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Demonstrating group selection: A comment on Janet Landa's 'The bioeconomics of homogenous middleman groups as adaptive units'

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Abstract Janet Landa provides an impressive historical tour of the development of her theory of homogeneous middlemen groups (HMGs), and how she arrived at the group selection approach. Despite her claim that the case studies she presents provide evidence for group selection in human societies, we argue that such a conclusion is premature. We suggest that an evolutionary explanation of HGMs will be strengthened by greater attention to the details of the selective process.

Keywords Cooperation · Cultural evolution · Group selection

Janet Landa's (2008) target article summarizes the evolution and development of her thoughts on homogenous middlemen groups (HMGs) over the past several decades, describing her own transition from viewing HMGs through the lens of economic models to her current position, which views HMGs as adaptive units shaped by group selective pressures. The article is an important theoretical and empirical contribution to the small but growing literature on the adaptive design of groups (Wilson 2002; Richerson and Boyd 2005). Nonetheless, Landa's conclusion that her case studies of HMGs 'collectively demonstrate the existence and evidence of the importance of group selection in human society' is unwarranted. While these case studies are valuable, and Landa is to be commended for organizing and describing such a wide array of groups, they are insufficient to draw any conclusions concerning the selective pressures that have shaped HMGs.

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Wilson and colleagues have argued that evolutionary biology's focus on individual level selection is misleading (Wilson and Sober 1994; Sober and Wilson 1998; Wilson and Wilson 2007). Wilson contends that selection operates at multiple levels, but current methods of investigating adaptation make group-level adaptations invisible to evolutionary researchers. The fitness effects of between group and within group selective pressures are typically collapsed into a single measure, essentially defining the possibility of group selection out of existence. Sober (1984) has dubbed this approach the 'averaging fallacy'. To avoid the averaging fallacy, Sober and Wilson (1998) advocate a multi-level selection approach in which within-group (individual level) and between-group (group level) fitness effects are estimated. Multilevel selection is a potentially powerful theory for evaluating evolutionary dynamics, especially those that seem to defy individual-level or gene-level explanations. We think this approach holds great value for understanding the selective pressures operating on the trading groups Landa describes, but her article has only initiated this process. Considerable work remains.

Group selection concerns the differential fitness of groups. To show that selection is operating at the level of groups one needs to demonstrate that there exists a distribution of groups that exhibit quantifiable phenotypic variation relative to each other, that their differences are transmitted to future generations through some mechanism of heritability, and that there is differential reproduction of groups over time. These conditions are not met in the present study. Indeed, Landa fails to provide a context within which group-level competition is occurring. Landa describes the customs, dress codes, and beliefs of various successful trading groups, but to evaluate group-level adaptations we need to know the competitive context in which they evolved. What competing groups failed to fill this economic niche occupied by HMGs? What characteristics do these groups exhibit that made them less effective competitors than HMGs? How did HMGs out-compete these groups (displacement, reproduction, warfare, etc.)? Are these groups growing or shrinking over time? How common are group fission/fusion events? Are the economic niches filled by HMGs more profitable than other available economic activities?

While Landa claims to have demonstrated the existence of group selection in human society, her use of group selection is unclear. Are readers, whether from an economic or a biological background, intended to view Landa's account of HMGs as a description of a real evolutionary phenomenon or is Landa using group selection as an analogy? Her claims suggest the former but her evidence suggests that latter. Landa quotes (Metcalfe, 2008, p. 25): 'economic evolution is not biological evolution for [there is] nothing in the economic world to correspond to the exact processes of biological inheritance, sexual reproduction and gene transmission over time.' But this is only qualified by the statement that 'a basic GS theoretical framework can still provide a powerful bioeconomics framework for understanding how one trading group comes to dominate middleman-entrepreneurial roles.' Contrary to her claims, Landa has not demonstrated group selection. Group selection merely serves an analogical role in her argument. It is an organizing theme concerning which behaviors we would expect to emerge if selection had crafted highly cooperative groups among differentially reproducing units.

