Brent Emerson
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Being Precise about Levels of Selection

It's winter in a certain forest in North America. There are rabbits sitting all over the snow, nibbling on the last remnants of vegetation. All the rabbits are white, difficult to see unless we're looking for them carefully. Then a wolf steps into view, and we freeze frame, beginning to construct an adaptationist explanation of the uniformity before us. The wolf represents the first of three elements we require to implicate natural selection: a selection pressure. Letting the action continue, we follow the wolf as he passes by our previously noted rabbits and continues to search for food. Across a field, we see a dark brown rabbit, frozen in fear. The wolf jumps ahead to catch it as it scampers away. Freeze: we have variation, the second requirement. Given the background assumption of heritability—that rabbits produce near-copies of themselves, down to the color of their fur—our triad is completed and we have all the elements necessary in a story of adaptation by natural selection. Predatory wolves and a snowy winter environment constitute the selection pressure, differences in outer surface coloration constitute the variation, and the standard Mendelian or microbiological story applies to the heritability of the outer-surface-coloration trait in rabbits. Given the display just witnessed, we term this an example of selection of individual organisms.

We might then proceed to step down the reductionist pantheon, additionally calling it selection of genetic material, selection of molecules, selection of atoms, selection of subatomic particles, etc. But this would be unsatisfactory. Obviously the selection mechanism we have posited does have to select certain rabbit molecules from a pool of them, and therefore certain rabbit atoms from a pool, but we want to say something special about the 'organism' and 'gene' levels. To see what's different about these levels we merely have to look back at the requirements we put on selection in the first place; now these qualifications will be useful in identifying the levels at which selection occurs. Below the genetic level, molecules and atoms

do not reproduce themselves to pass on any unique characteristics, if they have any. Hence the heritability requirement is not met. While there are many different types of atoms (variation) it is a difference that goes unnoticed by the selection mechanism in question: white rabbits and brown rabbits contain atoms which are, in practice, indistinguishable from each other. We might note the neutrality of the selection mechanism here by identifying it as *selection from* molecules, atoms, etc.

To have *selection for* characteristics at certain levels of organization, we must see the requirements met. Already we've seen them at the single-organism level. To argue for selection for characteristics of genetic material, we note the gene-variation between brown and white rabbits, the gene's mechanism of heredity (generating a larger organism that reproduces it), and how the selection pressure interrupts this heredity by killing the larger organisms it depends upon. Thus we have natural selection at the genetic level. What about larger levels? Consider this event as an instance of selection between groups of similarly-colored rabbits. Clearly there is variation (groups of brown, groups of white) and the selection pressure remains. Groups of white rabbits produce groups of mostly white rabbits, groups of brown rabbits produce groups of mostly brown rabbits: heritability. Thus we can regard it as an instance of selection for groups of white rabbits.

So far it seems that selection for characteristics at one level implies selection at any other heritable level. In tandem with the reductionist tendency to characterize only the simplest or physically smallest level as 'real', this assumption has certainly fueled arguments that group selection is always individual-organism selection and hence is 'really' individual-organism selection, that individual-organism selection is always selection for genes and hence is 'really' selection for genes. This tendency will be discussed later; for now I want to illustrate just why this easy reduction is sometimes invalid.

Back to the forest: selection has rendered most rabbits white. However, we discover several populations of rabbits which are almost exclusively brown. This naturally surprises us, given the results we witnessed earlier. A wolf approaches a group of these brown rabbits. Then something odd happens: the rabbits form immediately into groups of three. One in each group hops up and down, one turns around and around in a circle, and one runs on a line between the other two. The wolf seems confused, looks around, and spots a brown rabbit who's sitting alone. He leaps over and gulps down this lone rabbit, then takes his leave. The rabbits relax and take up their nibbling. Another wolf enters the scene, and this time two rabbits attempt to form the protective triangle but can't find a third: they just hop and turn. Their behavior has no effect on the wolf, and they get eaten.

Now we're hard pressed to provide an evolutionary explanation for this behavior. If it is construed as a response to selection pressure, it seems to be effective. And there is clearly variation: a rabbit who doesn't manifest the triangle behavior exists and consequently soon doesn't exist anymore. Incomplete manifestations also exist and also are not effective. If we can find a mechanism for heritability, it seems that a selection mechanism is an adequate explanation. But (let's say) it soon becomes apparent that individual rabbits only know and manifest one single behavior (i.e., either hopping, turning, or running), so the whole complex can't be explained as anything heritable between individual rabbits. Then as selection for individual organisms, the explanation seems to fail. But each behavior does seem to be heritable: somehow (either via genetics or instruction, we're not sure) a rabbit's progeny almost always manifest exactly the same behavior as their parent. So groups of rabbits do have a heritable characteristic: either they contain all types of rabbits (and hence their progeny almost definitely will) or they don't (and hence their progeny almost definitely won't). Thus we can attribute the behavior to a selection for certain groups of rabbits.

Obviously, this rabbit-triangle example is meant to represent high-level social structure. And it's clear that it is a case of group selection that can't also be considered selection at the level of the individual organism. It's phrased in a cute simplistic bunny-and-wolf way, but it's probably not so far-fetched: examples of this type of structure probably occur in animal social behavior all the time. Examples in the human-society context might include sex/gender systems and economic systems, cases where high-level structures has arisen and propagated themselves in a way that can't be analyzed completely at the level of the individual organism, rather in the same way that selection for the individual organism can't be analyzed at the level of the cell.

So we can safely say that there are cases of group selection that aren't cases of selection for individuals. There is a more fundamental thing to be explored, though: this grounding tendency to always be searching for the *primary* unit of selection, as if one level of analysis can be established as how things *really are* once this basic unit is identified. Dawkins thinks he's found it in the 'gene', Hull in the 'gene lineage', others in the individual organism, the species, or some other group.

There may be extra-scientific, perhaps political, reasons for adopting a thesis. The evolutionary primacy of the individual seems to underwrite the political liberalism that locates the ultimate source of value in the individual, while Dawkins' thesis of the primacy of the gene seems to attempt to subvert this significance. Similarly, Marxian theorists might invoke quasi-biological theses to support the primacy of a larger social group (e.g., the 'State'), while someone focused on an important line drawn between humanity and other animals might argue for the species as primary unit. There seems to be no other reason why a single level of analysis would be given such ultimate significance.