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A Modular Approach to Teaching Multilevel Selection

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ABSTRACT

Multilevel selection is a controversial theory in evolutionary studies and is oft ignored in evolution education. It is, however, a powerful tool in that it is the only one that considers the simultaneous and independent effects of both group- and individual-level selection. This article provides a modular approach to teaching multilevel selection by: listing the main ingredients essential to any unit on multilevel selection; providing individual curriculum components that address each of these ingredients; and describing examples in which these classroom materials are combined to create a complete unit on multilevel selection. These examples include an introductory- and upper-level treatment of the topic. All materials are made available in Online Teaching Materials.

KEYWORDS

Multilevel selection; evolution education; cultural evolution

INTRODUCTION

Group selection is an aspect of evolutionary theory with a long history of controversy. Many of its early proponents made major mistakes by assuming that traits could evolve by providing benefits to the group—or even worse, the species—without considering the consequences of such tendencies on an individual's own fitness (e.g. Wynne-Edwards, 1962). As a result, this naïve approach to group selection was soundly rejected by the scientific community (Williams, 1966). Since then, further work on traits that benefit the group has led to a more sophisticated model termed multilevel selection (Sober & Wilson, 1998). As its name implies, multilevel selection simultaneously considers the distinct pressures acting upon all levels of organization, from the gene, to the individual, to the group, and even the multi-species community. Evolutionary change can then be attributed to the direction and strength of selection acting upon each level of organization. Despite this stricter reformulation, however, many theorists are still opposed to the

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employment of group-level explanations for the evolution of traits that directly benefit others (West, El Mouden, & Gardner, forthcoming), and prefer models that calculate fitness exclusively at the level of the individual (e.g. inclusive fitness theory).

This debate is active within the field, with two separate sparring matches occurring in the pages of *Nature*, one following Wild, Gardner & West's (2009) article on the evolution of virulence, the other Nowak, Tarnita & Wilson's (2010) paper on the evolution of eusociality. Nonetheless, multilevel selection is almost completely absent from biology and evolution education. Most texts reject group-level selection wholesale, often limiting treatment of the subject to the naïve group-level selection of the early 20th century (e.g. Alcock, 2009). Many cite examples similar to Wynne-Edwards' (1962) model of waterfowl reproduction. Noting that the success of any flock of ducks or geese is constrained by the local abundance of resources, Wynne-Edwards argued that mothers then limit the size of their own egg clutches in order to avoid overpopulation. He referred to this as an adaptation that exists "for the good of the group," a phrase that has often been associated with naïve group selection, and has a major logical weakness. While some mothers are repressing their own reproductive success, they are being outcompeted by those that are not doing so, precluding the evolution of a trait by so simplistic a model.

Critiques of multilevel selection over-emphasize these examples, however, and fail to acknowledge its explanatory power when used properly. It is in fact possible that strong between-group competition can select for groups of geese whose females lay fewer eggs, but only if these between-group forces are stronger than competition between individuals within groups. Among other things, this makes it a particularly useful model for the sustained cooperation between non-kin that is observed in human societies. It is also an essential ingredient to understanding the role of inter-group conflict in cultural evolution. Some approaches, like inclusive fitness theory, describe these same phenomena by simplifying evolution to individual-level outcomes, collapsing a variety of interacting processes into a single result. Multilevel selection, on the other hand, maintains the separation between each level of selection, providing a richer depiction of how a single phenomenon might arise from a combination of forces. All told, multilevel selection is a useful tool for any evolutionist, especially one who focuses on human affairs.

This article presents a modular approach to teaching multilevel selection, which is to say that curriculum components are organized around a set of essential ingredients that a unit on multilevel selection must cover. In the first section, I identify these main ingredients. I then describe a list of curriculum components that address each ingredient, and provide examples of how these have been combined to create complete units on multilevel selection. All materials are available in the Online Teaching Materials associated with this manuscript at http://evostudies.org/evos-journal/evos-journal-teaching-materials/.

Essential Ingredients

When taking a multilevel perspective, one must assess the relative strength of selection pressures acting at all levels of organization, from genes to communities. In this article and in my classroom, the focus is on the interplay between selection for traits that benefit individuals and for those that benefit groups,

which is the most straightforward and common example of a multilevel interpretation. Because individual-level selection is the most prominent evolutionary force, it is necessarily the first thing taught in a course on evolution. In turn, standard pedagogical procedures for individual selection provide a good outline for introducing group-level selection. The students at this point are aware of the three main components of natural selection: variation, consequences for reproduction, and heritability. Assuming the last to be true for the sake of simplicity, we are left with two main ingredients necessary for group-level selection to be a relevant factor: between-group competition, and between-group variation that influences that competition. Once they understand when and how group-level selection is possible, the students are prepared for the third ingredient: assessing the strength of group-level pressures relative to concurrent individual-level selection. Viewing the way these two processes can independently influence evolutionary outcomes, students are made aware of the reductionism that occurs by isolating analysis to the individual level, which is included here as a fourth and final ingredient for a unit on multilevel selection.

