FEATURE ARTICLE

Teaching Evolution Using Semester-Long Student Investigations of Adaptation by Natural Selection

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Abstract

Case studies are valuable tools for instruction but are often limited to a single topic and a single class period. Courses such as evolution that synthesize multiple concepts around a common theme, however, can use a single case study type project that extends over the entire semester to develop and link core concepts. A central theme in evolutionary biology is determining if complex biological traits represent adaptations that arose by natural selection. The instructional model presented here engages students in a step-by-step process to answer this question of adaptation for a trait of their choosing. In this process, the instructor first introduces the major concepts required to address adaptation. As each major concept is developed in class, students apply this concept to their particular trait, using information gathered from published studies. Students then report their research back to the class. At the end of the semester, each group synthesizes their evidence into a paper developing an argument as to whether or not their trait fits the criteria of being an adaptation. This project provides students with ownership of course material, gets students to act as practicing scientists, and helps them integrate and apply theoretical material to real questions.

Key Words: *natural selection; fitness; active engagement; collaborative groups; evidence; case study.*

○ Introduction

Active engagement in course material can enhance student learning, but getting and maintaining student engagement in the classroom can be challenging. When students have the opportunity to use and apply new information, they tend to better understand and retain the lessons (Gormally et al., 2009; Schank et al., 1999). One common and highly successful method of actively engaging students in learning is through case studies (see National Center for Case Study Teaching in Science; https://www.nsta.org/case-studies). Most case studies are of short duration and focus on a single topic leading to potentially high-quality but short-term engagement in a single topic. The instructional model presented here takes the key components of case study instruction and expands the process over the majority of the semester. This provides an overall course structure that actively engages students with core course content at a deep level and provides student ownership of the material. A sense of ownership is important for student success (O'Neill, 2005). This unique course structure was designed and implemented in an upper-level undergraduate evolutionary biology course and will be described here in this context. However, this model may be applicable to other courses where there is a major overarching question central to that field that can be broken into multiple conceptual steps.

Getting students to understand evolution is important because the concept of evolution links all of biology together and is fundamental to understanding biology (Dobzhanski, 1973). However, students tend to have a poor understanding of this core idea in science (reviewed in Gregory, 2009), and cognitive biases can significantly interfere with student learning of evolutionary concepts (Barnes et al., 2017). For example, teleological reasoning, or explaining something by its end result rather than what caused it, often plays a large role in impairing student understanding of natural selection. As evolution is a unifying, cross-disciplinary concept in science (Gould, 2002), it also requires students to understand and apply material from other fields such as genetics. Yet genetic mechanisms important to understanding evolution, such as mutation and random variation, can also be particularly difficult for students to grasp (Morabito et al., 2010).

> *The semester-long case study model presented here for examining the process of adaptation by natural selection helps students contextualize and apply many major concepts in evolution.*

In the instructional model presented here, students work in groups to develop and present arguments for five different major conceptual issues that apply to whether a phenotypic trait should be considered an adaptation. The students' arguments are based on evidence they find in the primary literature. Lecture and lab exercises add additional content

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while scaffolding the material to help students make conceptual connections between their individual research goals and specific course content. When argumentation is made an explicit part of instruction, it appears that understanding of content can improve (Asterhan & Schwarz, 2007; Zohar & Nemet, 2002). Students also develop arguments based on evidence that crosses disciplinary fields, such as applying genetics to development of phenotypes.

The process of adaptation by natural selection, how complex traits of organisms develop and come to fit their environment so well, is a core concept in evolutionary biology and remains an active area of investigation. Over the course of the semester, each group of students finds and evaluates evidence for the hypothesis that a particular biological trait is an adaptation that arose by natural selection. Figure 1 presents a visual summary of the timeline of different activities outlined here and provided in detail in the course description section below.

At the beginning of the semester, each of several student groups picks a different complex biological trait to investigate. Examples of traits students have used are provided in Table 1. Evidence required to test the hypothesis that a trait is an adaptation is broken into five main criteria that also represent major conceptual areas in evolutionary biology and major learning goals of the course (Table 2; Brandon, 1991). During the semester, each group applies each of these five major concepts one by one to their particular trait.

