Take-home exam exercise for EEB 5449, Fall, 2014. C. S. Henry
ANSWER BOTH QUESTIONS BELOW. Please restrict the length of your ENTIRE exam to **6 double-spaced pages**. Note that the questions are of equal credit. **Due end of 17 Oct**.

QUESTION 1.

You are an evolutionary biologist interested in speciation. You've encountered a species of planthopper, *Nilaparvata beigei* (Hemiptera: Auchenorrhyncha: Delphacidae), with an Holarctic geographical distribution, which is a generalist feeder on grasses. It's a dull brown insect, showing very little morphological variation across its huge range. All attempts by you and other trained systematists to separate this monolithic species into separate species based on color patterns, setal (hair) locations and patterns, wing venation, and ecology have failed. There is some anecdotal evidence that some individuals seem to prefer tall-grass hosts, while others prefer short-grass hosts, but there still remains the problem of telling the putative "ecotypes" apart.

For years, biologists thought that planthoppers had simple mating behavior: the male approaches the female from the side, sits there for a few minutes, then dashes up and copulates. Yet more recent work has shown that these insects produce vibrational signals within their substrates, using tymbal organs on the sides of the body and touching their bodies to the surface while "buzzing." It turns out that both sexes sing identical 'songs' and duet with each other before they will copulate. The songs are complex, and you've discovered that the single 'species' *Nilaparvata beigei* in fact is a swarm of at least 12 cryptic morphs (or species?), each singing a different song. In many regions, distinct cryptic song species occur sympatrically, often two or more on the same grass tussock.

In addition to what is described above, you also have this additional information:

- Insects are not brainy: the songs are totally hard-wired, not learned.
- Long-grass stems are better at propagating vibrational signals of certain characteristics, while short-grass stems are better at propagating signals of other, different characteristics.
- Behavior choice tests indicate that neither females nor males respond to the songs of 'heterotypic' (i.e., not their own) morphs, rejecting heterotypics completely if given a choice of heterotypic vs. homotypic partners.
- Most of the cryptic morphs are interfertile when taken into the lab, confined together, and given no choice; both F_1 and F_2 generations are viable and show little reduction in either fertility or fecundity.
- With one exception (see below), hybrids between song morphs, based on possession of intermediate songs, have not been found in the field, despite extensive collecting.
- The diversity of song morphs living sympatrically is higher in mountainous regions — e.g. the Coast Range and Sierras of western North America, the Alps of central Europe, the

Himalayas and surrounding highlands of central Asia, the mountains of China — than it is in non-mountainous regions.

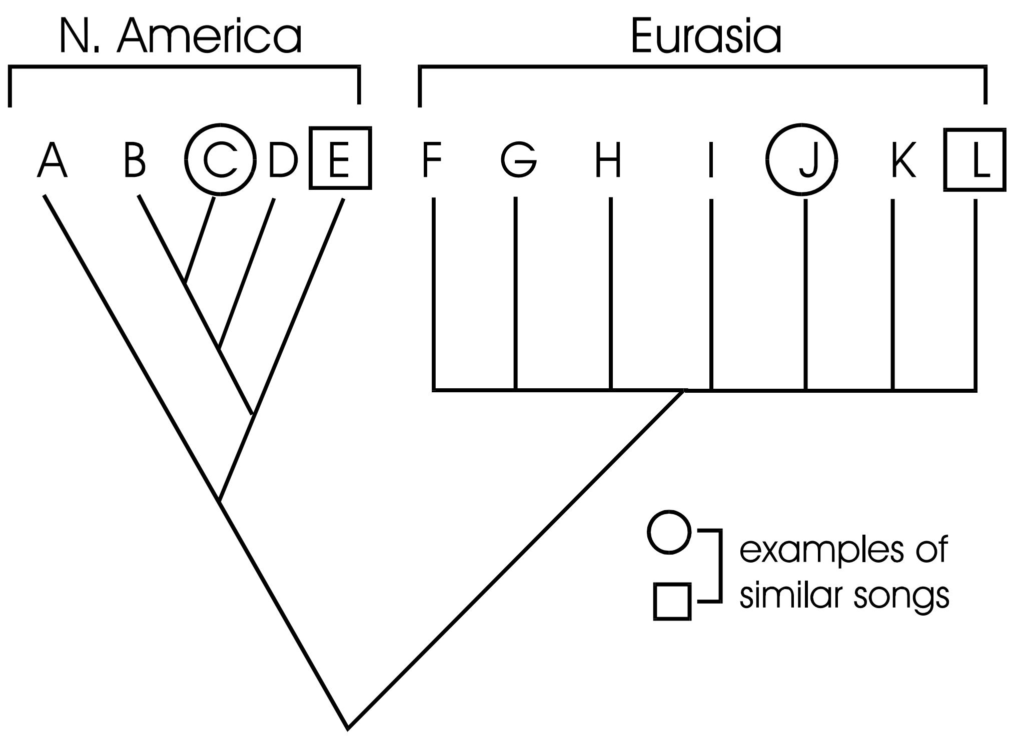
- Songs of potentially sympatric song morphs are more distinct from one another than are songs of morphs whose geographic ranges do not overlap.

