generalized host debilitation (Holmes and Bethel 1972). The infected intermediate host must be eaten by a suitable vertebrate definitive host for parasite transmission to occur. In this case, it is especially tempting to invoke the altered behaviors as adaptive for transmission. They may, however, be a defensive response on the part of the host (e.g., Smith Trail 1980; Boorstein and Ewald 1987; Horton and Moore 1993), or a reflection of overall pathology.

Our comparative study of hosts examined behavioral alterations in cockroach hosts that are infected by the acanthocephalan, *Moniliformis moniliformis*. We studied an acanthocephalan because altered intermediate host behavior is a trademark of the phylum. We chose *M. moniliformis* because it develops in several species of cockroaches that are amenable to comparative laboratory study and alters a variety of cockroach behaviors. Our studies compared individuals of each of seven cockroach species to infected conspecifics in a variety of tests that examined behaviors thought to be important to predator avoidance or host defense: substrate orientation (horizontal, vertical), substrate color choice (black, white), open field activity (three indices), and three types of responses to illumination (Carmichael and Moore 1991; Allely et al. 1992; Gotelli and Moore 1992; Moore and Gotelli 1992; Moore et al. 1994). In addition, a total of 29 species

of cockroaches were examined for resistance to infection by *M. moniliformis* (Freehling and Moore 1993; Moore and Crompton 1993). Although it would be desirable to have more than seven host species for the behavioral study, most other acanthocephalan-arthropod systems would have yielded far fewer tractable combinations. We compared altered host behaviors and host susceptibility to a cladogram of the cockroaches constructed from morphological characters (McKittrick 1964).

## MATERIALS AND METHODS

### Reconstruction of Cockroach Phylogeny

Ideally, the construction of a cockroach phylogeny should be conducted by an insect systematist. Early in this study, we contacted a number of arthropod specialists (J. Carpenter, B. Thorne, I. Huber, and L. Roth), none of whom were aware of ongoing studies of cockroach phylogeny at the subfamily level. Recent studies have addressed the phylogenetic status of the primitive cryptocercid roaches (Thorne 1990; DelaPorte 1992), but we know of no study using modern phylogenetic methods that addresses relationships among cockroach subfamilies. The definitive work on this topic continues to be McKittrick's (1964) monograph. She provided detailed descriptions of morphology and musculature of representative species from different cockroach subfamilies and produced from these a dendrogram of subfamily relationships. Although her monograph predates modern phylogenetic methods, her results were summarized in tabulature form and included discussions of presumed ancestral and derived character states. We therefore rely on our own phylogenetic reconstruction of McKittrick's (1964) data (Table 1).

Table 1 of McKittrick (1964) lists 27 discrete characters for 20 cockroach subfamilies. Six taxa had character states identical with those of other subfamilies and so were not included in the cladistic analysis. Of the 27 characters, five are based on oviposition behavior, five on male genitalia, 10 on female genitalia, and seven on the cockroach proventriculus. Some of these characters are nonindependent. Her characters 3, 4, and 5, which describe oviposition behavior, are not independent of character 1, mode of reproduction. Similarly, her characters 23, 24, 25, and 27 describe dentition patterns, and are not independent of character 21, presence or absence of the dental belt. Tree structure and consistency indices were similar with and without these nonindependent characters. However, the full character set gave better resolution of the basal subfamilies. Character states are summarized below (see Table 1).

(1) Life history, two states: oviparous (0), false ovoviviparous or false viviparous, (1).
(2) Ootheca rotation, two states: ootheca held dorsal (0), ootheca rotated 90° (1).
(3) Oviposition digging, three states: with mouthparts (0), with legs (1), no oviposition digging (2).
(4) Oviposition behavior, four states: walk forward to oviposit (0), oviposit before site is prepared (1), back over hole to oviposit (2), no oviposition (3).
(5) Reduction in oviposition digging, three states: reduction

TABLE 1. Character-state distribution used in the phylogenetic analysis of cockroaches, adapted from McKittrick (1964).

| Subfamily | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Polyzosteriinae, Blattinae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Lamproblattinae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Cryptocercinae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| Polyphaginae | 0 | 0 | ? | ? | ? | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 6 | 2 | 2 | 1 | 2 |
| Holocompsinae | 0 | 0 | ? | ? | ? | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 6 | 2 | 2 | 0 | 2 |
| Anaplectinae | 0 | 0 | ? | ? | ? | 0 | 1,2 | 0 | 1 | 1,2 | 1 | 1 | 1 | 1,2 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0,2 | 1 | 0 | 0 | 0 |
| Plectopterinae | 0 | 0 | 1 | 2 | 1 | 0 | 2 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 2,3 | 1,2 | 0 | 0 | 1,2 |
| Blattellinae | 0 | 1 | 1 | 2 | 1 | 0 | 2,3 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 2 | 2 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 1 |
| Ectobiinae | 0 | 1 | 1 | 2 | 1 | 0 | 3 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 2 | 2 | 1 | 0 | 0 | 4 | 1 | 0 | 0 | 1 |
| Nyctiborinae | 0 | 1 | ? | ? | ? | 0 | 3 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 2 | 2 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 1 |
| Epilamprinae, Perisphaeriinae | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 0,1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 4 | 2 | 1 | 1 | 1 |
| Panchlorinae, Zetoborinae | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 4 | 2 | 1 | 1 | 1 |
| Blaberinae, Oxyhaloinae, Diplopterinae, Panesthiinae | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 5 | 2 | 1 | 1 | 1 |
| Pycnoscelinae | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 4 | 2 | 1 | 1 | 1 |

in terminal phase (0), reduction in subterminal phase (1), no oviposition (2).

(6) Laterosternal shelf membrane, two states: short (0), expanded into brood sac (1).

(7) Spermathecae, four states: forked (0), single (1), 1 pair (2), 2 pair (3).

(8) Spermathecal glands, two states: absent (0), present (1).

(9) Basivalvulae, three states: short, in genital chamber roof (0), elongate, in genital chamber roof (1), elongate, lateral in genital chamber (2).

(10) Valvifer arms, three states: none (0), short (1), long (2).

(11) Crosspieces, two states: absent (0), present (1).

(12) Laterosternites IX, two states: large and heavy (0), small, lightly sclerotized or absent (1).

(13) Spermathecal plate, two states: posterior (0), anterior (1).

(14) Genital papillae, two states: absent (0), present (1).

(15) Dorsal extensions of first valvifer arms, two states: absent (0), present (1).

(16) Ventral phallomere, three states: unreduced (0), reduced (1), absent (2).

(17) Median sclerite, two states: absent (0), present (1).

(18) Hook on phallomere, three states: left, nonretractable (0); right, retractable (1); left, retractable (2).

(19) Convoluted sclerites on phallomeres, three states: right and left (0), left (1), right (2).

(20) Basal sclerite (R3), two states: present (0), absent (1).