Between-Group Competition

Group-level selection is dependent on active competition between groups that results in differential reproduction for their respective members. This can occur with varying severity, ranging from war at one end of the spectrum (Richerson & Boyd, 2004), to resource competition in pack hunters (Heinsohn & Packer, 1995), to seemingly non-social example, like stands of plants having differential seed production (Weinig, Johnston, Willis, & Maloof, 2007). In these contexts, it is important to note that an individual's success is necessarily correlated with that of his or her neighbors. Whether the group's goal is to take territory, tangible resources, or merely to avoid overexploiting those same resources (as in the case of the plants), the reproductive success of individual members becomes incumbent upon the group's success. If the group achieves its goal, then all members are benefited; if the group fails, then all members are similarly hindered in their own reproductive success. Thus, a trait that benefits the group can be selected for as these benefits can be transmitted back to the individual trait holder via the success of the group. The strength of this between-group competition is determined by the local ecology. If the ecology provides challenges to survival that are best surmounted by group coordination, or resources that are best accessed through cooperation, it is likely to induce between-group competition. If these sorts of challenges and resources are not present, then between-group competition will be limited.

This brings up the curious question of how to define groups. Clearly, there must be some level of delineation between sets of individuals; it would otherwise be impossible for individuals to reap any gain from inclusion in something that does not actually exist. On the other hand, groups need not be completely isolated, either physically or temporally. As Wilson (1975) pointed out in his formulation of trait groups, groups need only be sets of individuals that preferentially interact in order for selection to operate at the group level. In the absence of clear divisions between groups, this definition allows for individuals to be considered differentially involved in

multiple groups, deriving greater benefit from the success of those groups they are more strongly associated with. This point is more appropriate for advanced courses. When teaching introductory evolution, I find it sufficient to stick to examples in which distinctions between groups are obvious, like pack hunters.

Between-Group Variation

The competition and consequent selection described above is only relevant if there is variation to act upon and if this variation influences said competition. Otherwise, selection might be differentiating between groups, but without favoring one trait over another. In this case one cannot use group-level selection to make a systematic prediction about the final condition of the population. Variation that is pertinent to group-level competition comes in two forms. The more commonly discussed example is when populations have different compositions regarding a particular trait, which is most often discussed in the context of cooperation. Groups with a greater proportion of cooperators are often able to outperform those with fewer cooperators in certain tasks. The second form of variation is in the form of group-level traits, which is a particularly important consideration when discussing cultural evolution. A popular example concerns religions with doctrines that promote war in the name of the religion itself (David Sloan Wilson, 2003). If its followers are successful in their attempts to impose the religion on other groups, the religion and its aggressive belief system will be propagated.

Addressing Group- and Individual-Level Selection Simultaneously

Taken alone, the previous two ingredients are not multilevel selection, but something akin to naïve group selection. The final step that students must take to fully comprehend multilevel selection is that selection is occurring at all of these levels at all times. Sober & Wilson (1998) liken this to a pool ball in the middle of a billiard table. If two independent forces are working upon it (let us say, blowing fans), the final location of the ball will be decided by the direction in which each force is pushing, and how hard each is doing so. Turning again to the example of cooperation, groups with many cooperators hold an advantage over groups with few cooperators in certain contexts. On the other hand, individual non-cooperators surrounded by cooperators outcompete their neighbors by free-riding during collective effort, and not reciprocating the goodwill of others. Thus, we see group-level selection promoting cooperation, and individual-level selection working against it. It is at this point that one must determine which force is more emphasized by the local ecology. A good example for this comes from Henrich et al.'s (2004) comparison of prosociality in fifteen world societies. They found that the cross-cultural variation correlated positively with the payoffs the local ecology offered to cooperative groups—a variable that greatly influences the balance between group- and individual-level competition. The most cooperative society in their study was the whale-hunting Lamalera of Indonesia, and the least cooperative society was the Quichua of the Amazon, who live on family farms and rarely have any resource interactions with non-kin.