- In fact, there are at least two examples of nearly identical songs, characterizing morphs in western North America versus central Asia (C and J, E and L; see cladogram below).

- Sequence data from the mitochondrial genome indicate that the cryptic song morphs are no more different from one another (measured by percent sequence divergence) than local populations are for most other insect species.

- The sequence data above, from four mitochondrial genes, have been used in a phylogenetic analysis; the resulting hypothesis of relationships is shown in Figure 1. Despite lack of resolution within the Eurasian complex, there is 100% confidence in the North American/Eurasian split.

- Song morphs F and G are apparently producing intermediate hybrid singers in a narrow region of the Pyrenees mountains separating Spain from France; the hybrids are rare and are found only in a band 4 km wide.



Issues you should address are listed below. You need to develop convincing arguments consistent with the available evidence. Invent as few *ad hoc*, unsupported assumptions as possible: rampant speculation is frowned upon by your readers. Also, keep it concise!

(a) Should these song morphs be considered real species? Why or why not? Include the issue of different species concepts in your discussion.

(b) How do you interpret the extreme morphological similarity among these song morphs? Things that you might address include extent of genetic divergence, rates of evolution, time(s) of divergence, mode of communication, reproductive isolating mechanism, etc.

(c) How do you interpret the fact that these bugs are more diverse in mountainous areas than elsewhere?

(d) How do you interpret the fact that songs are more distinct between (among) morphs in sympatry than they are in allopatry? Include the issues of reproductive character displacement, reinforcement, or alternative explanations.

(e) What's going on, in an evolutionary sense, with the morphs F and G in the Pyrennées? That is, fit this situation into your developing suite of consistent hypotheses regarding this planthopper system.

(f) Are there problems with the molecular phylogeny? How could you improve its resolution? (you might want to include this in your "what I would do" section, below).

(g) Discuss the likelihood of chance versus convergence as explanations of similar songs in species-pairs C + J and E + L. What tests would you use to figure out what's really going on? (one approach: Think in terms of testing for adaptation, and show specifically how you'd do it here).

(h) Assume for the moment that the hypothesis of convergence is supported. Discuss how this might give the Biological Species Concept precedence over alternative views of species isolation and barriers to gene flow between species (at least in this system).

(i) Present a convincing hypothesis of evolution and (possibly, depending on your view earlier) speciation in this planthopper taxon.

(j) What needs to be done in this system? That is, what would you do, and how, if you were writing a grant proposal to the National Science Foundation?

QUESTION 2.

You are a high-powered scientist who knows everything there is to know about every aspect of evolutionary biology – in fact, that's why you were selected by the Highly Prestigious journal PNAS to review a paper that needs to be published Right Away because the authors are very high-powered, too.

Here's the article, with the electronic link to it:

Opie, C., Q. D. Atkinson, R. I. M. Dunbar, and S. Shultz. 2013. Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 13328-13332.

Link: <http://www.pnas.org/content/110/33/13328.full.pdf+html?with-ds=yes>

Write a review of this paper, assuming it is a 'new submission.' When you are done, decide whether it should be (1) accepted with no changes, (2) accepted with minor changes, (3) reconsidered after major revision, (4) rejected but with the possibility of resubmission, or (5) rejected without reconsideration.

A good review should follow the guidelines below, though not necessarily in any particular order; nor do you need to include every bulleted point. And feel free to add others.

- Give a brief summary of the study, including the background, key hypotheses, results found, conclusions drawn, and the stated importance of the study to its field.

- The questions examined in the paper should be significant ones; what important evolutionary issues does this particular study address, and (briefly!) why are they important?

- Is the writing style clear, concise, engaging, and sufficiently free of jargon?

- Is the paper too long for a relatively trivial result, or does it beg for elaboration? If too long, is this because of repetition? Specify which text sections (if any) can be removed without compromising the paper – or, what text should be added.

- Are hypotheses clearly described, along with their predictions? Do the authors clearly enumerate and explain explicit tests of those predictions that they plan to carry out? And are the methods for testing those hypotheses well designed?

- Are the results and conclusions properly supported by tables, figures, and statistical tests? Are all tables and figures easy to interpret and necessary? Are the statistics appropriate, unambiguous, and easy to understand, at least after you as the reviewer have done a little homework? Should the authors have included additional or alternative tables and figures or applied different statistical tests to their data?

- Do you think that there are more convincing interpretations of the results than what the authors have considered, and if so, what are they and why are they preferable?

- Is the study properly placed in a broader context, such that its significance to the field of evolutionary biology is made clear? And related to this, for what audience might the authors be writing, associated with which particular sub-discipline? In your opinion, does the paper hit its mark, or go astray?

- Does the study have broader significance, e.g. to the general public, and if so (and we hope so), is that broader significance articulated well?

- Should the authors do more work before the paper will be acceptable for publication, and if so, what specific recommendations do you have for them?