Groups follow a jigsaw format to investigate and present each criterion as it is introduced and developed over the semester. Following the in-class introduction to each criterion, one student from each group takes the lead and researches the primary literature, looking for studies that investigate that particular concept/criterion with respect to their group's trait. These lead students review the available data and develop an argument based on that evidence as to whether or not that criterion supports the hypothesis that their trait is an adaptation that arose by natural selection. Then the student who did the research from each group presents their argument to the class. First, these students work together to give a brief panel presentation providing an overview of the importance of that criterion to the process of adaptation. Then each of these lead students presents the evidence they found for this particular criterion as it applies to their group's specific trait. This process proceeds in

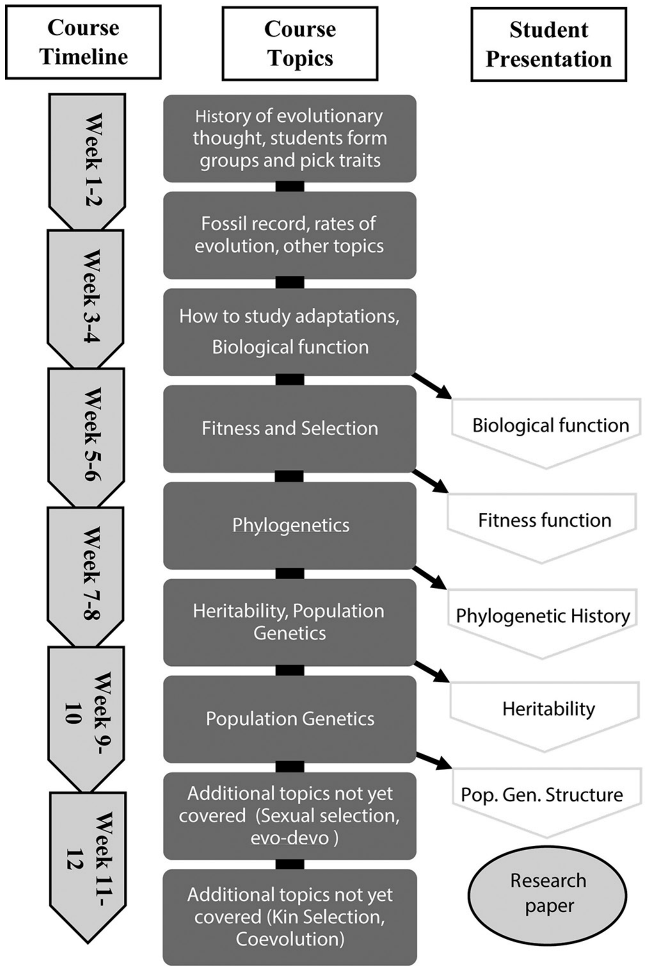

Figure 1. Course structure. The first column gives the approximate time in the semester each event takes place. The second column gives the order of content presented in the course. The third column gives the criteria for adaptation under study and approximate timing of each set of student presentations.

Table 1. Topic choices: A sample of potential traits for this case study. Many phenotypic traits could be used in this case study. The trait should be fairly unique and distinct enough to allow students to clearly define the phenotype. It is important that there are published studies to provide enough information for the students to develop some conclusions.

Trait	Description
Rattlesnake rattle	One group of pit vipers has developed a modified tail that makes noise.
Siblicide	Booby (blue-footed and Nazca) chicks will kill their younger brothers and sisters. How can this be an advantage?
Human speech	One of the things that really sets us apart.
Paedomorphosis in salamanders	Sometimes adult tiger salamanders do not turn into terrestrial adults but stay in their larval form.
Alternative mating strategies in male sunfish	Some males are territorial while others use sneaky strategies to mate.
External testes in some mammals	Most vertebrates have internal testes. However, in some mammal species, the testes move out of the body during development.
Altruism in humans	Why do some people risk their lives to help others?

Deciduous leaves	Oaks (for example) occur in both the temperate and tropical regions. Here they drop their leaves all at the same time. Is "fall" adaptive?
Flower color	We mostly think about plants as being green. However, the reproductive organs of many (flowers) are very brightly colored.
Armor in male stickleback fish	These little fish, found in both salt water and fresh water, are covered in armor-like plates and have spines that stick out.
Feathers	One of the characteristics associated with birds and their relatively unique ability to fly are feathers.

