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THE LEVELS OF SELECTION DEBATE: TAKING INTO ACCOUNT EXISTING EMPIRICAL EVIDENCE

El debate sobre niveles de selección: teniendo en cuenta la evidencia empírica existente

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ABSTRACT

For over five decades the dominant neo-Darwinian view is that natural selection acts only at the genic and organismal levels, but the ignored empirical evidence of multilevel selection occurring in nature obtained over the last fifty years does not agree with it. A long exchange of mathematical and theoretical arguments about the levels at which natural selection acts constitutes what is known as the 'levels of selection debate'. The large amount of empirical evidence, studied by quantitative genetics means, specifically contextual analysis, indicates that natural selection acts on levels of the biological hierarchy above and below that of the gene and organism, from the molecular to the ecosystem level, thus supporting what is called the multilevel selection theory. Beyond theoretical arguments, if empirical evidence for multilevel selection and contextual analysis results are carefully examined, the debate on the levels of selection is easily resolved: natural selection occurs in nature at different levels of biological hierarchy. This text provides an overview of such empirical evidence.

Keywords: biological hierarchy, contextual analysis, group selection, multilevel selection, natural selection.

RESUMEN

Por más de cinco décadas la visión neo-darwinista dominante de la selección natural es que esta actúa únicamente a nivel génico y organísmico, pero la ignorada evidencia empírica de selección multinivel ocurriendo en la naturaleza obtenida durante los últimos cincuenta años no es consecuente. Un largo intercambio de argumentaciones matemáticas y teóricas sobre los niveles en los que actúa la selección natural constituye lo que se denomina como el "debate de los niveles de selección". La gran cantidad de evidencia empírica, estudiada mediante métodos de genética cuantitativa, específicamente el análisis contextual, indica que la selección natural actúa en niveles de la jerarquía biológica por encima y por debajo del nivel del gen y organismo, desde el nivel molecular hasta el ecosistémico, apoyando así lo que se denomina la teoría de selección multinivel. Más allá de argumentos teóricos, si se examina cuidadosamente la evidencia empírica de selección multinivel y los resultados del análisis contextual, se resuelve de forma sencilla el debate de los niveles de selección: la selección natural ocurre en la naturaleza en diferentes niveles de la jerarquía biológica. Este texto ofrece una revisión general de dicha evidencia empírica.

Palabras clave: análisis contextual, jerarquía biológica, selección de grupo, selección natural, selección multinivel.

INTRODUCTION: THE LEVELS OF SELECTION DEBATE

Does natural selection operate at different biological levels besides these of the organism and/or gene? Is group selection a significant evolutionary force? Are neo-Darwinian theories as kin selection and direct reciprocity the exclusive explanations of cooperation and social behavior? These questions have overwhelmed entire generations of evolutionary biologists, generating hundreds of mathematical and theoretical papers in what is called the "levels of selection debate". However, in the discussions about the level at which selection occurs, empirical evidence has not been taken into account (Eldakar and Wilson, 2011). There is abundant empirical evidence of multilevel selection processes occurring in nature (Table 1; Stevens *et al.,* 1995; Tsuji, 1995; Banschbach and Herbers, 1996; Campbell *et al.,* 1997; Solis *et al.,* 2002; Aspi *et al.,* 2003; Donohue, 2003; Donohue, 2004; Weinig *et al.,* 2007; Eldakar *et al.,* 2010; Formica *et al.,* 2011; Laiolo and Obeso, 2012; Moorad, 2013; Pruitt and Goodnight, 2014; Searcy *et al.,* 2014; Campobello *et al.,* 2015). The above listed questions can be largely answered if empirical evidence is seriously taken into consideration. Of course there are instances when the empirical evidence contradicts long-held theoretical arguments, but should this happen, the theory must be adjusted to the evidence rather than the evidence being adjusted to fit the theory.