(21) Dental belt, two states: present (0), absent (1).

(22) Sclerotization, three states: confined to dental belt (0), also on 1° valvular plicae and/or pulvilli (1), no dental belt (2).

(23) Teeth, seven states: sculptured (0), bladelike (1), bottle shaped (2), sclerotized, with tubercle (3), only tubercle sclerotized (4), unsclerotized (5), no teeth (6).

(24) Intercalaries, three states: present (0), absent (1), no teeth (2).

(25) Interdentaries, three states: present (0), absent (1), no teeth (2).

(26) Symmetry of 1° valvular plicae, two states: radial (0), bisymmetrical (1).

(27) Symmetry of armarium, three states: radial (0), bisymmetrical (1), no teeth (2).

We used a branch-and-bound analysis in PAUP (Swofford, 1990) to construct parsimonious cladograms for these data. Character states were left unordered (Fitch parsimony) although similar results were obtained with ordered characters (Wagner parsimony), using character polarizations based on McKittrick's (1964) discussion. The tree was rooted with the Cryptocercidae, which exhibit many morphological similarities with termites (McKittrick 1964; but see Thorne 1990).

Branch-and-bound analysis of the 27 characters and 14 unique subfamilies generated 99 equally parsimonious trees, each with a tree length of 61, a consistency index (CI) of 0.902, and a rescaled CI of 0.844. Figure 1 shows the 50% majority-rule consensus of these trees, along with the proportion (> 0.50) of 100 bootstrap replications (Felsenstein 1985a) that support each branch. Not all authors accept the validity of consensus trees (Carpenter 1988), although the primary objection is that consensus trees have been used to resolve molecular and morphological phylogenies (Hillis 1987; Barrett et al. 1991). The bootstrap results should at least reflect the uncertainty associated with soft polytomies (Maddison 1989) that cannot be resolved by simple parsimony methods.

The major branches of the cladogram are relatively stable, and the cladogram is consistent in its general features with McKittrick's (1964) dendrogram and with Roth's (1970) scenario for the evolution of cockroach life history. McKittrick (1964) depicted the subfamilies Anaplectinae, Blattellinae, Nyctiborinae, Plectopterinae, and Ectobiinae as a natural grouping (Family Blattellidae), whereas our analysis suggests this is a paraphyletic grouping. Although our analysis did not resolve the polytomy of the Blattellinae-Ectobiinae-Nyctiborinae branch, we have behavioral and prevalence data only for the Blattellinae, so this is not a problem for the analyses that follow. From our perspective, the most important uncertainty in the tree is the placement of the Plectopterinae, which may be either basal or proximal to the Blattellinae polytomy. Analyses of behavioral and prevalence data using both placements gave comparable results.

Cryptocercinae

Blattinae, Polyzosteriinae

Lamproblattinae

Polyphaginae

Holocompsinae

Anaplectinae

Blattellinae

Ectobiinae

Nyctiborinae

Plectopterinae

Pycnoscelinae

Epilamprinae,    Perisphaeriinae

Panchlorinae, Zetoborinae

Blaberinae, Oxyhaloinae,
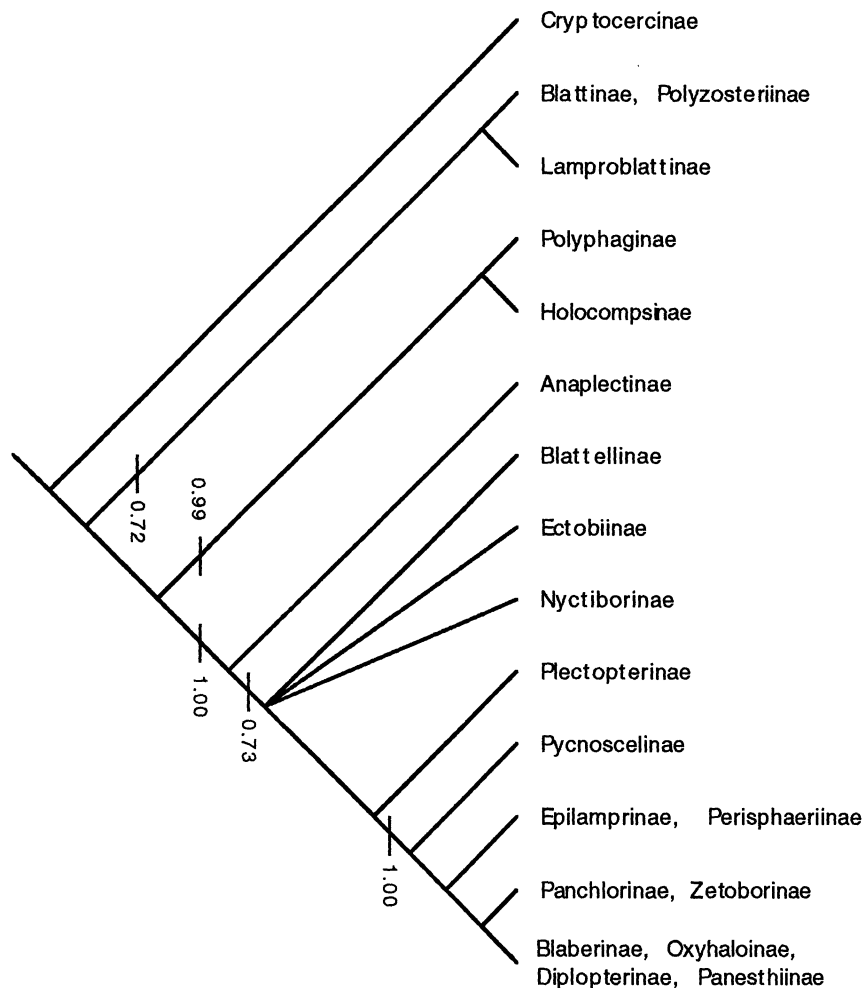Diplopterinae, Panesthiinae

0.72    0.99    1.00    0.73    1.00

Fig. 1. Fifty percent majority consensus tree for cockroach subfamilies. Numbers along branches indicate proportion of 100 trees retained (> 0.50) in branch-and-bound bootstrap replication. Multiple names on the same branch indicate subfamilies with identical character states that were not included in the analysis.

More detailed studies of cockroach phylogeny would be desirable, but the cladogram in Figure 1 at least provides an adequate hypothesis of relationships for us to compare with prevalence and behavior data. As Felsenstein (1985b) has noted, it is probably better to use phylogeny crudely than to ignore it entirely. Although there are some ambiguities in the cladogram, the important point is that the behavioral and susceptibility data we are analyzing are *completely independent* of the morphological and reproductive characters used to reconstruct the phylogeny (Coddington 1988, Brooks and McLennan 1991).