Table 2. Criteria used to make an argument that a trait is an adaptation that arose by natural selection (Brandon, 1991). The only real restriction to the order is that biological function needs to come first so that the phenotype under study is clear to all following group members.

Criteria	Brief Descriptions of Criteria
1) Biological function	Description of the phenotype students will be studying. What is the physiological, physical manifestation of the trait? This is also known as proximal function or how the trait functions in current ecological time.
2) Fitness function	How does the trait impact survival and/or reproduction?
3) Phylogenetic history	Is the trait evolutionarily new to the group under study? What was the ancestral state of the trait, and what is the distribution of the trait across the phylogenetic history of the groups that possess the trait?
4) Heritability	Is there a genetic basis for variation in the trait that can allow it to respond to selection?
5) Population genetic structure	Do past or current selective environments support the selective arguments being made above?

a stepwise (jigsaw) manner through the semester until each of the five conceptual areas has been developed formally in lecture and lab exercises, researched by the students, and finally presented to the class by a student from each group. Providing students with clearly defined roles within their group like this enhances the effectiveness of team building within groups (Salas et. al., 1999; Theobald et al., 2017).

Once students present on the last criterion, each group synthesizes its individual research findings on their trait into a single paper. This final paper presents all their accumulated evidence and evaluates how well the evidence from each conceptual component supports the hypothesis that their particular trait is an adaptation that arose by natural selection.

This teaching technique has been used in both an upper-level undergraduate evolution course for biology majors (class sizes have ranged from 8 to 26) and a second-year honors seminar course (20 students, not limited to science majors).

○ Course Description: Details of the Process Applied to Evolution

At the beginning of the semester, the instructor presents a brief overview of the case study goals and objectives to the students. The instructor also provides a description and introduction to each of the traits on the list the class will pick from to study (see Table 1 for a list of potential traits). Students then have the opportunity to form groups based on topic choice preferences and preferred group members. As there are five criteria, groups of five students work best so that each student can focus on a separate criterion. Students can also decide at this point whether they want to investigate a trait not on the list. The students must propose the trait for approval by the instructor, who then evaluates the appropriateness of the trait for this process. If it is a trait the instructor is not very familiar with, the instructor will need to do enough of a survey of the literature to determine whether there are sufficient studies available for this trait that address the key criteria for this study of adaptation.

The instructor then introduces the concept of adaptation and major approaches to studying adaptation. Discussions of papers like "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" (Gould & Lewontin, 1979) and the first three chapters of *The Blind Watchmaker* (Dawkins, 1986) support these objectives well. As the case study process does not cover all course content, those topics not covered, such as the history of evolutionary thought, geologic record, rates of evolution, kin selection, evo-devo, coevolution, and sexual selection, can be bookended to the beginning and end of the semester. This can be done with lectures and presentations, as preferred by the instructor, and help provide a framework for what evolution is about before jumping into the details of natural selection and adaptation.

The instructor then introduces the specific format of the case study model they will be utilizing for the rest of the semester to examine the process of adaptation (see Figure 1). This model is based around five criteria or levels of evidence required to determine whether a trait is an adaptation that arose by natural selection as outlined by Brandon (1991). In brief, these five criteria for the traits are (1) biological function, (2) fitness function, (3) phylogenetic history, (4) heritability, and (5) population genetic structure. These five criteria are defined in Table 2, and a more detailed handout of these definitions can be found in the Supplemental Material available with the online version of this article. Each student within the different groups picks one of these five criteria and will take the lead on researching and presenting it with respect to their group's trait.

After choosing a topic to investigate, students begin by reading general introductions to their topic area (e.g., textbooks, book chapters, web pages) and collecting sources. Each group then works together to write a prospectus outlining how they propose their trait will fit each of the criteria. The prospectus is brief and simply involves writing about the five major questions that must be addressed to establish that a trait is evolved and how those questions are to be phrased with respect to their topic. This document is intended to help students focus on what they will be looking for in their reading.

Biological function is the first criterion to develop, as it defines the phenotype (structurally and functionally) on which the rest of the group members will be focusing their efforts. The focus in this first section is on describing the proximal function of the trait. Once provided with the conceptual background, students who picked the biological function criterion search for primary literature that describes the details of the phenotype of their trait. The material presented in class, meanwhile, moves on to the concept of evolutionary fitness, the second major criterion. Clearly separating the proximal biological function of a trait from the fitness implications of the trait helps students break the cycle of teleological thinking about natural selection. By having to clearly articulate how the phenotype interacts with the environment to promote fitness, students can better understand the context dependence of selection.

