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 genético y organismico, 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 que del gen y organismo, desde el nivel molecular hasta el ecosistémico, apoyado además de la teoría de selección multinivel. Más allá de argumentos teóricos, si se examina cuidadosamente la evidencia empírica de selección multinivel y los resultados de 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 those 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; Benschbach 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) | Benschbach 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:

\[ W_{ij} - W = \beta_{i1}(z_{1ij} - z_{1.}) + \beta_{i2}(z_{2ij} - z_{2.}) + \cdots + \beta_{in}(z_{nij} - z_{n.}) \\
+ \beta_{c1}(z_{1ij} - z_{1.}) + \beta_{c2}(z_{2ij} - z_{2.}) + \cdots + \beta_{cn}(z_{nij} - z_{n.}) + \\
+ \beta_{c_{n+2}}(y_{2i} - y_{2.}) + \cdots + \beta_{c_{n+m}}(y_{mi} - y_{m.}) + \epsilon_{ij} \]
Where the relative fitness ($W$) from the individual $i$ belonging to the group $j$, depends on: the individual regression coefficients ($\beta_i$) of the individual traits ($z_1, z_2, ..., z_j$), the aggregate regression coefficients ($\beta_c$) of the aggregate traits (the group average excluding the focal individual), and the emergent regression coefficients ($\beta_{c+a}$) 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 ‘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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REFERENCES
Aspi J, Jakäläniemi A, Tuomi J, Siikamäki P. Multilevel phenotypic selection on morphological characters in a metapopulation
of Silene tatarica. Evolution. 2003;57(3):509-517. DOI:http://dx.doi.org/10.1554/014-3820(2003)057[0509:MPSOMC].2.0.CO;2

Banschbach VS, Herbers JM. Complex colony structure in social insects. II. Reproduction, queen-worker conflict, and levels of selection. Evolution. 1996;50(1):298-307. DOI:http://dx.doi.org/10.2307/2410801

Biernaskie JM, Foster KR. Ecology and multilevel selection explain aggression in spider colonies. Ecol Lett. 2016;19(8):873-879. DOI:http://dx.doi.org/10.1111/ele.12622

Campbell DR, Waser NM, Melendez-Ackerman EJ. Analyzing pollinator-mediated selection in a plant hybrid zone: hummingbird visitation patterns on three spatial scales. Am Nat. 1997;149(2):295-315. DOI:http://dx.doi.org/10.1086/285991

Campobello D, Hare JF, Sarà M. Social phenotype extended to communities: expanded multilevel social selection analysis reveals fitness consequences of interspecific interactions. Evolution. 2015;69(4):916-925. DOI:http://dx.doi.org/10.1111/evo.12629

Darwin CR. The descent of man, and selection in relation to sex. London: John Murray; 1871. p. 166.

Donohue K. The influence of neighbor relatedness on multilevel selection in the great lakes sea rocket. Am Nat. 2003;162(1):77-92. DOI:http://dx.doi.org/10.1086/375299

Donohue K. Density-dependent multilevel selection in the great lakes sea rocket. Ecology. 2004;85(1):180-191. DOI:http://dx.doi.org/10.1890/02-0767

Eldakar OT, Wilson DS. Eight criticisms not to make about group selection. Evolution. 2011;65(6):1523-1526. DOI:http://dx.doi.org/10.1111/j.1558-5646.2011.01290.x

Eldakar OT, Wilson DS, Dlugos MJ, Pepper JW. The role of multilevel selection in the evolution of sexual conflict in the water strider Aquarius remigis. Evolution. 2010;64(11):3183-3189. DOI:http://dx.doi.org/10.1111/j.1558-5646.2010.01087.x

Formica VA, Mcglothlin JW, Wood CW, Augat ME, Butterfield RE, Barnard ME, et al. Phenotypic assortment mediates the effect of social selection in a wild beetle population. Evolution. 2011;65(10):2771-2781. DOI:http://dx.doi.org/10.1111/j.1558-5646.2011.01340.x

Gardner A. Group selection versus group adaptation. Nature. 2015;524(7566):E3-E4. DOI:http://dx.doi.org/10.1038/nature14596

Gardner A, West SA, Wild G. The genetical theory of kin selection. J Evol Biol. 2011;24(5):1020-1043. DOI:http://dx.doi.org/10.1111/j.1420-9101.2011.02236.x

Goodnight C. On multilevel selection and kin selection: contextual analysis meets direct fitness. Evolution. 2013;67(6):1539-1548. DOI:http://dx.doi.org/10.1111/j.1558-5646.2012.01821.x

Goodnight CJ. Multilevel selection theory and evidence: a critique of Gardner, 2015. J Evol Biol. 2015;28(9):1734-1746. DOI:http://dx.doi.org/10.1111/jeb.12685

Goodnight CJ, Stevens L. Experimental studies of group selection: what do they tell us about group selection in nature?. Am Nat. 1997;150(S1):S59-S79. DOI:http://dx.doi.org/10.1086/286050

Goodnight CJ, Schwartz JM, Stevens L. Contextual analysis of models of group selection, soft selection, hard selection, and the evolution of altruism. Am Nat. 1992;140(5):743-761. DOI:http://dx.doi.org/10.1086/285438

Grinsed L, Bilde T, Gilbert JDJ. Questioning evidence of group selection in spiders. Nature. 2015;524(7566):E1-E3. DOI:http://dx.doi.org/10.1038/nature14595

Hamilton WD. The evolution of altruistic behavior. Am Nat. 1963;97(896):354-356. DOI:http://dx.doi.org/10.1086/287114