### Behavioral Data

We used the results of coordinated studies of the effects of *M. moniliformis* on cockroach behavior (Carmichael and Moore 1991; Gotelli and Moore 1992; Allely et al. 1992; Moore and Gotelli 1992; Moore et al. 1994). We were influenced in our choice of species by the availability of cockroaches, and by the susceptibility of those roaches to infection by *M. moniliformis*. Seven species were tested for behavioral alterations: *Periplaneta americana, Periplaneta australasiae,*

*Periplaneta brunnea, Blatta orientalis, Supella longipalpa, Diploptera punctata,* and *Blattella germanica.* Four of these species are in the same subfamily (Blattinae), and three of those are in the same genus (*Periplaneta*).

Under comparable laboratory conditions, control and parasitized roaches of these seven species were tested for differences in activity, substrate choice, and photic response (for experimental and statistical details, see Gotelli and Moore 1992). Activity tests were conducted in open-field arenas. Response variables include the percentage of time an individual was active during a 15-min test interval, average velocity during periods of movement, and total distance traveled. Substrate choice was also studied in an open-field arena in which roaches could move freely between black and white vertical and horizontal surfaces. The response variable is the percentage of time spent on each of these four surfaces. Photic responses included tests for photokinesis (freeze time in response to a directed light source), phototaxis (directional movement in response to a directed light source), and photophilia (percentage of time spent in light). Activity and substrate choice were measured under both red and white light conditions.

TABLE 2. Altered host behaviors data matrix. 0, host behavior unaltered; 1, reduction in host behavior when parasitized; 2, increase in host behavior when parasitized. Activity time, percent time active in open field arena tests. Distance, distance traveled. Velocity, velocity during time of travel. BH, use of black horizontal surfaces in behavioral choice arena; WH, use of white horizontal surfaces; BV, use of black vertical surfaces; WV, use of white vertical surfaces. Photokinesis, freeze time in response to light; Photophilia, percent time spent under shade; Phototaxis, directed movement in response to directional light source.

| Species | Activity time | Distance | Velocity | BH | WH | BV | WV | Photokinesis | Photo-philia | Phototaxis |
|---|---|---|---|---|---|---|---|---|---|---|
| Periplaneta americana | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| Blattella germanica | 0 | 1 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 |
| Periplaneta brunnea | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 |
| Supella longipalpa | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 |
| Diploptera punctata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Blatta orientalis | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Periplaneta australasiae | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

For each species, repeated-measures analyses of variance (ANOVA) were used to assess significant effects of parasitism on host behavior. Although the substrate preference categories are not entirely independent of one another, the comparisons are between control and parasitized groups, so that an increase in the use of one substrate due to parasitism does not automatically entail a reduction in use of the other substrates.

Table 2 summarizes those results as discrete characters for cladistic analysis: 0, no significant alteration in behavior, 1, reduction in behavior due to parasitism, 2, increase in behavior due to parasitism. We used the conventional level of statistical significance ($P \le 0.05$) and the mean responses of control and parasitized animals to code the responses for each species. Comparisons are based on the behavior of male cockroaches under red light conditions. Three behaviors—use of white vertical surfaces, velocity, and phototaxis—were unaffected by parasitism in any species. These traits were excluded from our cladistic analyses.

### Susceptibility Data

We used a data set on the susceptibility of 29 species of cockroaches (representing 12 of the 20 subfamilies) to infection by *M. moniliformis* (Freehling and Moore 1993; Moore and Crompton 1993). Susceptibility was determined through oral exposure of cockroaches to acanthocephalan eggs, and, for some species, confirmed through direct injection of hatched parasites into the hemocoel (Moore and Crompton 1993). Although injection is *not* a natural route of infection and therefore has no direct evolutionary significance, it does allow us to distinguish among a few potential mechanisms of apparent resistance (see below). Our measure of susceptibility was prevalence (percentage of individuals that became infected). For some species, more than one set of prevalence data was available. In these cases, we used the largest value measured for the species, reasoning that the maximum represents most nearly the optimal conditions for infection. In four subfamilies (Blattinae, Blattellinae, Oxyhaloinae, and Blaberinae) data on several species were available, and in these cases, prevalence was compared among subfamilies with a one-way analysis of variance, treating each species as a replicate. The distribution of prevalence values across species is distinctly bimodal. For most species with "intermediate" prevalence, only small samples were tested.

In the cladistic analysis, we treated susceptibility as a dichotomous character and used 15% prevalence as a cutoff for assignment to the susceptible or resistant state.

Three species presented a special problem. *Nahublattella fraterna, Eurycotis floridana,* and *Gromphadorhina portentosa* did not become infected, but only five or six individuals of each species were available for exposure. Consequently, these observations may represent false negatives that could affect the results of our susceptibility analysis. Although the response of *Gromphadorhina* was similar to that of other Oxyhaloinae, *Eurycotis* is our only representative of the subfamily Polyzosterinae and *Nahublattella* is the only species in the Blattelliinae that did not take the infection. If these data are treated at face value, they indicate additional evolutionary steps in the reconstruction of susceptibility as a cladistic trait. We repeated our analyses with and without these questionable data and obtained similar results, so we have presented results from the full data set.

### Cladistic Analyses of Behavioral and Susceptibility Data

To analyze behavioral and susceptibility data, we first created reduced dendrograms from the information in Figure 1. These dendrograms summarize the relationships among the subset of taxa for which we have behavioral or susceptibility data. Intervening nodes, for taxa with unknown behaviors or susceptibility, are not included in these diagrams. We wish to determine whether there is an unusually small amount of homoplasy when behavioral and susceptibility data are mapped on to the dendrogram. Significantly low levels of homoplasy can be taken as a signature of a phylogenetic effect and would indicate that the distribution of behavioral traits is nonrandom with respect to phylogeny. We use the consistency index (CI) as a simple measure of the degree of congruence between the dendrogram and the behavioral and susceptibility data. High values of the CI indicate low homoplasy and few steps needed to account for the distribution of the character (Goloboff 1991).

The number of evolutionary steps needed to reconstruct the history of a character will depend on underlying assumptions about character change. For the behavioral data, we considered three models of character change: (1) Fitch parsimony. Under this model, changes among the states of unaltered (0), decreased (1), or increased (2) behavior are equiprobable and nonadditive; (2) Wagner parsimony. For

this model, we recoded the data in Table 1 as decreased (0), unaltered (1) or increased (2) behavior. The model assumes that the traits are ordered and additive. Thus, altered behaviors can evolve only from an unaltered state, and vice versa; (3) Fitch parsimony (II). For this model, we recoded any alteration (increase or decrease) as (1) and retained the unaltered state as (0). This model is consistent with the scenario that any deviation from unaltered behavior is important and that the direction of change (increase or decrease) does not matter. For the susceptibility analyses, we also used Fitch parsimony, because there are only two possible character states (susceptible, resistant). We never polarized characters in any of the analyses, because one of our goals was to infer the ancestral state of each character from the phylogenetic reconstruction.