About one and a half weeks into the evolutionary fitness material, students who picked the biological function criterion present their research findings to the class. Presentations begin with a short panel where the presenters from all the groups work together to give a brief explanation of what the criterion is and how it fits into the context of the study of adaptation. In the individual presentations that follow, students present the specific evidence they found in the literature to show how this criterion for adaptation is supported for their trait. Typically, individual presentations last 8–12 minutes. These first presentations on biological function are fairly descriptive in nature but are very important for setting the stage for the other researchers in their groups by clearly describing the phenotype and how it functions biologically in the environment.

After completing classroom material on the second conceptual criterion, evolutionary fitness function, the student from each group who selected this criterion has a basis from which to now look for and understand studies measuring fitness and selection on their trait. Meanwhile, lecture and lab topics move onto phylogenetics. Students learn about phylogenetic tree construction, ancestral state reconstruction, and phylogenetic comparative methods, with a break for the presentations by the students who researched the fitness function criterion. As students gain an understanding of phylogenetics, the ones who chose the phylogenetic history criterion research the origins of their trait, where it arose in the phylogeny, how the trait is distributed across the phylogeny, and what the ancestral condition was likely to have been. The goal here is to see if the trait arose in the group in which it is proposed to be an adaptation. As the course content moves onto topics of heritability and population genetics, the phylogenetic students present their findings to the class. Heritability can be a challenging topic, and additional lessons in genetics may be appropriate to add here.

Classroom instruction supporting the final criterion, population genetic structure impacting the process of adaptation, can focus on processes of genetic drift, gene flow, mutation, and/or inbreeding. Students developing this criterion may focus their research in a variety of different directions depending on what studies are available for their trait and what material has been developed in previous presentations. In some cases, direct tests of gene flow and genetic drift may be available and appropriate. In others, students can use a historical perspective to develop an argument for whether or not selective environments proposed to have led to the trait were present at the time and place the trait was thought to have arisen (building on the phylogenetic history material presented previously).

After covering population genetic topics, the remainder of the semester in class can be dedicated to treating any additional areas of evolutionary biology not yet covered. After about a week and a half into this material, the students who were researching population genetic structure present their findings to the class, thus completing the presentation part of the case study.

Following the last presentations, students focus on the second major product of this case study, the group papers. These papers are a synthesis of the research each group member did during the semester. The papers typically consist of seven sections: an introduction that explains the overall model used here for studying adaption, five separate sections presenting the evidence for each different criterion, and a conclusion that summarizes the group's final argument for how well their trait met the criteria for being an adaptation that arose by natural selection. Each student is expected to act as lead author of the section on which they presented but is also expected to help the others with the conceptual synthesis and writing. The more students work together on this final synthesis, the more opportunity there is for reinforcement of the concepts for which they were not lead author.

○ Supporting Student Learning and Assessment

This project has numerous "checkpoints" built into it, where the instructor provides direction, feedback, and support. Since student ownership is a core part of this learning experience, guidance is often built into the feedback on different parts of the assignment that can be applied to the next step, rather than presented to the students as up-front directions. Table 3 presents the relative point value of each of the assignments and whether it is graded as an individual or group project.

The prospectus is an early group assignment designed to help group members begin to articulate their understanding of their topics at this early stage. Feedback on this assignment allows the instructor an initial opportunity to clarify misunderstandings students may have of the five questions and provide direction to their research. This is an opportunity for the instructor to suggest key search terms and important authors to the students.

Reading primary literature is challenging. Early in the semester, papers from the literature on adaptation are assigned and discussed in class. While learning about how we study adaptation is a key goal of this activity, during these paper discussions students are also asked to examine the structure of the scientific papers and are guided toward how to find the key evidence of the study. To build

Table 3. Breakdown of grading of major assignments. Some assignments are graded individually, while others represent group efforts. The case study represents 39% of the overall grade in the course, and this is further broken down in the third column.