Since 1960s, the controversy over the level at which selection occurs has been particularly strong. With the publication of *Animal Dispersion in Relation to Social Behavior* (Wynne-Edwards, 1962), a *naïve* vision of multilevel selection was developed. This early definition of multilevel selection suggested that natural selection acts by the good of the group, or in other words, natural selection only operates at levels higher than that of the individual. Multilevel selection, as the name implies, is now known to operate at a minimum of two levels of the biological hierarchy. Of course, the work of Wynne-Edwards (1962) was immediately and famously criticized (Hamilton, 1963; Hamilton, 1964a; Hamilton, 1964b; Maynard-Smith, 1964; Williams, 1966; Maynard-Smith, 1976). During the 1970's, several seminal works concerning cooperation and social behavior also appeared (Wilson, 1975a and *Sociobiology* by Wilson, 1975b). More recently, the controversy has revived. Nowak *et al.* (2010), Nowak *et al.* (2011) and Wilson and Nowak (2014) have made strong criticisms against the theory of inclusive fitness (Hamilton, 1964a; Hamilton, 1964b). These authors have shown mathematically that this theory applies to very limited cases. As such, they suggest choosing a social behavior model much closer to the concept of multilevel selection.

Table 1. Strength and direction of natural selection acting on two levels of the biological hierarchy. The studies were conducted on different traits and organisms, and contextual analysis was used.

Organisms	Selection	Reference
Plants	**I+<G- (6)**, I+ (1), **G+ (1)**	Stevens *et al.,* 1995
Ants	I+ (1), **G- (2), G+ (1)**	Tsuji, 1995
Ants	I+ (1), **G+ (2)**	Banschbach and Herbers, 1996
Plants	**I+<G+ (1)**, **G+ (1)**	Campbell *et al.,* 1997
Plants	**I+<G- (5)**, I+>G- (5), I+ (10), **G- (2)**	Solis *et al.,* 2002
Plants	I+>G+ (1), I+>G- (1), **G+ (1)**	Aspi *et al.,* 2003
Plants	I+>G+ (1), **G- (1)**	Donohue, 2003
Plants	**I-<G+ (1)**, I+>G- (1)	Donohue, 2004
Plants	I+>G- (3), I+>G+ (1), **G- (3)**	Weinig *et al.,* 2007
Water striders	I+>G- (1)	Eldakar *et al.,* 2010
Beetles	I+>G- (5)	Formica *et al.,* 2011
Birds	I->G+ (1), I+>G- (1)	Laiolo and Obeso, 2012
Humans	I+>G+ (1), **I+<G+ (1)**	Moorad, 2013
Spiders	I+<G- (1)	Pruitt and Goodnight, 2014
Salamanders	I-<G+ (1)	Searcy *et al.,* 2014
Birds	**G+ (1)**, **G- (1)**	Campobello *et al.,* 2015

[1] For the same trait, 'I' represents the individual regression coefficient, and 'G' represents the aggregate regression coefficient (the group average, excluding the focal individual). [2] '+' and '-' represent the sign of the coefficient, and '<' and '>' represent, respectively, if the individual regression coefficient is lower or higher than the aggregate regression coefficient. [3] In brackets are presented the number of traits that share the same condition respective to the sign and value of the coefficients. [4] In bold: the cases in which, for a trait, selection at the higher level ('group selection') is higher than selection at the lower level ('individual selection').

THE CONCEPT OF MULTILEVEL SELECTION

Multilevel selection occurs when natural selection acts simultaneously on two or more levels of the biological hierarchy (Heisler and Damuth, 1987). Thus, starting from the molecular level, to the genetic, cellular, organismal, family, deme, group, sub-population, population and even to the community or ecosystem level, it is possible for natural selection to occur given that the principles of evolution by natural selection are met: phenotypic variation, heritability and differential fitness (Lewontin, 1970). In addition, the strength and direction of natural selection acting on each hierarchical level may different (Goodnight *et al.,* 1992). One of the main consequences of multilevel selection is that selfish individuals, meaning the lower level, outcompete altruistic individuals within the group, the higher level, however altruistic groups outcompete selfish groups (Darwin, 1871; Wilson and Wilson, 2007). When the strength of selection at a higher level of the biological hierarchy is strong enough for individual selection to be suppressed, a major transition in evolution occurs (Michod and Roze, 2001; Okasha, 2006; Szathmáry, 2015). Famously, there are three common features to a major evolutionary transition: entities capable of independent replication before the transition can only replicate as parts of a larger unit after it, labour division and changes in information storage and transmission (Szathmáry and Maynard Smith, 1995).