In addition to the model of character change and the amount of homoplasy in the data, the CI is influenced by the number of taxa and the number of characters. Comparison with an appropriate null model is essential for evaluating whether an observed CI is unusually small or large (Archie 1989). The null-model we have used is one that simply reshuffles the observed character states among extant taxa, using the "shuffle" algorithm available in MacClade (Maddison and Maddison 1992). We repeated the shufflings 100 times and used MacClade to reconstruct the character states of the interior nodes under the three models of character change. We then compared the observed CI with the histogram of simulated values to evaluate the probability of obtaining a CI as large or larger than that observed.

This is by no means the only null-model possible. For example, if we had information on evolutionary change in both host and parasite clades, we could have used an evolutionary arms-race model (Weis et al. 1989) to generate expected character changes. Alternatively, if we had some measure of host vulnerability to predation, we could have searched for significant clusters of association between vulnerability and altered host behavior, using Maddison's (1990) test of concentrated character changes. But lacking this detailed information, we feel a simple randomization test is most appropriate for measuring the degree of association between phylogeny and altered behavior or susceptibility.

This reshuffling assumes implicitly that amounts of character change in the branches of the reduced dendogram are approximately equal. If this is not the case, then some branches of the tree will have had less time or opportunity for character divergence than others (Harvey and Pagel 1991). The effect of unequal character change will probably be to bias the test towards rejecting the null hypothesis in favor of finding unusual synapomorphies. Knowing the biases inherent in the test and conducting the test at different phylogenetic levels allows us to gain insights into patterns of behavioral alteration and susceptibility.

A second assumption of our analyses is that susceptibility (or altered behaviors) seen in different taxa is caused by a common mechanism. This assumption allows us to treat susceptibility as a single "trait." But if the mechanism of susceptibility differs among lineages, concordances with phylogeny may be distorted.

We assume a common mechanism for three reasons. First, the relatively large size (0.02 mm; Moore 1946) of the hatched acanthor (the invasive stage of the acanthocephalan) means that encapsulation is the most likely defensive response to be used. Other defensive compounds are more effective against smaller pathogens. Second, failure to observe developing acanthocephalans in the hemocoels of representatives of some cockroach species may have indicated passive "resistance," for example, failure to hatch or to successfully penetrate the intestine. Direct injection of hatched acanthors into the hemocoel would obviate such barriers. In no case did this treatment result in "susceptibility" in an otherwise resistant species (Moore and Crompton 1993). Finally, precise mechanisms controlling host susceptibility and altered behaviors in cockroaches are poorly known (see Discussion), and in the absence of information that implicates a diversity of such mechanisms, we assume common ones.

## RESULTS

### Behavioral Alterations

Figure 2 illustrates the reduced dendogram for the seven host species we tested, and shows the mapping of one of the behavioral traits, use of black horizontal surfaces. Data in McKittrick (1964) do not allow us to resolve the polytomy of the three species of *Periplaneta*. Because the branch lengths are grossly unequal in this tree, the analyses are probably biased towards finding unusual synapomorphies.

In particular, we expected, a priori, that behavioral responses of the *Periplaneta* species would be extremely similar, but this was not the case. Figure 3 illustrates the CI for the set of behavioral data, compared with null expectations under three scenarios of character evolution. In all scenarios, there were certain character distributions that would have caused us to reject the null hypothesis of random levels of homoplasy. In other words, the histograms of CIs for randomized character distributions show that certain configurations of the trait would have allowed us to conclude that homoplasy was unusually low (= large CI). Thus, the tests were sufficiently powerful to detect a strong match between the cladogram and the behavioral data. The null hypothesis was never rejected in these analyses; the CI for the behavioral matrix when mapped on this dendogram was no greater than would be expected if the observed character states were distributed at random. This pattern holds for all three models of character evolution.

Table 3 shows that none of the individual behavioral traits formed a concordance (=synapomorphy) on this tree. For these simple trees, probabilities of homoplasy can be easily calculated (Moore and Gotelli 1990). For example, if only two extant taxa show an altered behavior, there are $\binom{7}{2} = 21$ unique pairwise arrangements on the tree in Figure 2. By inspection, four of these arrangements would be concordant with phylogeny (=synapomorphic). The probability of a synapomorphy is thus $4/21 = 0.19$, so the probability of a homoplasy $= 1 - 0.19 = 0.8$. With six behaviors showing homoplasy, the joint probability of this event is 0.38 (One behavior [photophilia] showed an autapomorphy). Thus, for each individual behavioral trait, and for the group of traits collectively, the degree of concordance with host phylogeny would be expected by chance.

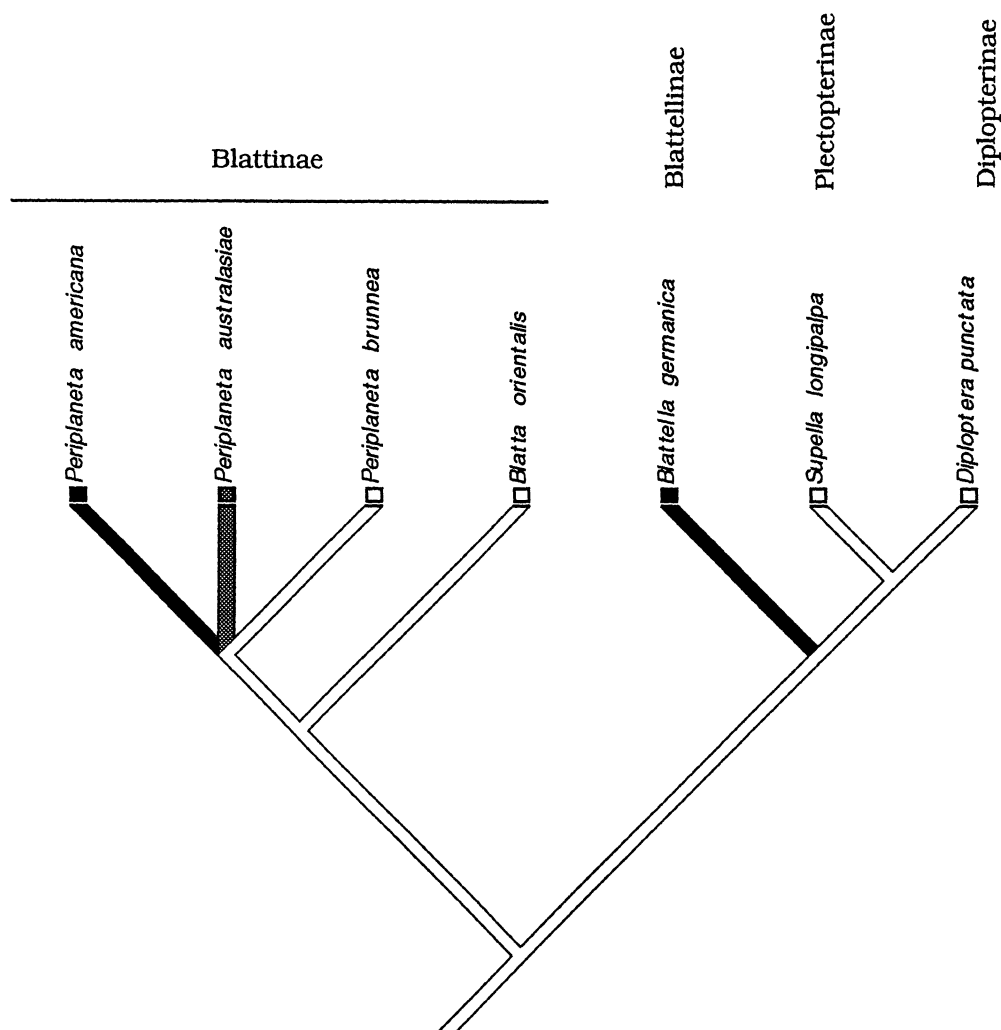Finally, we used a parsimony reconstruction of the interior