Assignment	Individual/Group	% of Total Grade
Prospectus	Group	1
Annotations	Individual	4
Presentation	Individual	12
Questions on presentations	Individual	1
Adaptation paper section draft	Individual	2
Final paper	Group	15
Group development of trait	Group	4
Other assignments from class (exams, debate, paper discussions, worksheets, participation)	Mixture	61

on these initial lessons about reading primary literature, students complete three article annotations that are due two class periods prior to their presentations. For these article annotations, students pick what they think are the three most relevant research papers they found so far in their research. A sample article annotation worksheet (available in the Supplemental Material online) functions to help guide students in their reading of the articles. Students first write a summary of the key points of the paper. Students then answer questions that focus their reading of the articles on how each criterion in the study of adaptation was specifically addressed, if it was at all. The annotation form further asks them to identify literature cited in the paper that looks useful for their own specific goals and the goals of the other members of their group. From these annotations, the instructor can (1) determine if the student found appropriate papers and, if not, direct them toward the correct literature before they give their presentation; (2) see if the student can summarize the main points of the paper correctly and, if not, provide feedback to help them see where these points were; and (3) see if the student can identify and articulate the points that are most relevant to their specific goals. The timing of these annotations allows the instructor to see if students are finding the appropriate sources while judging the students' level of understanding and also to provide the above feedback before their presentation, when this feedback is directly applicable to their giving a successful presentation. A fourth article annotation is due later in the semester, before the written paper is due, giving students a chance to use the prior feedback and gain further directed practice in reading the relevant literature.

In a typical case study, the instructor supplies the material and questions. Allowing students to explore the literature to find the key papers on their own more closely aligns this to how science is practiced. Similar to what scientists do when they are developing projects, the students must be able to clearly articulate the question and how the criteria they are investigating apply to their trait, figure out what type of data they need to address that question, and find the appropriate literature resources that show what is already known about the topic. It is important for the instructor to be familiar enough with the traits to be able to help guide the students to the appropriate key words and sources. An alternative to this more open approach is to only use traits the instructor has already researched and provide the key literature sources directly to the students. While this eliminates the research component, the instructor can focus on more directly guiding the reading and extracting of information from the literature.

Presenting scientific evidence clearly is an important skill for scientists. Before the first presentations (on biological function of the traits), the instructor provides details about how to give a scientific presentation to the entire class, along with specific expectations. By showing examples of high-quality and low-quality presentation slides, the instructor can help model these expectations to the students. After each set of presentations, the instructor provides detailed written feedback to those students who presented, to help them understand the strengths and weaknesses of their research presentations, with an eye toward what they need to fix or add to the written component of the project (see sample presentation rubric in the Supplemental Material online). This is another point in the process where the instructor can correct any errors in logic or recommend any important literature these students missed. These issues can then be addressed by the students in the final written paper. Students are more likely to incorporate feedback when it includes points they will need to address in a later assignment and the feedback can focus on ideas and concepts, rather than lower-order issues such as presentation style or grammar (Szymanski, 2014). Students are encouraged to share the feedback with their group members so they all benefit and are less inclined to repeat any mistakes.

To support student practice of critical thinking during presentations, each nonpresenting student submits to the instructor three questions they came up with during the presentations. These questions, if deemed appropriate by the instructor, can be incorporated into the instructor's written feedback to the presenters. These student-generated questions provide feedback from the perspective of their peers and often help uncover misconceptions of both presenters and observers. For example, if students submit questions that show they did not understand a key component of the presentation, the instructor can clarify that point to the entire class.

Communicating scientific evidence and arguments through writing is another important skill scientists use. Each group produces a final paper that synthesizes all their evidence, with each student acting as the primary author for their own section. To support this effort, all the students who presented a given section read that section from all the groups. Students submit drafts to the instructor for feedback, and a rubric is provided to help guide the students' writing. Students are also reminded to use feedback from their presentations. A sample paper grade sheet/rubric is available in the Supplemental Material online.

Much science is done by working in collaborative groups. Successful completion of this project requires collaboration among group members. This component is assessed in part through peer review of group members that focuses on each group member articulating their own contribution to the overall project and their perception of the contributions made by the other group members. The instructor also looks for how much each group worked together and contributed to individual presentations and how well the final paper integrates each independent section into a coherent whole. For example, if a mistake is pointed out in feedback in an early presentation and the same mistake is repeated in a later presentation, it is apparent the feedback was not shared among group members. This falls under the grade category "group development of the trait."

