Tulane University

Department of Ecology and Evolutionary Biology

March 1, 2007

Dear volunteers,

I am writing this letter from my office in uptown New Orleans, where things are starting to feel normal – I even moved out of my FEMA trailer recently. While over half of New Orleans is still empty and rotting, there is still hope here that we can successfully rebuild the city and set an example for how to prepare cities and manage ecosystems for rising sea levels and an increasingly variable climate. I also hope that Tulane University can continue to be a leader in the New Orleans renewal and in conducting the research necessary for managing wild and urban ecosystems. As a part of that research effort, I was happy to have the help of six Earthwatch teams here in New Orleans. I was also happy to spend some time away from New Orleans and out in the field with four successful teams in Arizona, Costa Rica, and Ecuador. I really hope the final report provides you with a sense of how successful the Forest Caterpillars project has been because of your excellent field assistance.

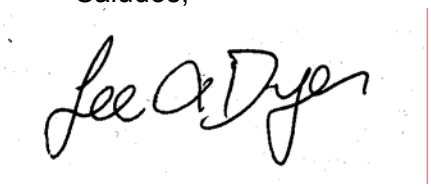
I have been impressed with the amount of high quality data that Earthwatch volunteers have collected with us over the past 10 years. I am sure that I will continue leading this research for at least 20 more years, and I hope to keep discovering new species and new associations. Perhaps the most important paper that we have completed from these data is our paper that is currently in review to the journal *Nature*. We found that diets of tropical caterpillars are more specialized than their temperate forest counterparts. We hope that this paper helps resolve issues about how diversity is maintained and debates about how many species of animals are on earth. We have also been making improvements to the web page (caterpillars.org), including extensive plant species pages for Ecuador, enhanced pages in Spanish, and pages for parasitoids. In many ways, the web pages contribute to science and education more quickly and efficiently than any of our publications.

If you are wondering about the rest of the team of plant/caterpillar/enemy investigators, feel free to send an email asking for their addresses. The Ecuadorian gusaneros, Maria, Rafael, and Wilmer are all still working on the project, collecting and rearing amazing numbers of caterpillars. Beto, Gerardo, Grant, Genoveva, Angela, Tara, Clark, Michael and Mark are still working full-time with me on various projects, including the caterpillar work. Mike Singer is still in Connecticut and hopefully will be with the team in Arizona again this year. Harold Greeney is still up in the cloud forest chasing after butterflies, helping researchers, and transforming Yanayacu into a major research center.

I would like to thank all of you for your hard work. As an extended team, we have a strong database and positive memories of great people. My collaborators and I have enjoyed working with the volunteers, and our project

would not be successful without your help. We also want to thank all of you for sending us great emails, cards, pictures, slides, and other thoughtful items. We definitely appreciate this correspondence. Please feel free to keep in touch and we will do our best to respond. Hopefully we'll see you again in the field.

Saludos,



Lee Dyer, gusanero

EARTHWATCH INSTITUTE FIELD REPORT

Project Title: Forest Caterpillars

Principal Investigator: Lee Dyer

Position/Affiliations: Professor, Tulane University

Research Sites and Local Management Status:

Napo, Ecuador, -0.583, -76.13, Biological Reserve, National Park
Sarapiqui, Costa Rica, 10.4, -82.0, Biological Reserve, National Park
Arizona, USA, 31.88, -109.2, Biological Reserve, National Forest
New Orleans, LA, USA, 31.00, -90.15, City

Scientific names of primary species being studied:

Lepidoptera, Hymenoptera, Diptera, Angiosperms, Nemata

Key Research Objectives:

- Are tropical caterpillars more specialized than temperate caterpillars?
- What affects diversity and abundance of caterpillars and parasitoids in natural forests and adjacent agriculture (banana and alfalfa)?
- What parasitoids might be good candidates for biological control in banana plantations and alfalfa fields?
- How do variation in precipitation and temperature affect levels of parasitism (and subsequently affect caterpillar densities)?