FIG. 2. Homoplasy in altered behavior patterns. Reduced dendrogram depicting relationships among seven cockroach host taxa and pattern of altered behavior for use of black horizontal surfaces. Subfamilies are listed above species names. White, unaltered host behavior; black, increase in use of black horizontal surfaces by parasitized animals; shaded, decrease in use of black horizontal surfaces by parasitized animals.

nodes of the dendrogram to evaluate the ancestral state of behaviors. For six of the seven behaviors, the most-parsimonious reconstruction was that the unaltered state was ancestral. For the use of black horizontal surfaces, either the altered or unaltered ancestral state was equally parsimonious (Table 3). Thus, assuming that unaltered behaviors were ancestral for the cockroaches, the tree length of the behavioral data was only 15 steps, compared with 24 steps if we assume that altered behaviors are ancestral (Table 3). Using a paired $t$-test for each character state, the difference between these tree lengths is statistically significant ($t = 4.38$, $P = 0.002$). This test assumes that the behavioral characters are independent of one another.

### Susceptibility Analyses

Figure 4 shows the dendrogram of resistant and susceptible cockroach species. Twelve host species were resistant to infection, so a maximum of 12 character-state changes are possible, which would be the case if each species evolved re-

sistance independently. The most-parsimonious reconstruction requires only five state changes. The CI of 0.20 for this tree was significantly greater than expected by chance (Fig. 5A). Parsimony analysis of interior nodes suggests that susceptibility to parasitism was the ancestral state for the cockroaches, although only one additional step (from 5 to 6) is required if resistance was the ancestral state. There was significant variation in resistance among subfamilies (Fig. 6): species in some subfamilies (Blaberinae and Oxyhalinae) tended to be highly resistant to parasitism and species in other subfamilies (Blattinae) tended to be highly susceptible.

The cladistic analysis of susceptibility assumed that branch lengths were approximately equal, which was clearly not the case for species and genera in different subfamilies. Branch lengths may be more nearly equal in an analysis of subfamilies with and without resistance. The dendrogram of resistance in Figure 4 was collapsed to the subfamily level, so that individual species were no longer treated as replicates (Fig. 7). At this level of analysis, the randomization test no longer revealed any tendency toward a large CI (Fig. 5B).
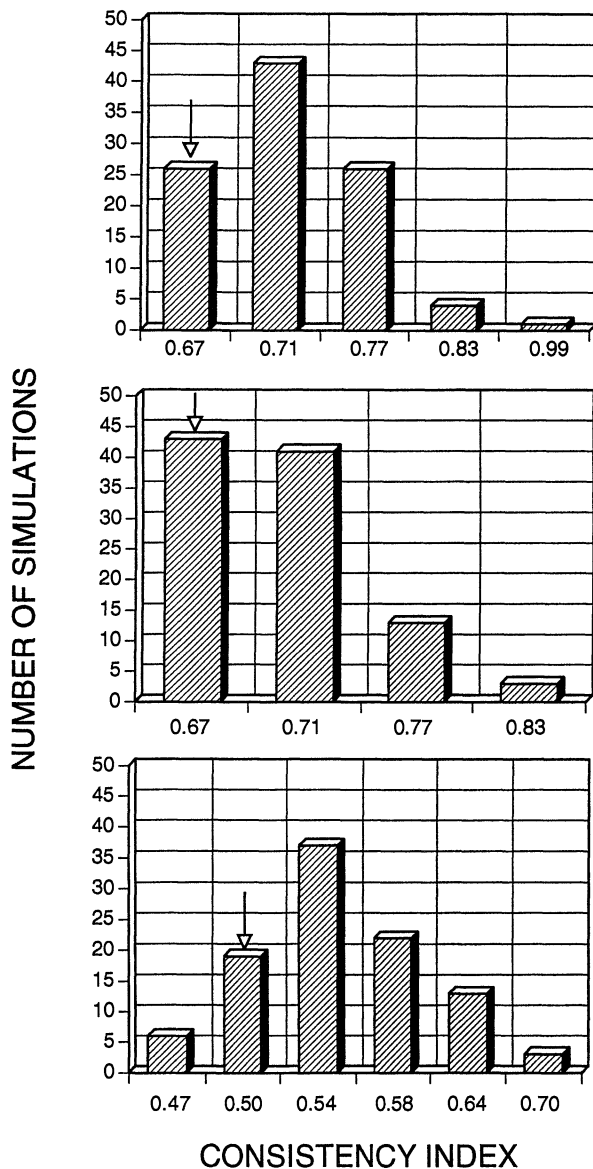
FIG. 3.   Histogram of consistency indices for 100 reshufflings of behavioral data matrix (Table 2) mapped onto reduced host dendrogram (Fig. 2). Observed CI for the data is indicated by an arrow. (A) Fitch parsimony. Observed CI = 0.67; $P$ (CI) ≥ observed = 1.00; (B) Wagner parsimony. Observed CI = 0.67; $P$ = 1.00; (C) Fitch parsimony (II). Observed CI = 0.50; $P$ = 0.94. See text for model details.

TABLE 3.   Cladistic analysis of behavioral traits. The probability of a homoplasy for the tree topology in Figure 2 is calculated from Moore and Gotelli (1990). Parsimonious ancestral state minimizes tree length for behavioral matrix in Table 1. Invariant traits (WV, phototaxis) deleted.

| Trait | Number of steps | Pattern | $P$ (homoplasy) | Parsimonious ancestral state |
|---|---|---|---|---|
| Activity time | 2 | homoplasy | 0.8095 | unaltered/alt |
| Distance | 2 | homoplasy | 0.8095 | unaltered |
| BH | 3 | homoplasy | 0.9429 | unaltered |
| WH | 3 | homoplasy | 0.9429 | unaltered |
| BV | 2 | homoplasy | 0.8095 | unaltered |
| Photokinesis | 2 | homoplasy | 0.8095 | unaltered |
| Photophilia | 1 | autapomorphy | — | unaltered |

cockroaches would hold more physiological traits in common than distantly related ones would. Thus, if behavioral alterations result from physiological disruptions (neurological, hemolymph components, and so on) in one cockroach species, we would expect such alterations to be shared more readily by close relatives than distant ones, regardless of the adaptive nature of those alterations in every association. Therefore, this absence does encourage increased consideration of the possible species-level adaptive value these altered behaviors may confer on either cockroach or acanthocephalan.