Here are the arguments that support the existence of multilevel selection in nature (Okasha, 2006): i) the abstract nature of the concept of natural selection, derived from the concept of evolution by natural selection, which always occurs in entities which possess phenotypic variation, are heritable, and have differential levels of fitness (Lewontin, 1970), ii) the existence of a biological hierarchy, meaning that to achieve the complexity of a gene or a multicellular organism, natural selection must have occurred at lower levels of the biological hierarchy, i.e., a major transition in evolution, and iii) the abundant empirical evidence showing cases in which natural selection operates at different biological levels besides that of the gene or the multicellular organism. Having stated these three arguments, what is the strength of natural selection at higher biological levels, the group, compared to lower levels of the hierarchy, as the individual? Although in the 1960's it was argued that group selection was theoretically possible, it has also been argued that its strength would be irrelevant and ultimately suppressed by the strength of individual selection (Williams, 1966). However, the empirical evidence, derived from quantitative genetics, suggests that this is not always the case in nature. In many cases, the strength of natural selection at the group level is higher than at the individual level. Also, manipulative experiments that have artificially imposed group selection indicate that its strength is much higher than expected (Goodnight and Stevens, 1997).

RESOLVING THE DEBATE: CONTEXTUAL ANALYSIS AND EMPIRICAL EVIDENCE

Rather than having long argumentative exchanges, a simple way to resolve this 50-year old debate is to simply look at the empirical evidence, which is strongly based in theoretical grounds and empirical methods from quantitative genetics. One of the main sources of evidence supporting multilevel selection theory is derived from quantitative genetics, specifically from contextual analysis. Contextual analysis (Heisler and Damuth, 1987; Goodnight *et al.,* 1992) is a type of multiple regression whereby the effect of phenotypic traits on relative fitness is assessed. Contextual analysis takes into account individual traits, aggregate traits, which are the group means excluding the focal individual, and emergent traits, which can only be measured in the context of the group, such as density. This type of regression method is similar to that which has been widely used to measure natural selection in nature (Lande and Arnold, 1983), but it is extended to aggregate and emergent traits. Through methods such as path analysis, contextual analysis (Stevens *et al.,* 1995; Weinig *et al.,* 2007) has been used to correctly detect multilevel selection processes occurring in nature.

The original formula (Heisler and Damuth, 1987) for computing contextual analysis is as follows:

$$W_{ij} - W = \beta_{I1}(z_{1ij} - z_{1..}) + \beta_{I2}(z_{2ij} - z_{2..}) + \cdots + \beta_{In}(z_{nij} - z_{n..})$$
$$+ \beta_{C1}(z_{1ij} - z_{1..}) + \beta_{C2}(z_{2ij} - z_{2..}) + \cdots + \beta_{Cn}(z_{nij} - z_{n..}) +$$
$$+ \beta_{Cn+2}(y_{2i} - y_{2.}) + \cdots + \beta_{Cn+m}(y_{mi} - y_{m.}) + \epsilon_{ij}$$

Where the relative fitness (W) from the individual i belonging to the group j, depends on: the individual regression coefficients (β_I) of the individual traits (z_1, z_2, ..., z_n), the aggregate regression coefficients (β_C) of the aggregate traits (the group average excluding the focal individual), and the emergent regression coefficients (β_{Cn+1}, β_{Cn+2}, ..., β_{Cn+m}) of the emergent traits (y_1, y_2, ..., y_m). Goodnight (2015) indicates that caution should be placed on the distinction between aggregate and emergent traits as both aggregate and emergent traits are traits 'which are experienced by the individual'. Thus, for example, each focal individual experiences a unique average height, an aggregate trait, and a unique density, an emergent trait.