Conflict between selection pressures at the group and individual levels is the most commonly discussed example of multilevel selection, and likely the best place for a student to begin. However, it is possible for group- and individual-level selection to push in the same direction, or for one to be neutral in relationship to a particular trait. In these cases, the final outcome is more obvious, but the magnitude of selection remains dependent on the strength of each force. Students may have difficulty seeing why a multilevel perspective is still informative in these cases, but referencing the example of the pool ball can be useful in reminding them that, even though they are both pushing in a single direction, the two forces are still independent.

Comparing Multilevel Selection to Other Frameworks

Following the rejection of naïve group selection, a variety of theories arose for how individual selection could permit the evolution of cooperation and other behaviors that aid one's neighbors. The most prominent examples of this are kin selection (investing in related individuals promotes one's own genes; Hamilton, 1963, 1964a, 1964b), direct reciprocity (cooperating only with those who cooperate back; Trivers, 1971), and indirect reciprocity (cooperating with those that can be expected to cooperate with other potential social partners; Nowak & Sigmund, 2005). Any unit on multilevel selection must address these models, their relationship to multilevel selection, and the advantages that multilevel selection provides. Conveniently, the relationship between them is closely related to multilevel selection's strengths. When one looks closely at kin selection and direct reciprocity, they are just specialized versions of multilevel selection. In both cases, individuals are investing in other cooperative individuals, and the benefits accrued from this behavior are dependent on the success of the group as a whole. In the case of kin selection, the cooperative behavior is only adaptive if it aids the family in survival. In the case of direct reciprocity, benefits from cooperation are dependent on the success of the dyad. The complex social situation described by indirect reciprocity is by all standard definitions a group!

Acknowledging that each of these three models is just a specific manifestation of multilevel selection is an important step in recognizing its value as a theory. The way it conceptualizes evolution, however, gives it an extra advantage. Each of these three models seeks to explain how group-level benefits accrue to the individual, and, in the process, flatten selection at the group- and individual-levels into a single outcome. Returning to the pool ball example from above, Sober & Wilson (1998) point out that these approaches can identify where the pool ball has moved to, but not the multiple forces that interacted to move it there. Multilevel selection, on the other hand, identifies the relative strength of these independent forces, giving a richer depiction of how evolutionary change occurs.

Curriculum Components

Emphasizing each of these ingredients in a classroom context can take numerous forms. Obviously, they could be summarized in a lecture. For those who have the opportunity to dedicate multiple class periods to the subject, however, I

provide a list of in-class activities that I have developed with colleagues for courses at Binghamton University. These activities are categorized according to the main ingredient they best address, though some can be used to illustrate more than one. All items described in this section are available in the Online Teaching Materials at http://evostudies.org/evos-journal/evos-journal-teaching-materials/.

Between-Group Selection

Board Games about Colonization

In this activity, all members of the class take part in a game in which "cultures" compete in the colonization of unsettled lands. In my classes I have tended to use a simplified version of the game Catan©, in which up to four players compete to take control of an unsettled island. A similar board game (i.e. Risk©) could be used, or certain computer games might be equally useful (e.g. Sid Meier's Civilization© or Age of Empires©). What is important is that the activity places an individual player in charge of a culture or society that is competing with others. It is valuable to emphasize how the individual student is responsible for an entire society within the context of the game, otherwise this could be misconstrued as individual-level selection. Also, if students recognize that certain strategies give someone a better chance of winning, this activity can easily lead to a discussion on the role of between-group variation.

National Geographic's "Eternal Enemies"

Though less interactive, this documentary provides a very clear picture of between-group selection. The video follows a pack of lions and another of hyenas—cast as eternal enemies—on the African savannah. The focus on pack hunters leads to a variety of scenes in which group coordination is necessary, be it in catching food or defending territory. A variety of individuals experience damaging and even fatal encounters with members of other species during the movie, allowing instructor and student alike to easily identify events that could contribute to group-level selection and individual-level selection. In addition, one can easily note events in which an individual's compromised functioning had impacts on the group's success. This can be valuable for emphasizing how, in group-living species, one's own fitness is inherently linked to that of the other members.

Between-Group Variation

Sequential Prisoner's Dilemma

Behavioral economists have developed a variety of protocols for measuring social behavior. The same simplicity that facilitates easy experiments that can be conducted in a variety of contexts also makes them engaging and demonstrative teaching tools. Picking from these, I tend to use the sequential Prisoner's Dilemma (SPD) in my classes because it provides three easily interpreted measures in one game. In the SPD, players are placed in pairs, and players can either cooperate or

defect, with two cooperators each receiving a greater amount than two defectors ($30 vs. $15), but a mixed interaction resulting in a lower payoff for the cooperator than the defector (often $10 vs. $45). A "first-mover" elects to cooperate or defect, enabling the second player to choose on the basis of the first player's decision. A player may have to choose between cooperation and defection in one of three circumstances: as a first mover (trust), a second mover with a cooperator (trustworthiness), or a second mover with a defector (self-sacrifice). I tend to play the game in such a way that all students determine how they would play in each circumstance. This can be followed by playing the game again with a new rule: players can invest their winnings to punish non-cooperators. For every $1 invested, the non-cooperator loses $5.