We wish to stress that increased vulnerability to predation is not the only adaptive scenario for altered behavior in intermediate hosts. As Brassard et al. (1982) noted with parasitized guppies, if an unsuitable predator responds, altered behaviors do not necessarily result in increased transmission, although they may result in increased predation. Bethel and Holmes (1977), however, described behavioral alteration differences among parasitized individuals of several species that apparently increased the likelihood of encountering an appropriate definitive host.

On the other hand, some altered behavior may be essentially defensive; optimal microhabitats may differ for infected and uninfected conspecifics (Boorstein and Ewald 1987). Kin-selected suicidal behavior is another possible antecedent for some behavioral alterations (Smith Trail 1980). Although this is an unlikely historical scenario for most acanthocephalan-host associations (Moore 1984), behavior that is consistent with kin-selected suicide can be observed in aphid-parasitoid associations (McAlister and Roitberg 1987).

Another explanation for altered behavior is pathology, which can often be seen as a neutral or nonadaptive explanation for altered behavior; pathology can, however, possess both historical and adaptive components. The extent of pathology itself is probably strongly influenced by natural selection (Ewald 1983). Because site selection may have a historical basis (Brooks 1980), and may also be critical to pathology, the relationship among pathology, adaptation, and history may be difficult to clarify. For instance, trematodes that encyst in the lens of the eyes of fish may be thought to exhibit an adaptation that increases fish vulnerability to predation and subsequent parasite transmission. On the other hand, such a developmental site could be favored by natural

## DISCUSSION

### Altered Host Behavior

Our analyses indicate no obvious phylogenetic component to behavioral alterations of cockroaches by *M. moniliformis*. Even within the genus *Periplaneta,* behavioral responses to infection were widely divergent. The absence of a phylogenetic pattern for altered behavior is surprising, because many behavioral traits themselves seem related to phylogeny (Brooks and McClennan 1991). Moreover, it is reasonable to expect that aspects of cockroach physiology are shared by descent from a common ancestor and that closely related
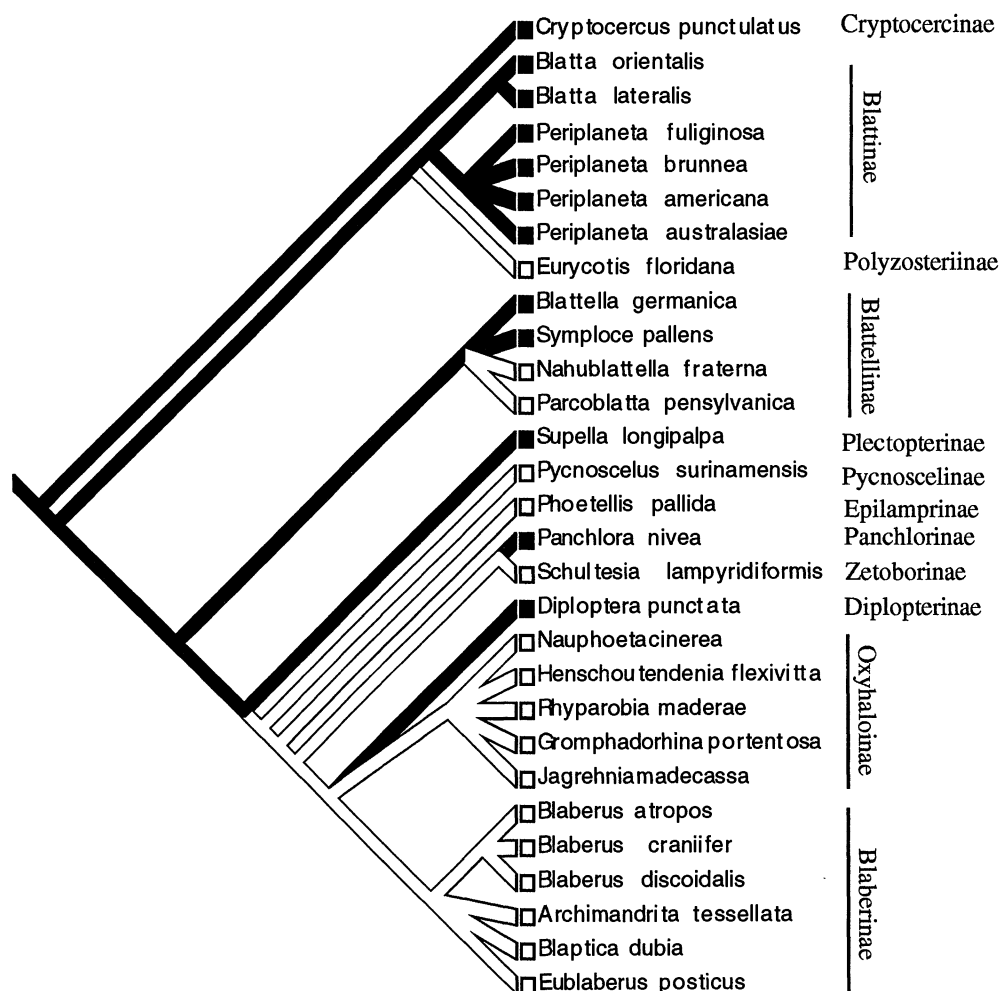
Fig. 4.   Dendrogram of resistant and susceptible cockroach host species. Polytomies represent species within genera or genera within subfamilies. Subfamilies are listed above species names. Black, susceptible; white, resistant.

selection because it is immunologically protected; the behavioral alterations and associated transmission benefits associated with the site would then be secondary (Szidat 1969). In like manner, the host may also have special metabolic requirements as a result of being parasitized, and these may affect behavior, even to the point of increasing risk-taking behavior (Milinski 1985; Hart 1988; Smith and Kramer 1987). Such a metabolic requirement may be a constraint of host-parasite metabolism, or may (also?) be favored by natural selection acting on parasite transmission rates.

