In forested habitats, harvestmen (Opiliones) are among the most conspicuous arthropods; however, relatively little is known about the ecology of most species (Machado et al. 2007). Factors including a general secretive nature, small body size, and nocturnal behavior have contributed to the general paucity of information concerning the symbiotic relationships of harvestmen with other organisms (Cokendolpher 1993, Cokendolpher and Mitov 2007). The most investigated interactions are those that involve ectoparasitic larval mites, especially erythraeid mites of the genus *Leptus* that parasitize temperate species of sclerosomatid harvestmen of the genus *Leiobunum* (Åbro 1988, Cokendolpher 1993, Guffey 1998, McAloon and Durden 2000, Cokendolpher and Mitov 2007). Mites are presumed to feed upon the hemolymph and tissues adjacent to the attachment site (Åbro 1988). They attach preferentially to the femur and tibia of the leg but also attach to the ocularium and dorsal surface of the scutum (McAloon and Durden 2000). Larval mites may remain with the same host for weeks or months before dropping off to become free-living as adults (Southcott 1989, 1992). Generally, little is known about the effects of parasitic mites upon the survival, locomotion, or reproductive capacity of their arthropod hosts (Guffey 1998).

Relatively few quantitative studies have examined mite–harvestmen interactions. The prevalence of infestation (the percentage of individuals that are parasitized) has been reported to vary from 0.5% for *Leiobunum formosum* (Wood) in Virginia (Townsend et al. 2006) to 61% for *L. formosum* in Tennessee (McAloon and Durden 2000), but it may fluctuate seasonally or annually (Townsend et al. 2006). The intensity of infestation (mean number of mites per individual that is parasitized) also may vary from one mite per host for *L. formosum* (Townsend et al. 2006) to four mites per individual for *L. nigripes* in Louisiana (Guffey 1998). Maximum reported intensities are 14 mites for *L. formosum* in Tennessee (McAloon and Durden 2000) and 32 mites for *Zachaeus crista* in Bulgaria (Mitov 2000).
Little is known about larval mites that parasitize Neotropical harvestmen, although there are records of infestation for the Gonyleptidae and Cosmetidae (Cokendolpher 1993, Cokendolpher and Mitov 2007). Before our research, there were no records of erythraeid mites parasitizing harvestmen on the Caribbean island of Trinidad, although these mites occur in Venezuela (Southcott 1989). The main objective of our study was to examine interspecific variation in the prevalence and intensity of mite infestations upon harvestmen in Trinidad. In addition, we also compared mite parasitism rates between harvestmen collected from different habitats.

Materials and Methods

From 10 July to 3 August 2005, we collected 415 adult harvestmen representing 12 species and seven families (Table 1) from crappo-cocorite forest (CCF), seasonal deciduous forest (SDF), lower montane rainforest (LMF), and upper montane rainforest (UMF) on the island of Trinidad. These habitats differ markedly with regards to physical characteristics and vegetation (Beard 1946, Murphy 1997). Along the northern coast, CCF receives <0.2 m of rain annually, occurs in the lowlands (below 243 m), and it has a relatively high canopy (30–46 m) with a well-developed understory. The rainfall and canopy of SDF are similar, but the understory is not as prominent and this habitat occurs throughout the northern, central, and southern ranges. In contrast, LMF receives 0.2–0.4 m of rain annually, is found at intermediate elevations (243–760 m), and has a slightly lower canopy (21–30 m) with a poorly developed understory. Occurring at the highest elevations in the northern range (above 760 m), UMF receives >0.5 m of rain annually and features a closed canopy, with trees ranging from 15 to 18 m and a well-developed understory of small palms and ferns.

On 10 July 2005, we searched for harvestmen in SDF on the slopes of Mt. Tamana in the Central Range (10°28’15.5” N, 61°11’50.5” W; datum WGS84; elevation 150 m). From 12 to 15 July, we sampled CCF adjacent to the beaches of Gran Tacarib and Petite Tacarib along the northern coast (10°47’39” N, 61°13’33” W; datum WGS84; elevation 15 m). On 30 July and 6 August, we collected in LMF along the Lalaja Trace, near the village of Brasso Seco in the northern range (10°44’47” N, 61°15’54” W; datum WGS84; elevation 260 m). From 23–26 July and 2–3 August, we sampled in UMF along Morne Bleu Ridge in the northern range (10°43’53” N, 61°15’08” W; datum WGS84; elevation 823 m).