○ Potential Learning Benefits

The semester-long case study model presented here for examining the process of adaptation by natural selection helps students contextualize and apply many major concepts in evolution. Students are encouraged to become active researchers in evolutionary biology. A strong case has been made for evolution instruction to not only integrate instruction in supporting fields such as genetics, but also include science practices (Beardsley et al., 2011; Catley et al., 2005). Researchers found that when students were given the opportunity to use science practices in evolution instruction, positive impacts on learning were observed (Glaze & Goldston, 2015). Students observe and read how researchers develop and apply evidence in evolutionary biology, then model this process using that evidence to develop their own arguments. Table 4 provides a brief summary of major learning benefits not necessarily specific to evolution that students felt they gained from this course design.

By applying the course material they recently learned about in class to their own particular trait and having to explain it back to the class along with supporting evidence they found, students benefit from reinforcement of core lessons, and misconceptions become apparent and can be addressed. Having a clear and unique goal for each student's research also moves the challenging process of reading primary literature from just-in-case to just-in-time learning (Schank et al., 1999). Research papers are being read not because the instructor assigned them, but rather because the student needs the information to answer their own unique question that they are responsible for to their group and have to present to their classmates.

Since groups work on a single trait throughout the semester, and since workload is split among members of the group, with each student focusing on a single component of the argument, a strong sense of ownership of course material can develop without it being all-consuming. Support of learning across each conceptual topic is provided by within-group collaborations (on the same trait but across different criteria). For example, many published studies do not focus on one student's particular goal but may actually provide information about multiple criteria. Students benefit by sharing and discussing these papers with other group members who also have a stake in understanding those research papers. Presentation class periods provide powerful reinforcement for each concept, as each presentation addresses the same major evolutionary concept but applies it to a different trait, so students watching the presentations see a variety of approaches and applications for each major concept.

In preparing their presentations, students practice critically evaluating evidence (data) found in primary literature and developing an argument using that evidence. They are encouraged to present and explain evidence from original figures found in the research papers. This also provides students practice interpreting and presenting data in graphical format. Collaborating with group members who focused on different types of evidence helps students synthesize ideas from different fields of biology. By having to link different types of evidence to address a single large question, students learn how to frame very specific arguments into a conceptual whole. The final paper in particular helps students build a multilayered complex argument from many detailed, often very specifically focused, studies that had different goals from those of the students.

Table 4. A summary of major learning benefits not necessarily specific to evolution that students felt they gained from this course design. These points were taken from discussions with students who took the course.

Contextualizing and applying major concepts in evolution
Increasing ownership of course material
Applying knowledge from lecture/lab directly to their question
Becoming active researchers in evolutionary biology
Reading the primary literature with a purpose (just-in-time not just-in-case learning)
Critically evaluating evidence (data) presented in primary literature
Interpreting and presenting data in graphical format
Presenting evidence about hypotheses in which they are invested
Collaborating with team members to synthesize ideas from different fields of biology
Learning to frame a specific argument into a conceptual whole
Building a multilayered complex argument from many detailed, specific studies

Flexibility of the Instructional Model

This case study model can be readily integrated into an evolution course currently taught with a lecture format. Each of the five major conceptual criteria are themes that are typically stressed in undergraduate evolution courses, and thus little or no content should be lost when adopting this model. Main adjustments to a lecture-based course may include changing the order of the presentation of topics, and changing five lecture days, or partial lecture days, to presentation days.

While ideal group size is five, smaller or larger groups can be accommodated by having students collaborate on one or more of the criteria. Larger class sizes can be accommodated by having shorter presentations, by not having every group present during each presentation day, or by having poster presentations that would allow a concept to be presented for many different traits at the same time. It may also be possible to apply this approach to students earlier in their academic development by supplying the groups with key papers to focus on (with question sets designed to help scaffold the material) rather than having them go into the primary literature on their own.

The course structure described here works for evolution in part because evolution is a topic that synthesizes information from across different areas of biology. A similar approach could be developed in other disciplines, provided there is an overarching question that can be partitioned into discrete units and the question can be applied to different situations/traits that allow each group to explore in their own direction.

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Supplemental Material

- Five Criteria to Test Adaptation Hypothesis
- Presentation Grade Rubric
- Paper Grade Sheet/Rubric
- Article Annotation Worksheet

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