The value and sign of each selection coefficient indicate the strength and direction of natural selection in each trait. For a given trait, when the regression coefficients are compared at the individual level, by means of the individual coefficient, and group level, by means of the aggregate coefficient, the strength and direction of natural selection at two levels of the biological hierarchy are being compared. Goodnight (2013) has shown that although contextual analysis and inclusive fitness basically originate from the same equation, inclusive fitness measures evolutionary change using a fitness optimization and evolutionary rates at equilibrium (Gardner *et al.,* 2011), while contextual analysis measures evolutionary change when populations are far from optimal, i.e., the strength of selection in a population (Goodnight, 2015). Taking into account their different approaches and objectives, these two metrics for explaining social behavior and cooperation appear to be complementary (Taylor *et al.,* 2007; Goodnight, 2013; Goodnight, 2015).

For decades the main focus of research has been placed on demonstrating that group selection occurs in nature, and traditionally 'groups' are thought of as groups of organisms, and no other entities in the biological hierarchy. Yet to date, most of the empirical evidence of multilevel selection acting in nature through contextual analysis (Heisler and Damuth, 1987; Goodnight *et al.,* 1992), has been obtained for individual organisms and groups of organisms ranging from ants and plants to birds and humans. Two important exceptions of this include studies at the community level. Campbell *et al.* (1997) used contextual analysis to measure multilevel selection in pollinator visitation patterns in two species of *Ipomopsis* (Polemoniaceae), and recently, Campobello *et al.* (2015) also used contextual analysis to measure the strength of selection of individual and group activity in the nest and its effect on relative fitness in a community of two species of birds. For different organisms, Table 1 shows the strength and direction of natural selection acting on two levels, lower level as the individual, higher level as the group. From the results of these studies, and contrary to theoretical predictions (Maynard- Smith, 1964; Maynard-Smith, 1976), in nature, for many traits represented by numbers in parentheses in the equations of Table 1, the strength of natural selection at higher levels of the biological hierarchy is greater than at lower levels.

Another study of particular interest is that of Moorad (2013), which has indicated the existence of multilevel selection in human groups after following census records of more than a century in Iowa, USA. Moorad (2013) investigated whatever individual-level or family-level selection for both polygyny and polyandry, affects an individual's fitness. Analyzing census data from the predominately Mormon Iowa population, through contextual analysis Moorad (2013) detected family- and individual-level selection for polygyny, which were three times stronger than family-level selection for polyandry and more than an order of magnitude stronger than individual-level selection for polyandry. Additionally, the work of Solis *et al.* (2002) is notable; in this study, twenty plant phenotypic traits were measured, and their effect on relative fitness was evaluated at the population and meta-population levels. Lastly, the work of Pruitt and Goodnight (2014) has shown for the first time that selection at a higher level as the group can affect an aggregate trait such as the degree of docility/aggression in groups of spiders. Pruitt and Goodnight (2014) work and conclusions has caused strong controversies, coming from different evolutionary biology fields, as population genetics, quantitative genetics and evolutionary game theory (Gardner 2015; Grinsted *et al.,* 2015; Pruitt and Goodnight 2015; Smallegange and Egas 2015; Biernaskie and Foster 2016).

CONCLUSIONS

Constituting the basis of multilevel selection theory, Darwin (1871) postulated that selfish individuals outcompete altruistic individuals, however altruistic groups outcompete selfish groups. The substantial empirical evidence here provided shows that natural selection acts simultaneously on at least two levels of the biological hierarchy. Further studies are needed, especially at levels well above or below the organismic level, as studies clearly showing cell or ecosystem selection. Finally, stronger and broader theoretical and mathematical models, which besides quantitative genetics incorporate evolutionary game theory and population genetics frameworks, are strongly needed.

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