In general, collections took place during daylight hours between 0730 and 1700 hours. Harvestmen were found by turning and breaking apart logs and palm frond sheaths and carefully searching the surfaces, crevices, and the litter associated with tree buttresses. All harvestmen were captured by hand and immediately placed in 70% ethanol or 10% buffered formalin. In August, specimens preserved in formalin were transferred to 70% ethanol for long-term storage. Specimens were carefully examined with the aid of a stereomicroscope to determine the presence and number of parasitic mites. Identifications of adult harvestmen were made with the aid of the original taxonomic descriptions and from comparisons with type materials borrowed from the American Museum of Natural History (AMNH).

Variation in the prevalence of infestation was assessed using either a chi-square test or Fisher's exact test and 95% confidence intervals (CIs) were obtained by Sterne's exact method (Rózsa et al. 2000, Reiczigel and Rózsa 2005). Mean intensities are reported with 95% CIs calculated using a bias corrected accelerated (BCa) bootstrap with 2,000 replicates. Median intensities are presented with either a chi-square test or Fisher's exact test and 95% confidence intervals (CIs) were assessed using either a chi-square test or Fisher's exact test. To test the robustness of the observed Kruskal–Wallis statistic, we used a randomization test of 2,000 iterations.

During sampling, we collected 92 nymphs of species for the families Cosmetidae, Cranidae, and Sclerosomatidae. We excluded these immature individuals from the statistical analyses because they could not be identified to genus. However, it seems possible that there may be ontogenetic variability with regard to the susceptibility of harvestmen to mite infestation. There

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Table 1. Sample sizes for 12 species of harvestmen collected in forested habitats (CCF, SDF, LMF, and UMF) from 10 July to 3 August 2007.

| Taxa             | CCF | SDF | LMF | UMF |
|------------------|-----|-----|-----|-----|
| Agoristenidae    |     |     |     |     |
| Trinella sp.     | 0   | 0   | 0   | 7   |
| Cosmetidae       |     |     |     |     |
| Cryptopelmadia   | 161 | 11  | 14  | 20  |
| Fascielma inae    | 26  | 8   | 0   |     |
| Cranidae         |     |     |     |     |
| Phaeoeciraenus    | 5   | 6   | 0   | 9   |
| Santinodactylina  | 4   | 2   | 0   | 8   |
| Manoaobidæ       |     |     |     |     |
| Cranella montgomeri | 0  | 0   | 0   | 5   |
| Rhopalocarus      | 34  | 7   | 0   | 3   |
| Samoidea         |     |     |     |     |
| Maracagynatium    | 0   | 0   | 4   | 0   |
| trinidadense      | 0   | 0   | 1   | 0   |
| Pellobunus longipalpus | (Goodnight & Goodnight, 1947) |     |     |     |
| Sclerosomatidae   |     |     |     |     |
| Pisonostemna sp.  | 23  | 19  | 2   | 4   |
| Stygnidae         |     |     |     |     |
| Stygnoplus clavotibialis | (Goodnight & Goodnight, 1947) |     |     |     |
| Unidentified species | 1  | 0   | 0   | 0   |
were no nymphs in our sample that had parasitic mites. Voucher specimens of harvestmen were deposited into the collections at Virginia Wesleyan College (Norfolk, VA), AMNH, Louisiana State Arthropod Museum (LSAM), and California Academy of Sciences (CAS). Additional voucher specimens with attached larval mites were deposited in the collection at the CAS.

To identify larval mites, we carefully examined specimens collected from multiple locations. Leg segments of harvestmen bearing mites were carefully removed, dehydrated in a graded ethanol series, and chemically dried using hexamethyldisilazane (Nation 1983). Specimens were mounted on aluminum stubs with double stick tape, sputter-coated with 10–15 nm of gold, and examined at an accelerating voltage of 15 kV with the Hitachi S-3000N scanning electron microscope (SEM) in the Electron Microscopy Center at the University of Louisiana at Lafayette.