Data Collection and Results

Diversity and caterpillar specificity
For many animals, species richness is much higher in tropical compared to temperate habitats. A major challenge in community ecology and evolutionary biogeography is to determine what creates these differences. For herbivorous insects, one such mechanism leading to an increased number of species in a given locale could be increased ecological specialization, resulting in a greater proportion of insect species with narrow resource requirements within a community. We used data from all of our Earthwatch sites along with collaborators' data to test this hypothesis by comparing host specialization in larval Lepidoptera (moths and butterflies) at eight different New World forest sites from southern (Table 1).

We found that diets of tropical caterpillars are more specialized than their temperate forest counterparts: tropical species on average feed on fewer plants species, fewer plant genera, and fewer plant families than do temperate caterpillars (Figure 1). This contrasts recent studies (by V. Novotny) that suggest that tropical herbivores are not more specialized and that conclude that there are fewer than 4 million species of animals in the world (compared to estimates of 30-80 million species made with the

assumption that tropical herbivores are specialized). The Novotny study used only 8 focal species of plants, which can yield misleading results (Figure 1).

Table 1. Caterpillar rearing databases used for the current study. Rearings include only those portions of the databases used for analyses in this study. Sampling area was estimated for Canada, Louisiana, Arizona, and Ecuador, where multiple sites were sampled. Hours of search effort were estimated for Panama but were not estimable for Canada and Connecticut. For number of caterpillar or host plant taxa, fam = families, gen = genera, spp = species. All vascular plants were sampled for all sites but Canada, where only trees were sampled. Earthwatch sites are Arizona, Louisiana, Costa Rica, and Ecuador.

Study Site	Median Latitude	Sampling Area (ha)	Rearings	Caterpillars (fam, gen, spp)	Host Plants (fam, gen, spp)	Effort (hours)	Years
Canada	47° 15' N	80,000,000	131,431	28, 280, 653	27, 59, 155	Unknown	20
Connecticut	41° 30' N	1,437,100	3,158	19, 166, 252	12, 13, 14	Unknown	5
Arizona	32° 13' N	1,000,000	7,601	20, 136, 184	50, 104, 161	9,000	10
Louisiana	31° 00' N	500,000	2,300	19, 98, 127	48, 77, 106	5,000	6
Brazil	15° 56' S	10,000	5,614	43, 264, 565	44, 80, 109	8,000	12
Costa Rica	10° 25' N	2,400	22,348	29, 223, 509	72, 176, 281	52,000	15
Panama	9° 10' N	1,600	4,536	30, 384, 401	57, 139, 209	8,000	9
Ecuador	0° 25' S	30,000,000	24,413	13, 65, 192	53, 110, 177	72,000	6

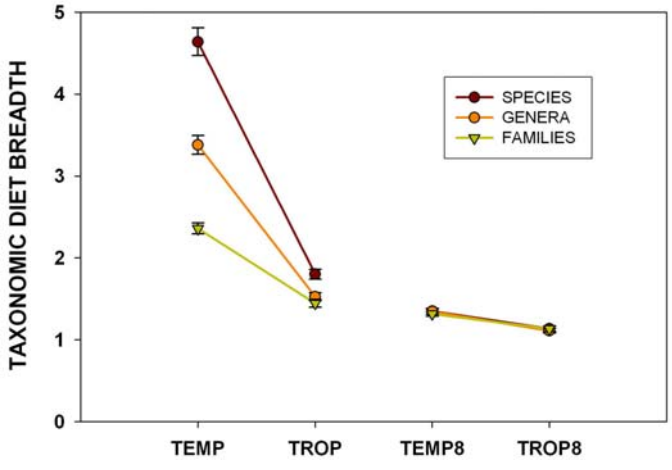


Figure 1. Mean caterpillar diet breadth (± 95% confidence intervals) for 1052 temperate caterpillar species (TEMP) from two subtropical and two temperate sites and 1585 tropical caterpillar species (TROP) from four sites in Central and South America. Diet breadth was measured as the number of taxa (families, genera, species) of host plants per caterpillar species. When eight focal host plant species were chosen randomly from each site, to reflect previous diet breadth studies, the difference between temperate (TEMP8) and tropical (TROP8) diet breadths are greatly reduced.