According to our analysis, behavioral alterations induced by the same parasite in several cockroach species are derived traits that are capable of appearing repeatedly in different cockroach lineages in ways that do not conform to our hypothesis of cockroach evolution. Given that history is relatively unimportant, the distribution of altered behaviors might reflect cockroach ecology instead. A cursory examination of ecological similarities among cockroaches could support this interpretation: *D. punctata* is the only cockroach we studied that typically does not live inside human dwellings, and it is the only cockroach that fails to exhibit alterations in the behaviors we examined. It is also limited in

distribution to the tropics. This cockroach does live in the vicinity of humans, however, and it is hard to argue on ecological grounds alone that *D. punctata*'s participation in the parasite life cycle is any less than that of other cockroaches. The remainder of the cockroach species that we studied are domiciliary pests, but they do show some variation in their use of such domiciles (Cochran 1982, Cornwell 1968). These microhabitat preferences are not reflected in our phylogenetic hypothesis.

### Susceptibility

There are two phylogenetic results from our comparison of cockroach susceptibility to *M. moniliformis*. First, species within the same subfamilies tend to have similar susceptibility patterns, and most of the susceptible subfamilies are close to the root of the tree. Our analysis therefore suggests that susceptibility is ancestral, and this agrees with the fact that *M. moniliformis* has been recorded from other insect groups, such as beetles (Schmidt 1985; see also Lackie and Lackie 1979). Our second observation, however, is that resistance, although derived, can be lost again in unrelated
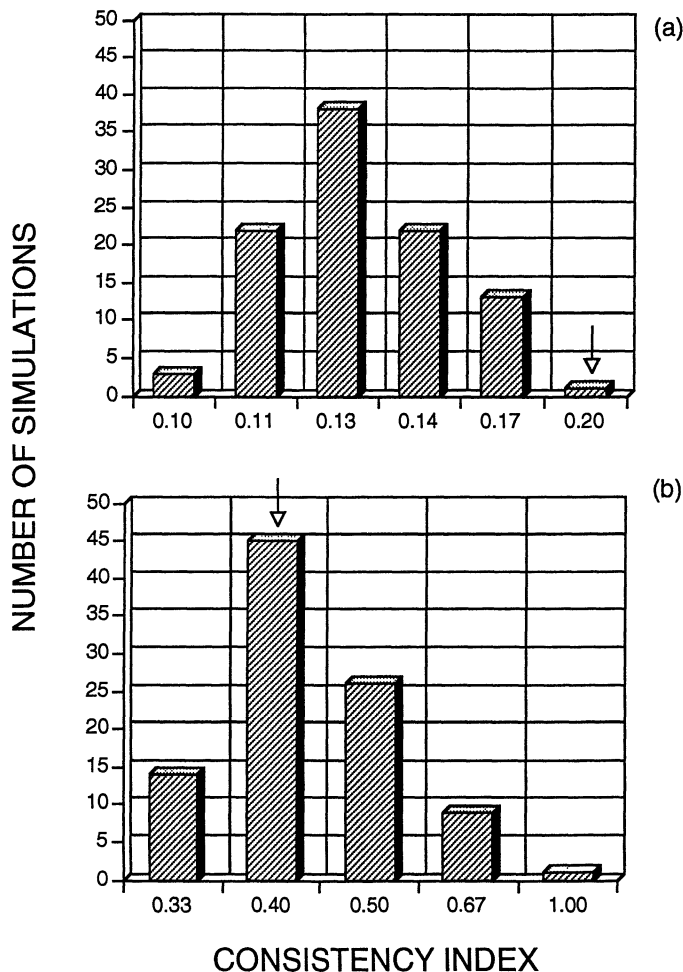
FIG. 5.  Histogram of consistency indices for 100 reshufflings of species susceptibility data. (A) species susceptibility data from Figure 4. Observed CI = 0.20; $P$ = 0.01; (B) subfamily susceptibility data from Figure 7. CI = 0.40; $P$ = 0.86.



FIG. 6.  Average susceptibility (prevalence) to oral infection by $M.$ $moniliformis$ within cockroach subfamilies. Species function as replicates, with sample sizes indicated in parentheses. Vertical lines are 1 SD F = 45.9, df = 3,18; $P < 0.0001$.

lineages; these cannot be predicted based upon their position in the tree. This result held even when, on the basis of low sample sizes in species that were therefore deemed resistant, we treated the Blattellinae as monomorphically susceptible and excluded the Polyzosteriinae from the analysis.

Our results are consistent with the status of the blaberids as a highly derived cockroach family with distinctive life-history modifications, including retention of oothecae until hatching. $Diploptera$ $punctata$ is especially notable in this regard, as it actually provides internal nourishment for young, and exhibits false viviparity (Cornwell 1968). The divergent qualities that characterize blaberids, including physiological correlates of reproductive innovations, may be related to their ability to resist $M.$ $moniliformis$ infection. This requires further investigation, but one result of our study is the consistency of our susceptibility data with the pattern of altered behaviors across taxa; that is, $D.$ $punctata$ is from a lineage that in general does not become infected with $M.$ $moniliformis,$ and $D.$ $punctata$ itself is not an optimal host (Moore and Crompton 1993). Of the cockroach species studied, $D.$ $punctata$ was alone in demonstrating no evidence of behavioral
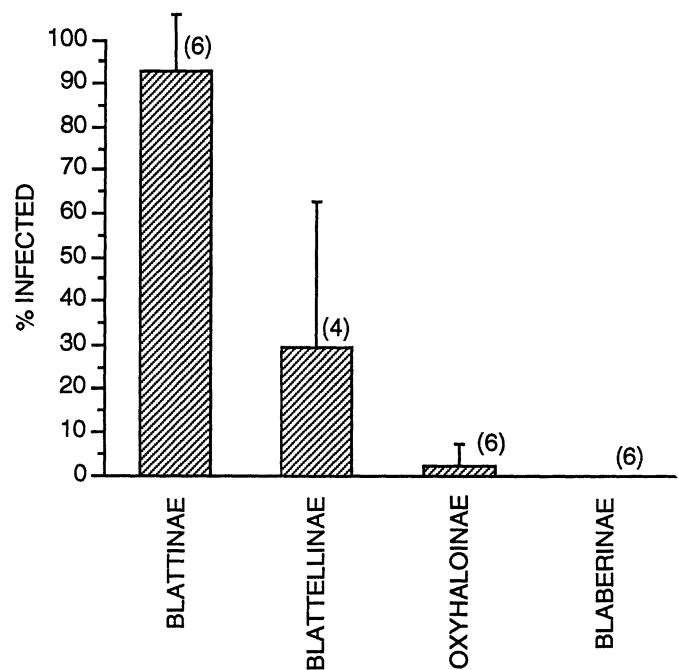
alteration (Allely et al. 1992). The possibility of similar results from other blaberids is tantalizing; unfortunately, blaberids have proven notoriously difficult to infect, even when hatched acanthors are injected directly into the hemocoel (Moore and Crompton 1993)!

## Mechanisms

In general, the studies of resistance and behavior can be pursued at several levels: mechanism, the phenomenon itself, and the ecological and evolutionary implications. Knowledge of the underlying neuroethological and immunological mechanisms for both altered behavior and variation in susceptibility is highly desirable. Similar responses might result from different underlying mechanisms, or the converse may occur, given interspecific divergence.