The problem with using biological analogies in human cultural behavior is that while often apt, they remain stories unless they are tightly linked to mechanistic causal processes. The evidence in Landa's article has several different interpretations when viewed from various evolutionary analogies. For example, in MacArthur and Wilson's (1967) theory of island biogeography, extinction risk and species turnover are highest on small islands far away from the mainland. By analogy, these minority ethnic groups are far-flung from 'the mainland' and must have strong group cohesion to avoid dissolution. Distance from their home countries or communities, not economic performance, could be driving the evolution of high levels of trust and cooperation. Or, perhaps individual selection had been operating on skills relevant to performing the middleman function. Then the opening of a new economic niche sorted these already adapted individuals into groups. This is similar to a form of character displacement, the divergence of similar species in size or morphology, in which divergence is facilitated by pre-existing variation (Rice and Pfennig 2007). Group selection could be secondary, or even non-existent. The point is that without clearly elucidated, direct counterparts for heritability, variation, and differential reproduction, evolutionary analogs for processes of functional specialization remain unsubstantiated scenarios.

As Wilson (2000) recommends, finding cultural convergence toward certain adaptive features provides circumstantial evidence for the operation of a selective process, but this does not constitute a demonstration of that process. For example, baseball players in the United States and Japan both engage in highly idiosyncratic superstitious behavior, especially when future events are perceived to be based on luck (Burger and Lynn 2005). It is plausible to claim that this behavior is an adaptive response to environmental uncertainty that helps the members of the group earn their living and gain prestige. However, noting this cultural convergence is a far cry from demonstrating that baseball teams have undergone a selective process by which more superstitious teams have outcompeted less superstitious teams over time. The observation that HGMs in varied geographical, yet economically similar, environments converged on the possibly adaptive strategies of free-rider deterrence and discretionary lending based on trust is significant. The claim that it reflects a process of selection at the group level requires much more empirical corroboration.

Landa describes middlemen trading groups as homogenous, supporting her contention that they can be viewed as adaptive units, but in some ways this description is misleading. While these groups do share similar language, dress, customs, and beliefs, as Landa has carefully documented, there is considerable intragroup cultural variance within these groups as well (e.g., Sosis 2008). More importantly, there is no evidence that they are homogenous regarding reproductive decisions as would be expected if group selection were the primary force shaping these groups. This intragroup differential reproduction will result in strong selection pressures at the individual level. Indeed, group ideologies and social punishments coercing cooperative and trusting behavior can be understood as cultural mechanisms that attempt to limit the potency of these selective pressures. Wilson (2002) has convincingly argued that religious teachings are aimed at encouraging members to behave for the benefit of the group. It appears that group-level ideologies are necessary precisely because we are not likely to act for the benefit of the group when it is not in our own individual interests. The reason we are exhorted by religious specialists, politicians, and other group leaders to dedicate

ourselves to the group is because we are not likely to make group sacrifices at the expense of our individual fitness without significant coercion (Cronk 1994).

We encourage Landa to continue to explore HMGs as adaptive groups, but we also suggest taking a closer look at the individual level selective pressures that may have shaped these trading groups. For example, Sosis (2005) has examined some of these groups using evolutionary signaling models and arrived at different conclusions than Landa, most notably that trust is largely absent among the ethno-religious trading groups he examined. To evaluate individual- and group-level adaptations we recommend the methods detailed by Sober and Wilson (1998). They outline a stepwise procedure to examine the relative strength of natural selection at multiple levels, simplified here (and in their book) to focus on individual- and group-level dynamics. The core of their procedure is as follows:

1. Determine what would evolve if group selection were the only evolutionary force.
2. Determine what would evolve if individual selection were the only evolutionary force.
3. Examine the basic ingredients of natural selection at the individual and group levels.
   a. Determine the pattern of phenotypic variation within and among groups.
   b. Determine the heritability of phenotypic differences.
   c. Determine the fitness consequences of phenotypic variation within and among groups.

We are not aware of any human studies that have fully carried out this program and thus were Landa to pursue such a task it would be a significant contribution to the emerging literature on cultural evolution. While Landa's case studies have already made a valuable contribution, they are simply a first step in analyzing potential group-level adaptations. It would be premature to draw conclusions concerning the demonstration of individual- or group-level adaptations from these data alone. We greatly look forward to Landa's future work in this area.

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