In the first game, about half of participants demonstrate trust and trustworthiness (self-sacrifice is quite rare). This provides ample variation to demonstrate how individuals differ in their cooperativeness, hence leading to groups with different compositions of cooperators and non-cooperators. Another feature is that individuals rarely choose to self-sacrifice to a non-cooperator, illustrating how non-cooperative groups will have difficulty fomenting collective effort if it is necessary. This point is emphasized even more strongly by the way punishment influences people's decisions during the game. Invariably, the proportion of students exhibiting trust and trustworthiness rises from around 50% to 80-90%. This makes it clear how a single social mechanism can greatly alter the behavioral composition of a group, and, consequently, its success as a unit. Connecting this to between-group selection can be done easily by pointing out that a cooperative dyad receives more money ($60) than a mixed dyad ($55) or a non-cooperative dyad ($30). The game can be cast as an ecology that promotes between-group selection, but changing the payoffs could easily alter this. See Online Teaching Materials for further description of how to implement the game in a classroom and how to manipulate payoffs.

"The Popsicle Stick Game"

An intriguing, more interactive manipulation of the logic underlying the sequential Prisoner's Dilemma was developed by Athena Aktipis and David Sloan Wilson. For lack of a better name, we refer to it as "The Popsicle Stick Game." In its simplest version, all members of the class are given two popsicle sticks, one with an "S" (Selfish) and another with an "A" (Altruistic) written on it. The class is then divided arbitrarily in half into altruists and selfish players (e.g. all people born before July are selfish). The students then wander around the room "interacting" with their classmates, and tallying points according to a matrix similar to that of the SPD. The only other rule is that students can only interact with each other student once. Following this, the game is played again, but individuals are allowed to interact with each other repeatedly. This essentially permits the formation of groups. Inevitably, those who were designated as cooperators have much higher scores at the end of this second round. The relative success of cooperative versus non-cooperative individuals demonstrates how groups of cooperators can arise and, in a favorable context, out-compete groupings of non-cooperators.

Addressing Group- and Individual-Level Selection Simultaneously

Placing group- and individual-level selection in the same context is something that logically comes at the end of the unit, as it involves the synthesis of current and past topics. I tend to focus on it mainly in a summary lecture and in independent assignments. In higher level classes, the first chapter of Sober & Wilson's (1998) Unto Others is an accessible reading that merges group- and individual-level selection. For specific examples of homework or test questions that probe this ability see the following section or the Online Teaching Materials.

Comparing Multilevel Selection to Other Frameworks

Because this ingredient requires at least a short history of theories for the evolution of cooperation, it is also best taught through lecture and independent assignments. A summary lecture, as mentioned in the previous section, can easily bring across all four elements while being oriented around the history of multilevel selection and related theories. Examples of such lectures and related homework and test questions are available in the Online Teaching Materials.

Example Units

As noted above, the intent here is to provide a modular approach to teaching multilevel selection. This means providing a core set of concepts that must be covered, and a set of curriculum components that address different aspects of these concepts. Instructors can then mix-and-match curriculum components in order to create a unit that provides coverage of the topic that is at once complete, and appropriate to their course's structure and broader learning goals. I have utilized this approach to teaching multilevel selection in two courses that are part of the Evolutionary Studies (EvoS) certificate program at Binghamton University. One is a large (~160 students), 100-level course called "Evolution for Everyone." It is cross-listed as a biology/anthropology course, and acts as the EvoS Program's introductory course, educating students of all academic backgrounds in the mechanisms of evolution and their application to human affairs. The second is a smaller (~30 students), upper-level course that educates students in cultural evolutionary theory. Here I describe the units on multilevel selection I have developed for each course. They are also summarized in Table 1. Both of these courses were taught in the 14-week semester format.