In addition to erythraeid mites, we examined a group of 30 mites that were found in association with a solitary adult Cynortula. These specimens were collected in July 2006 in CCF adjacent to Petite Tacarib. In contrast to larval erythraeids, these mites were considerably darker in color and thickly covered the dorsal surface of the body. In addition, we observed that they were not directly attached to the surface of the host but were actively moving. When placed in 70% ethanol, the mites floated or fell off of the harvestman rapidly. On the basis of these observations, we hypothesized that these mites were phoretic and not parasitic. In an effort to identify the mites, we prepared several individuals for SEM and also cleared and examined other specimens by light microscopy. Voucher specimens of these mites have been deposited into the collection at the AMNH. All specimens were legally collected and exported under permit numbers 000541 (to V.R.T. in 2005) and 001284 (to D.N.P. in 2006).
Results

Harvestmen were parasitized by two taxa of erythraeid mites, including a species of *Leptus* (Fig. 1A and B, D–F) and an unidentifiable species (Fig. 1C). The mode of attachment of these mites (Fig. 1, B and F) is generally the same as that used by larval mites that parasitize temperate species of *Leiobunum* (Åbro 1988). Mites preferentially attached to the tibia or femur of the leg of harvestmen in 175 of 178 instances. The remaining three mites were observed on the large dorsal spines on the body of three adult *P. inglei*.

Overall, the prevalence of infestation for larval mites upon adult harvestmen (N = 415) was 9.9% (BCa CI = 7.3–13.1%), with 41 individuals from six species parasitized (Table 2). Our observations represent the first records of erythraeid mite parasitism for each of these taxa. The prevalence of infestation ranged from 9.1% to 20% (Table 2) and was greatest for species of cosmetids, manaosbiids, and sclerosomatids, but not significantly different between these taxa ($\chi^2 = 5.204, df = 5, P = 0.392$). Intensity levels of mite infestation varied significantly ($H = 22.32, df = 5, P < 0.001$), and the mean intensity of infestation was highest for *Cynortula* sp. (7.2 ± 2.2 mites per host) with a maximum of 17 mites attached to a single host (Fig. 2). Of the 41 harvestmen infested by mites, *Cynortula* sp. had the nine most highly parasitized individuals. The mean intensity of infestation was considerably lower for the other species, ranging from 1 to 3.5 mites per host (Fig. 2).

The prevalence of infestation significantly varied across the four habitats ($P = 0.034$; Fisher exact), with

### Table 2. Prevalence (percentage) and intensity of mite infestation for 12 species of harvestmen from Trinidad

| Taxa                  | N  | Prevalence (95% CI) | Intensity range | Mean intensity (95% CI) | Median (exact CI) |
|-----------------------|----|---------------------|-----------------|-------------------------|-------------------|
| Agoristenidae         |    |                     |                 |                         |                   |
| *Trinella* sp.        | 7  | 0.0                 |                 | 0                       |                   |
| Cosmetidae            |    |                     |                 |                         |                   |
| *Cynortula* sp.       | 206| 9.2 (5.8–14.0)      | 1–17            | 7.2 (5.0–9.5)           | 5.0 (96.8% CI: 2–10) |
| *P. inglei*           | 36 | 19.4 (9.3–35.9)     | 1–7             | 2.3 (1.0–4.0)           | 1.0 (98.4% CI: 1–7) |
| Cranidae              |    |                     |                 |                         |                   |
| *P. calciferus*       | 20 | 0.0                 |                 | 0                       |                   |
| *S. serratotibialis*  | 14 | 142.2 (2.6–42.5)    | 1–6             | 3.5 (1.0–3.5)           | 3.5               |
| Manaosbiidae          |    |                     |                 |                         |                   |
| *C. montgomeryi*      | 5  | 20.0 (1.0–65.7)     | 1               | 1.0                     | 1.0               |
| *R. albilineatus*     | 44 | 9.1 (3.2–21.4)      | 1–4             | 2.3 (1.0–3.3)           | 2.0               |
| Samoidae              |    |                     |                 |                         |                   |
| *M. trinidadense*     | 4  | 0.0                 |                 | 0                       |                   |
| *P. longipalpus*      | 1  | 0.0                 |                 | 0                       |                   |
| Sclerosomatidae       |    |                     |                 |                         |                   |
| *Prionostemma* sp.    | 48 | 16.7 (7.8–30.0)     | 1               | 1.0                     | 1.0               |
| Stygnidae             |    |                     |                 |                         |                   |
| *S. clavotibialis*    | 29 | 0.0                 |                 | 0                       |                   |
| Unidentified species  | 1  | 0.0                 |                 | 0                       |                   |