As a result of the increased specificity, there is greater change in caterpillar species composition (greater β diversity) between tree species in tropical faunas than in temperate faunas – this means that you are more likely to find the same caterpillar species on different plants at the Arizona site compared to the Costa Rica site (Figure 2). These results help us understand the incredible diversity of the tropics and also push up estimates of animal diversity, since lower estimates of diversity assume that specialization is not as restricted as we have found.

We concluded that host plant specificity of herbivorous insects is, on average, greater in the tropics than at higher latitudes, and that a latitudinal gradient of dietary specialization is evident from our data. The evidence from this study is consistent with the hypothesis that ecological specialization is a factor in the origin and maintenance of high biodiversity in the tropics. Our previous Earthwatch results have indicated that this increased specialization in tropical herbivore communities may be due to more intense parasitism from wasps and flies and more toxic host plants – a specialized diet helps tropical caterpillars avoid these pressures. The underlying mechanisms for differences in specialization by latitude, and perhaps by longitude, will continue to be a focus of our Earthwatch research. While it is clear that a significant proportion of tropical animal diversity is a product of a higher number of plant species, our results also imply that greater ecological specialization contributes to the great diversity of herbivores in rainforests and lends support to higher estimates of the total number of species on earth.

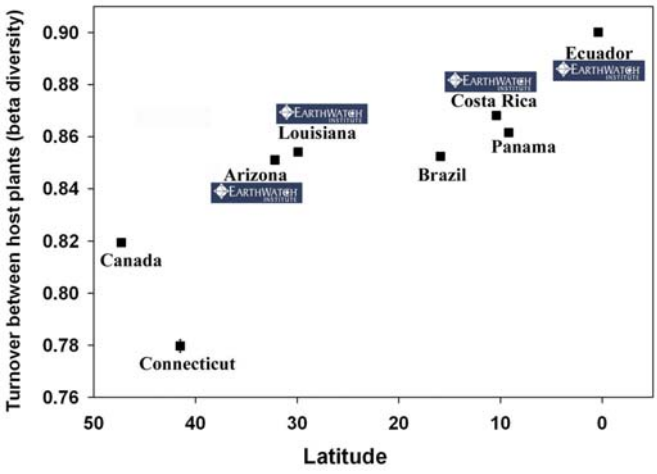


Figure 2. Diversity (β) of herbivores between plants for two temperate (Canada, Connecticut), two subtropical (Arizona, Louisiana), and four tropical (Brazil, Costa Rica, Panama, Ecuador) sites, ordered by an approximate modal latitude for each site. With this measure, insect species turnover across host plants is used as an index of host plant specialization, with higher values of β indicating higher levels of specialization. Symbol size indicates 95% confidence intervals. Earthwatch sites are marked with the Earthwatch logo.

Significance/Benefits of Research

Diversity and natural history

Our most significant accomplishment in 2006 is the compilation of natural history data related to approximately 3,200 species of caterpillars, plants and parasitoids. We share this natural history information with locals and scientists alike, including talks in Spanish to Costa Rican and Ecuadorian students, naturalists, and local workers; the local talks have increased awareness and respect for insect diversity. Many of the naturalist guides at our research sites use our data and images and find caterpillars during their tourist walks to discuss the role they play in the forest. We also share these data with anyone who has internet access by publishing it on caterpillar web pages at www.caterpillars.org. The web pages are constantly undergoing improvements and

should be a very useful tool for managing and studying biodiversity for many years to come. In addition, our basic research on diversity relationships between trophic levels will contribute to a growing understanding of how parasitoids and other natural enemies affect entire biotic communities.

Sustainable agriculture
Managers of banana plantations, alfalfa fields, and other agricultural systems who are attempting to control pests without using pesticides will benefit from increased knowledge of the parasitoid community. First, we discovered at least 35 new species of parasitoids in the families Braconidae and Tachinidae, all of which are potentially important biological control agents. Second, our modelling approach is being used to identify the most important biological control agents in tropical agriculture under different pesticide management, which allows plantation owners to manage for caterpillar pests without resorting to harmful insecticides.