Table 1. Two Example Units for Teaching Multilevel Selection, Organized around the Essential Ingredients

Course	Level	Between-Group Competition	Between-Group Variation	Merging Individual- and Group-Level	Comparing to Related Theories
Evolution for Everyone	Introductory	Eternal Enemies (movie)	Sequential Prisoner's Dilemma	Lecture, Homework	Lecture
Cultural Evolutionary Theory	Advanced	Board game	The Popsicle Stick Game	Lecture, Written Assignment	Lecture

Evolution for Everyone: An Introductory-Level Treatment of Multilevel Selection

Evolution for Everyone has a unique course structure that is framed around the scientific method. The course begins with an "introduction" section that summarizes the primary mechanisms of evolution. This phase lasts about one-third of the semester and is followed by a "methods & results" section that applies these mechanisms to a variety of topics that are important to human affairs, ranging from economics to mating and dating. For more on the structure of the course's curriculum, please see O'Brien & Wilson (2010).

The unit on multilevel selection, which marks the end of the introduction section, begins with the sequential Prisoner's Dilemma. The SPD takes place in the lecture hall, and takes about half of the hour-and-a-half class period. I begin the second half of the period by pointing out that, whether the other player chooses to cooperate or defect, it always pays more to defect ($45 over $30, $15 over $10). This then leaves open the question of why so many of the students cooperated anyway. Lecture then chronicles the history of theories for the evolution of group-beneficial traits, beginning with kin selection and moving through to multilevel selection. During the later parts of the lecture, punishment is described as a characteristic belonging to groups, and its impact is illustrated by straw-polling the students regarding their behavior in the game. This lecture is available in the Online Teaching Materials.

After this first day, the students are aware that between-group variation exists and that it might impact group functioning. They also have an evolutionary model that frames this phenomenon. In the following class, they watch Eternal Enemies, which emphasizes not only between-group competition, but how individual behaviors bear upon it. The sequence of events with individual- and group-level consequences provides a good lead-in to understanding that these two levels of selection are both operating at all times. The homework for the unit asks them to identify events in the movie that bear on selection at the individual level, at the group level, and at both. It also asks them more generally to identify how different levels of selection at the group and individual levels will lead to different outcomes in the evolution of social behaviors. These problem sets are available at Online Teaching Materials.

Cultural Evolutionary Theory: A More Advanced Treatment of Multilevel Selection

Multilevel selection is an immensely valuable tool for the study of cultural evolution as groups have imposed their cultural practices and ideals on others throughout modern history (Richerson & Boyd, 2004). In addition, models suggest that cultural evolution provides greater opportunity for the evolution of group-beneficial traits like cooperation (Bell, Richerson, & McElreath, 2009). Accordingly, I make multilevel selection and social behavior the central themes of the last third of my course on cultural evolutionary theory. The treatment of multilevel selection is thus quite a bit longer and in-depth than in Evolution for Everyone, which is also made possible by the students' more advanced experience with evolutionary theory.

The unit begins with the simplified version of the board game Catan©, emphasizing the fact that human societies often compete for resources. This game has no rules that permit war, thus all competition is based on the speed with which one can colonize the available lands. In the wrap-up, students discuss how different strategies lead to greater or lesser success, providing an early view of the variation that can underlie selection at the group level. This point is then the focus of the unit's second class meeting, which employs "The Popsicle Stick Game." Here it becomes more obvious how a specific trait (cooperation) can determine the relative fitness of members of one group versus another.

With the major elements of between-group competition and variation established, the remainder of the unit focuses on the way group-level selection interfaces with individual-level selection. This begins with the assignment of the first chapter of Sober & Wilson's (1998) *Unto Others*, which is discussed during the third class period. Finally, in the fourth meeting of the unit, a lecture similar to the one described above summarizes multilevel selection, and contextualizes it in the history of evolutionary theory.

The way this course is structured, evaluation is oriented around a handful of short papers on an "adopted" culture. At the beginning of the semester, each student chooses a culture (and time period, if appropriate) he or she would like to understand better through a cultural evolutionary framework. Each assignment then consists of a writing prompt that asks students to apply the most recent topic to their culture of choice. During the multilevel selection unit, students were asked to write a paper identifying an example of between-group competition in the culture's history, and the role this has played in the culture's evolution. The semester's final project is also oriented around multilevel selection. This much longer assignment asks students to discuss the social norms of their culture, the contexts in which other-oriented behavior is expected, and how these expectations are enforced. This is necessarily imbued with a multilevel selection perspective that identifies how the local ecology selects for this specific balance between self- and other-oriented attitudes. More complete descriptions of these assignments are provided in the Online Teaching Materials.

Conclusion

Multilevel selection is a valuable and utile theory that is particularly applicable to the evolutionary study of human affairs. It is also a complex model that can easily be misused, necessitating a strong pedagogical approach. This paper has provided a guide to the essential elements that a unit on multilevel selection must contain, and some curriculum components that can fulfill these requirements. The hope is that other educators will not only borrow these materials for their own classrooms, but also add to them with their own techniques that they have found to be fruitful.

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