The prevalence of infestation for the entire sample (N = 415) was 9.9%, with 41 harvestmen infested by 178 mites. Confidence levels are presented where it was possible to determine at least 95% CIs.

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**Fig. 2.** Box plot of the intensity of mite infestation for six species of harvestmen (N = 41). Boxes indicate interquartile range (IQR) between 25th and 75th percentiles. The central horizontal bar is the median and whiskers indicate values lying within 1.5 x IQR. Outliers are represented by “o”.
harvestmen from CCF exhibiting the highest overall prevalence of infestation at 12.7% (Table 3). In contrast, harvestmen from SDF and UMF had similarly low overall rates of 2.1 and 3.6%, respectively. The prevalence of infestation was nearly twice as high for Cynortula in CCF and SDF as it was in UMF (Table 3). Similar patterns of variation were evident for P. inglei and R. albilineatus.

The intensity of mite infestation did not vary between habitats ($H = 4.06$, df $= 3$, $P = 0.745$).

The 30 mites found on the dorsum of a Cynortula (Fig. 3) in 2006 represent the first report of phoresy for mites associated with harvestmen in Trinidad and also represent one of only a few instances reported in the literature (Cokendolpher and Mitov 2007).

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**Table 3. Prevalence of mite infestation (percentage) for harvestmen species collected from several habitats**

| Species               | OCF     | Prevalence | SDF     | Prevalence | LMF     | Prevalence | UMF     | Prevalence |
|-----------------------|---------|------------|---------|------------|---------|------------|---------|------------|
| Cynortula sp.         | 161     | 10.6       | 11      | 9.1        | 14      | 0.0        | 20      | 5.0        |
| P. inglei             | 26      | 23.1       | 2       | 0.0        | 8       | 12.5       | 4       | 0.0        |
| Prionostemma sp.      | 23      | 30.4       | 19      | 0.0        | 2       | 50.0       | 3       | 0.0        |
| R. albilineatus       | 34      | 11.8       | 7       | 0.0        | 4       | 0.0        | 5       | 0.0        |
| S. serratotibialis    | 4       | 50.0       | 2       | 0.0        | 8       | 0.0        |         |            |

**Discussion**

This study represents the first investigation of the prevalence and intensity of mite infestation for a community of Neotropical harvestmen. In Trinidad, harvestmen are parasitized by larval erythraeid mites in a manner similar to that reported for mites and their temperate host species (Guffey 1998, McAloon and Durden 2000, Townsend et al. 2006). In our study, we also found that mites preferentially attached to locations on the host, primarily leg segments, in frequencies that are also similar to those reported for temperate species (McAloon and Durden 2000). Observations of living and preserved harvestmen infested with mites indicate that hosts generally are not in poor condition nor do they have difficulty with locomotion; thus, they do not seem to suffer any immediate detrimental effects of mite infestation. However, most individuals in our sample were only infested with one to three mites (Table 2). During the course of the study, we collected several individuals that were infested by six to 10 or more mites (maximum observed intensity was 17 mites for Cynortula).

For these individuals, the short and long-term effects of heavy mite infestations upon the survivorship, fecundity, and locomotion remain to be determined. In other arthropods, high intensity mite infestations (six or more mites) have been found to severely impair reproduction, especially in males (Polak and Markow 1995).