Sustainable employment in the rainforest
Although it is not a direct benefit from the research, our Earthwatch project benefits the local communities by supporting the research stations and by continuing collaborations with local naturalists and scientists. Field stations generally benefit the communities by providing excellent employment opportunities that are not destructive to the forest and by boosting the economy. At the Costa Rica site, we continue to provide long-term employment to local naturalists, Gerardo Vega and Humberto Garcia; at the Ecuador site, we have provided long-term employment to at least 3 full time field assistants. We plan to continue hiring as many local naturalists as possible, depending on continued funding from other sources.

Environmental education
Finally, our work has directly benefited the educational community because many volunteers have been school teachers and have incorporated ideas learned from this project into their classes. In collaboration with volunteers on the New Orleans teams, we developed a web site for this educational outreach (http://www.tulane.edu/~ldyer/outreach/Welcome.html - it is currently being revised). As part of this outreach, our laboratory works with local schools (K-12) on insect ecology education. Our work has also indirectly benefited the educational community because the research addresses basic theoretical questions in ecology. For example, one of the most important issues to which our Earthwatch project has contributed is the idea of "trophic cascades." Theory predicts that the effects of predators and parasitoids on plant biomass and diversity should not be great in complex systems such as rainforests, but we have demonstrated that the enemies of caterpillars significantly enhance plant biomass and diversity by killing caterpillars. This means that the consequences of tropical predator extinctions are more severe than previously thought, and predators of all sizes and all predatory guilds (i.e. including parasitoids) should be a major focus for conservation efforts. These ideas are summarized in a book chapter (Dyer 2006, referenced below).

Dissemination of Results *(all publications below are available in pdf format at: http://www.tulane.edu/~ldyer/papers.htm)*

Peer reviewed articles and book chapters
Dyer, L.A., M.S. Singer, J.T. Lill, J.O. Stireman III, G.L. Gentry, R.J. Marquis, R.E. Ricklefs, H.F. Greeney, D.L. Wagner, H.C. Morais, I.R. Diniz, T.A. Kursar, and

P.D. Coley. *Revised, in review.* Host specificity of Lepidoptera in tropical and temperate forests. Nature.

Dyer, L.A. and D.K. Letourneau. 2007. Determinants of lichen diversity in a rainforest understory. Biotropica. *In press.*

Dyer, L.A. 2007. Insects in the dark. In: Adams, R. (ed.). Reflections by Moonlight. University Press of Colorado. *In press*.

Dyer, L.A. 2006. The ecology of tri-trophic interactions in the tropics. In: Carson, W.P. and S.A. Schnitzer (editors). Tropical Forest Community Ecology. Blackwell Science, Oxford, UK.

Presentations
University of Texas, Austin, 2006
University of Maryland, 2006
Wright State University, 2006
Southestern Louisiana University, 2006
Organization for Tropical Studies, 2007

Volunteer Tasks and Accomplishments

In our 10th year of funding by Earthwatch, we were fortunate to have the help of 49 volunteers. These volunteers helped us bring our rearing total up to approximately 2,100 species of butterflies and moths (35,000 individuals), over 400 species of parasitoids, and 750 plant species. The 10 teams participated in all aspects of our Forest Caterpillars project. Team members searched for and collected caterpillars, noted possible morphological or behavioral characters, and took care of the larvae. At La Selva, Tirimbina, and Yanayacu they also assisted with experiments on the understory pepper plants, *Piper* spp. and helped with encapsulation experiments. In New Orleans, volunteers helped get the laboratory back on its feet after disruptions from hurricanes, and helped kick off our project to examine the effects of the hurricanes on caterpillar outbreaks. In Arizona, the volunteers contributed to new design for determining altitudinal gradients in plant-caterpillar-parasitoid interactions, which will be a focus at all of our sites in the future.