Hamilton WD. The genetical evolution of social behavior. I J Theor Biol. 1964a;7(1):1-16. DOI:http://dx.doi.org/10.1016/0022-5193(64)90038-4

Hamilton WD. The genetical evolution of social behavior. II J Theor Biol. 1964b;7(1):17-52. DOI:http://dx.doi.org/10.1016/0022-5193(64)90039-6

Heisler IL, Damuth J. A method for analyzing selection in hierarchically structured populations. Am Nat. 1987;130(4):582-602. DOI:http://dx.doi.org/10.1086/284732

Laiolo P, Obeso JR. Multilevel selection and neighbourhood effects from individual to metapopulation in a wild passerine. PLoS ONE. 2012;7(6):e38526. DOI:http://dx.doi.org/10.1371/journal.pone.0038526

Lande R, Arnold SJ. The measurement of selection on correlated characters. Evolution. 1983;37(6):1210-1226. DOI:http://dx.doi.org/10.1371/journal.pone.0038526

Lewontin RC. The units of selection. Annu Rev Ecol Syst. 1970;1:1-18. DOI:http://dx.doi.org/10.1146/annurev.es.01.110170.000245

Maynard-Smith JM. Group selection and kin selection. Nature. 1964;201(4924):1145-1147. DOI:http://dx.doi.org/10.1038/2011145a0

Maynard-Smith JM. Group selection. Q Rev Biol. 1976;51(2):277-283.

Michod RE, Roze D. Cooperation and conflict in the evolution of multicellularity. Heredity. 2001;86(1):1-18. DOI:http://dx.doi.org/10.1038/2011145a0

Moorad JA. Multi-level sexual selection: individual and family-level selection for mating success in a historical human population. Evolution. 2013;67(6):1635-1648. DOI:http://dx.doi.org/10.1111/evo.12050

Nowak MA, Tarnita CE, Wilson EO. The evolution of eusociality. Nature. 2010;466(7310):1057-1062. DOI:http://dx.doi.org/10.1038/nature09205

Nowak MA, Tarnita CE, Wilson EO. Nowak et al. reply. Nature. 2011;471(7339):E9-E10. DOI:http://dx.doi.org/10.1038/nature09836
Okasha S. Evolution and the Levels of Selection. New York: Oxford University Press; 2006. 263 p.

Pruitt JN, Goodnight CJ. Site-specific group selection drives locally adapted group compositions. Nature. 2014;514(7522):359-362. Doi:http://dx.doi.org/10.1038/nature13811

Pruitt JN, Goodnight CJ. Pruitt & Goodnight reply. Nature. 2015;524(7566):E4-E5. Doi:http://dx.doi.org/10.1038/nature14597

Searcy CA, Gray LN, Trenham PC, Shaffer HB. Delayed life history effects, multilevel selection, and evolutionary trade-offs in the California tiger salamander. Ecology. 2014;95(1):68-77. Doi:http://dx.doi.org/10.1890/13-0120.1

Smallegange IM, Egas M. Good for the group? Explaining apparent group-level adaptation. Trends Ecol Evol. 2015;30(7):379-381. Doi:http://dx.doi.org/10.1016/j.tree.2015.04.005

Solis S, Mendlinger S, Ward D. Differentiation along a gradient of environmental productivity and predictability in populations of Hordeum spontaneum Koch: multilevel selection analysis. Biol J Linn Soc. 2002;75(3):313-318. Doi:http://dx.doi.org/10.1046/j.1095-8312.2002.00021.x

Stevens L, Goodnight CJ, Kalisz S. Multilevel selection in natural populations of Impatiens capensis. Am Nat. 1995;145(4):513-526. Doi:http://dx.doi.org/10.1086/285753

Szathmáry E. Toward major evolutionary transitions theory 2.0. Proc Natl Acad Sci USA. 2015;112(33):10104-10111. Doi:http://dx.doi.org/10.1073/pnas.1421398112

Szathmáry E, Maynard-Smith JM. The major evolutionary transitions. Nature. 1995;374(6519):227-232. Doi:http://dx.doi.org/10.1038/374227a0

Taylor PD, Wild G, Gardner A. Direct fitness or inclusive fitness: how shall we model kin selection. J Evol Biol. 2007;20(1):301-309. Doi:http://dx.doi.org/10.1111/j.1420-9101.2006.01196.x

Tsuji K. Reproductive conflicts and levels of selection in the ant Pristomyrmex pungens: contextual analysis and partitioning of covariance. Am Nat. 1995;146(4):586-607. Doi:http://dx.doi.org/10.1086/285816

Weinig C, Johnston JA, Willis CG, Maloof JN. Antagonistic multilevel selection on size and architecture in variable density settings. Evolution. 2007;61(1):58-67. Doi:http://dx.doi.org/10.1111/j.1558-5646.2007.00005.x

Williams GC. Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought. Princeton: Princeton University Press; 1966. 328 p.

Wilson DS. A theory of group selection. Proc Natl Acad Sci USA. 1975a;72(1):143-146. Doi:http://dx.doi.org/10.1073/pnas.72.1.143

Wilson DS, Wilson EO. Rethinking the theoretical foundation of sociobiology. Q Rev Biol. 2007;82(4):327-348. Doi:http://dx.doi.org/10.1086/522809

Wilson EO. Sociobiology: The New Synthesis. Cambridge: Harvard University Press; 1975b. 697 p.

Wilson EO, Nowak MA. Natural selection drives the evolution of ant life cycles. Proc Natl Acad Sci USA. 2014;111(35):12585-12590. Doi:http://dx.doi.org/10.1073/pnas.1405550111

Wynne-Edwards VC. Animal Dispersion in Relation to Social Behavior. London: Oliver & Boyd; 1962. 653 p.