In contrast to prior studies (Guffey 1998, Townsend et al. 2006), our investigation provides insight into associations between larval erythraeid mites and a diverse community of harvestmen in forested tropical habitats. In general, we found interspecific variation in the intensity, but not the prevalence of mite infestation. Taxa that were most commonly parasitized included species for the families Cosmetidae, Manaosbiidae, and Sclerosomatidae. These taxa were also the most abundant in our sample, accounting for 82% of all individuals (339 of 415). Larger samples of less common taxa including agoristenids, cranaids, samoids, and stygnids are needed before we have a clear understanding of the ecological and natural history traits that most contribute to mite infestation. In our study, we did find that the prevalence of infestation (but not inten-
sity) varied across habitat type, with the highest infestation rates observed at the lowest elevation in crappo-cocorite forest (CCF). In Trinidad, CCF represents a disturbed habitat ("jungle") that generally supports a more developed understory than other forest types. This habitat may be favorable for erythraeid mite development and reproduction. Presently, little is known about the natural history of adult erythraeid mites (Southcott 1992), the conditions that are favorable for their survival, or the cues used by larvae to find arthropod hosts.

Other major factors that could affect interactions between larval mites and host species of harvestmen include microhabitat and the size or age of the host. Adult erythraeid mites inhabit the litter community and deposit eggs in the soil (Southcott 1992). To become infested, harvestmen must encounter larval mites as they move through the leaf litter or when they shelter within or beneath refuges, e.g., logs or rocks, near leaf litter. We hypothesize that harvestmen that live in proximity to the forest floor are more likely to be parasitized and with greater intensities than individuals that occupy more arboreal microhabitats, e.g., tree buttresses or bromeliads in the canopy. With respect to age or body size, we did not observe any instances of parasitism by mites upon sexually immature individuals, i.e., nymphs. The ability of larval mites to distinguish between nymphs and adults has not been empirically established and seems rather unlikely in that larval erythraeid mites are generalist parasites with respect arthropod hosts. Because harvestmen, like other arthropods, molt as they grow and mature, larval mites that attach to nymphs are probably lost when the host exoskeleton is molted. Therefore, mite parasitism of nymphs may have been inadequately sampled in our study.

In general, most observations of harvestmen and phoresy involve the transport of pseudoscorpions (Cokendolpher and Mitov 2007). Our observation of mite phoresy for a Neotropical harvestman is the first report of this type of ecological interaction in Trinidad and the Caribbean. Species of oribatid mites have been observed to be phoretic upon coleopterans (Evans 1992), but they have not been previously reported from harvestmen (Cokendolpher and Mitov 2007). Because of the secretive nature and nocturnal habits of most species of harvestmen, it is difficult to assess the ecological significance of this observation. Given the size of our field collections in 2005 (N = 415), we infer that the prevalence of these interactions are rare. However, given the ability of harvestmen to wander considerable distances over time (up to 0.2 km per night; Grether and Donaldson 2007), the ecological significance of phoresy for mites upon harvestmen could represent an important means of dispersal for mites under specific environmental conditions.

Acknowledgments

We thank the Pacheco family in Brasso Seco Paria village, S. Broadbridge (Caribbean Discovery Tours), P. Resslar, D. Dardis, and L. Heltsley for assistance with logistics and field work. We thank P. Resslar, K. Carson, T. Pesacreta, D. Otis, and J. Easter for helping with sample preparation, photography, and scanning electron microscopy. We also thank E. Aird, J. Aird, L. Hultgren, B. Albertson, and L. Johnson for technical support. We are grateful to E. Pante for assisting with the R language and environment. We also thank N. Platnick (AMNH), L. Predini (AMNH), R. Mercurio (AMNH), C. Griswold (CAS), and C. Carlton (LSAM) for assistance with specimen loans and depositions. This research was supported by a VWC Summer Faculty Development Fund (to V.R.T.), a faculty development grant from the CLA at Mercer University (to M.K.M.), Beta Beta Beta Research Foundation grant (to J.A.T.), VA Academy of Sciences Small Projects grant (to V.R.T.), VA Federation of Independent Colleges Summer Undergraduate Research grant (to D.N.P. and R.K.H.), and the Virginia Wesleyan College Science Undergraduate Research Fund. We are especially grateful to the Forestry Division of the Ministry of Agriculture, Land and Marine Resources of Trinidad and Tobago.

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Received 3 March 2008; accepted 16 July 2008.