The 10 teams logged over 2,000 total person hours in the field, searching for and recording data on caterpillars and working on related experiments. At La Selva and Tirimbina, they found over 1,400 caterpillars belonging to 85 butterfly and moth species in 24 families; at least 12 of those were new species. From these caterpillars they reared over 20 species of parasitoid wasps and flies. At the Southwest Research Station, volunteers collected 400 individual caterpillars for a total of 40 species in 15 families. At least 12 species of parasitoids were reared. The teams in Ecuador contributed to our NSF funded biotic survey and inventory of the eastern slope of the Andes, collecting 2,200 caterpillars, including 90 species in 19 families, and a couple dozen new species. The site will continue to yield many new species of caterpillars and parasitoids (Figure 3). The host plant data at our four Earthwatch sites were used in our important new finding that tropical caterpillars are more specialized than temperate caterpillars.

Figure 3a. Two potentially new species in the family Sphingidae. These rare caterpillars were parasitized, so unless we find them again, they will not receive a scientific name. Yanayacu Biological Station, Ecuador.

Figure 3b. Cryptic geometrid caterpillars from the Southwest Research Station, Arizona (top image, *Synchlora* sp.), Reserva Tirimbina, Costa Rica (middle image, *Eois* sp.), and New Orleans, Louisiana (bottom image, *Antepione* sp.). All caterpillars were collected in survey plots that are utilized at the Earthwatch field sites. The plots and other survey work we completed at these research sites allowed us to complete the analyses of trophic interactions described in this report.

Figure 4. This new species of tachinid fly, *Hyphantrophaga* sp., emerged from an unknown skipper (Hesperiidae) caterpillar that it had parasitized. More information on this species is published on caterpillars.org, under the Ecuador pages.

Project Development

The data we have collected thus far at all sites support our hypotheses that the dynamics in these strikingly different habitats (Arizona, Ecuador, Costa Rica, Louisiana) are very similar, but the actors are different — species composition of the caterpillars and their parasitoids show very little overlap. The larvae that we studied exhibited a wide array of defenses, and we continued a focus on two specific defenses: frass-throwing and encapsulation. Several more years of data will allow us to make conclusions about how these defenses function against different types of parasitoids. For all sites, we will continue to focus on collecting new species (Figure 4), but we will also focus more on altitudinal gradients in parasitism, similar to the precipitation gradient that we've tested.

Educational Opportunities

Educational opportunities were provided to:

- Local communities. We employed six local naturalists and gave talks to local residents at all of the research sties.
- Students. Nine graduate students in Dyer's laboratory participated in the projects, either directly or by analysing data and working on papers. Seven undergraduates were also involved with the Earthwatch research. One PhD dissertation was completed with help from the Earthwatch funded work.
- Early career scientists. One post doctoral researcher (Gentry) and three Assistant Professors (Walla, Stireman, Singer) helped run Earthwatch teams.

Our Earthwatch project has united workers from Costa Rica, Ecuador, and the United States to maximize the effectiveness of caterpillar-parasitoid inventories. All of the research stations involved are centrally located near a wide variety of habitat types, including national parks and other protected areas. The research and associated educational activities enhance the educational and conservation missions of these field stations. More directly, the education and employment of local workers on the projects greatly enhance the credibility of conservation projects.

Acknowledgements

Research assistants:
Costa Rican paraecologists: Gerardo Vega, Humberto Garcia, Maylin Paniagua
Ecuadorian paraecologists: Rafael Maitio, Wilmer Simbana, Maria de los Angeles
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Collaborators:
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Dr. Grant Gentry, Tulane University, Ecology and Evolutionary Biology
Dr. Craig Dodson, Mesa State College, Chemistry
Dr. Thomas Walla, Mesa State College, Biology
Dr. Daniel Janzen, University of Pennsylvania
Dr. Deborah Letourneau, University of California, Environmental Studies
Harold Greeney, Yanayacu Biological Station
John Lill, George Washington University, Biological Sciences
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Scott Shaw, University of Wyoming, Entomology
Phil DeVries, University of New Orleans, Biology

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Organization for Tropical Studies
Tulane University

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