The neuroethology and immunology of a few cockroaches have been extensively studied, but most species remain unexamined. There have been very few neurophysiological studies of parasite-induced behavioral alterations in arthropods. One exception is the discovery that injection with serotonin elicits modified escape responses in gammarids that mimic those seen in amphipods infected with the acanthocephalan $Polymorphus$ $paradoxus$; some of these responses are eliminated by octopamine injection (Helluy and Holmes 1990). Similar information for cockroach-acanthocephalan associations currently does not exist.

In contrast, the immune response of cockroaches to $M.$ $moniliformis$ has been carefully scrutinized. In general, there are several ways to avoid encapsulation (e.g., hemocyte transformation, antigenic mimicry; Lackie 1980), and for quite some time, $M.$ $moniliformis$ was thought to evade recognition
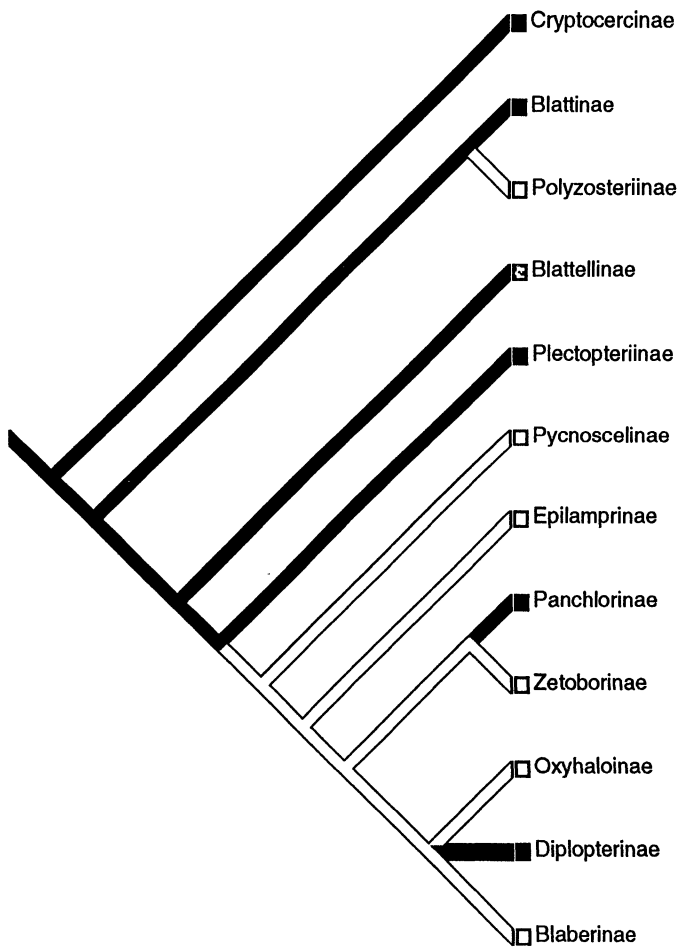
FIG. 7. Dendrogram of resistant and susceptible cockroach subfamilies. Same data set as in Figure 4, but replication of individual species is collapsed. Note polymorphism in Blattellinae (see Materials and Methods). Black, resistant; white, susceptible; stippled, polymorphic.

fully in cockroach species that were susceptible to oral exposure (Moore and Crompton 1993).

It is not clear that there are ecological correlates to the distribution of susceptibility that we find among cockroaches. Dunn (1990) has suggested that immunological memory may be more important in species with ecologically persistent individuals than in ephemeral species, which can escape invaders in space and time. By the same reasoning, investment in other defenses may be less crucial to relatively ephemeral species. Yet short-lived cockroaches (e.g., *B. germanica* and *S. longipalpa*) are susceptible, as are longer-lived *Periplaneta* species.

CONCLUSIONS

In summary, we have failed to find a particularly powerful role for phylogeny in the alteration of behavior that is associated with *M. moniliformis* infection in cockroaches. Of course, this is subject to several underlying assumptions, not the least of which are the assumptions that accompany phylogenetic analysis (e.g., Felsenstein 1981, 1982, 1983). Within this framework, we emphasize that our tree has a fairly stable topology and to a great extent, is consistent with the evolutionary presentation of McKittrick (1964). There is also the possibility that the cockroaches we used were somehow not representative of those species actively involved in *M. moniliformis* transmission. This is unlikely, given the overlap of the ranges of at least most of our species with those of known rodent hosts and the cosmopolitan distribution of the parasite. We acquired our cockroaches from laboratory colonies in several locations, and none of these laboratories were engaged in *M. moniliformis* research. Their colony maintenance and any subsequent effects of cockroach behavior were independent of acanthocephalan considerations. Finally, the behavioral alterations or susceptibility patterns that we observe in our cockroaches may not characterize entire species. This is less likely for at least some of the species tested for susceptibility: 13 of these species were tested in both the United States and Scotland, using different stocks of cockroaches, and they yielded the same results (Moore and Crompton 1993). Moreover, such variation, if it did exist in either data set, would simply do more to obscure the role of history. Our results indicate that both altered behavioral responses and susceptibility can evolve in cockroaches confronted with *M. moniliformis*, setting the stage for an adaptive interpretation of these phenomena.

It may be reasonable to expect that the constellation of behaviors that are altered in parasitized animals will be found to have multiple benefits for both parasite and host, and the relative allocation of benefits to each of the parties may be dynamic, shifting in time, and a heterogeneous environment. What we have done here is to assess for the first time the importance of host history as a potential constraint or influence on these potential benefits and on the capability of a parasite to invade a suite of intermediate hosts prone to such behavioral alteration. In the case of cockroaches and their acanthocephalan, we have found little evidence for such influence, with the exception of susceptibility at some taxonomic levels.

in *P. americana* by displaying some elements of host "self" (e.g., Lackie and Lackie 1979). Recently, however, Lackie and Holt (1988) discovered that *M. moniliformis* may also immunosuppress *P. americana* to some extent. The success of the latter strategy may depend on hemocyte density, which varies among species (Karp 1990). In general, the hemolymph of our largely resistant taxon, the Blaberidae, exhibits a milky appearance and is prone to rapid melanization, which may indicate particularly labile hemocytes (Lackie, pers. comm. 1992). Melanization of parasites may result from more than one biochemical pathway (Christensen and Tracy 1989); whether these comprise different evolutionary mechanisms is not well understood. Again, more detailed knowledge of mechanism is desirable. We do know that resistance of cockroach species to *M. moniliformis* does not depend on events in the intestine or intestinal wall; cockroach species that were resistant to infection with orally administered acanthocephalan eggs were also resistant to infection with hatched acanthocephalan larvae injected directly into the hemocoel. Hatched larvae from the same parasite population developed

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