

1 **More on the genetical theory of multilevel selection**

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7
8 **Abstract** – In my article *The genetical theory of multilevel selection*, I provided a
9 synthesis of the theory of multilevel selection (MLS) and the theory of natural
10 selection in class-structured populations. I framed this synthesis within Fisher’s
11 genetical paradigm, taking a strictly genetical approach to traits and fitness. I
12 showed that this resolves a number of longstanding conceptual problems that
13 have plagued the MLS literature, including the issues of “aggregate” versus
14 “emergent” group traits, “collective-fitness₁” versus “collective-fitness₂” and
15 “MLS1” versus “MLS2”. In his commentary, Goodnight suggests this theoretical
16 and conceptual synthesis is flawed in several respects. Here, I show this is
17 incorrect, by: reiterating the theoretical and conceptual goals of my synthesis;
18 clarifying that my genetical approach to traits is necessary for a proper analysis
19 of the action of MLS independently of non-Darwinian factors; emphasising that
20 the Price-Hamilton approach to MLS is consistent, useful and conceptually
21 superior; and explaining the role of reproductive value in the study of natural
22 selection in class-structured populations.

23
24 **Keywords** – breeding value, cancer, class structure, contextual analysis, group
25 adaptation, group selection, haplodiploidy, Price equation, reproductive value.

26

Introduction

27

28 In my article *The genetical theory of multilevel selection* (Gardner 2015), I
29 provided a synthesis of the theory of multilevel selection (MLS) and the theory of
30 natural selection in class-structured populations. I framed this synthesis within
31 Fisher's (1918, 1930, 1941) genetical paradigm, taking a strictly genetical
32 approach to traits and fitness. I showed that this resolves a number of
33 longstanding conceptual problems that have plagued the MLS literature,
34 including the issues of "aggregate" versus "emergent" group traits, "collective-
35 fitness₁" versus "collective-fitness₂" and "MLS1" versus "MLS2" (reviewed by
36 Okasha 2006).

37

38 Goodnight (2015) suggests this theoretical and conceptual synthesis is flawed in
39 several respects. He suggests that I did not adequately review the empirical
40 literature on MLS, that I employed a flawed definition of evolutionary traits, that
41 I framed my contribution within a flawed Price-Hamilton tradition, and that I did
42 not correctly describe MLS in the context of class-structured populations.

43

44 Here, I: (1) reiterate the theoretical and conceptual nature of my synthesis; (2)
45 clarify that my genetical approach to traits is necessary for a proper analysis of
46 the action of MLS independently of non-Darwinian factors; (3) emphasise that
47 the Price-Hamilton approach to MLS is consistent, useful and conceptually
48 superior; and (4) explain the role of reproductive value in the study of natural
49 selection in class-structured populations.

50

Evidences of multilevel selection

51

52

53 Goodnight suggests that I did not adequately review the empirical literature on

54 MLS, and he provides a brief overview to remedy this perceived oversight.

55 However, the empirical reality of various evolutionary phenomena that

56 researchers have referred to as MLS is not in dispute here. The real issue is that

57 MLS researchers have been unable to agree upon exactly what MLS and its

58 associated concepts actually mean, and it is this issue that provided the

59 motivation for my theoretical and conceptual synthesis. I made this clear in the

60 opening sentences of the Abstract:

61

62

The theory of multilevel selection (MLS) is beset with
conceptual difficulties. Although it is widely agreed that
covariance between group trait and group fitness may arise
in the natural world and drive a response to ‘group
selection’, ambiguity exists over the precise meaning of
group trait and group fitness and as to whether group
selection should be defined according to changes in
frequencies of different types of individual or different types
of group.

71

72 Nevertheless, Goodnight’s empirical overview does helpfully illustrate the

73 muddle of definitions that are being used in the study of MLS. Importantly, whilst

74 many of the studies that he mentions define group selection in terms of the

75 proliferation and/or extinction of groups (e.g. Pruitt & Goodnight 2014), others
76 define group selection in terms of the impact that an individual's group
77 environment has on her own fitness (e.g. Stevens et al 1995). These definitions
78 are not equivalent, and will often disagree with each other as to the existence,
79 magnitude and direction of group selection in particular scenarios (more on this,
80 below).

81

82 I do disagree with Goodnight when he suggests that these empirical studies have
83 vindicated the "old" group selectionism of Wynne-Edwards (1962). It is true that
84 artificially-imposed, industrial batch-level selection in chickens may lead to
85 increases in yield (Muir 1996), but this is a world away from Wynne-Edwards'
86 claim that whenever selection acting within wild populations is in opposition to
87 selection acting at the between-population level, it is the latter that must prevail,
88 such that adaptation in the natural world is always "for the good of the group".
89 Both of these points serve to illustrate the conceptual confusions that abound in
90 the MLS literature.

91

92 **Multilevel selection is not evolution**

93

94 Goodnight suggests that my theoretical synthesis is flawed on account of my
95 conception of evolutionary traits being defined only for well-mixed populations.
96 This is incorrect. The definition that I used is valid, conventional and appropriate
97 to the aims of my study. My impression is that confusion has arisen out of MLS
98 being conflated with total evolutionary change.

99

100 Here is how I introduced the genetical approach to traits:

101

102

The character under selection is the heritable portion of the

103

individual's phenotypic trait, g ; that is, a weighted sum of

104

the frequencies of the alleles that the individual carries, the

105

weights being decided by linear regression analysis... This

106

quantity is also known as the individual's 'breeding value'

107

108

109 This linear-regression approach to describing the genetical component of the

110 phenotype was introduced by Fisher (1918) and it is conventionally termed

111 "breeding value" (Falconer 1981). The application of breeding values within the

112 context of Price's equation was spelled out by Price (1970), and they are clearly

113 defined even for populations that are not well mixed (Falconer 1985). Indeed, it

114 is the variance in breeding value that actually defines the "additive genetic

115 variance" (Falconer 1985) that is central to Goodnight's own approach to MLS in

116 structured populations (see below). If breeding value were really undefined

117 except for in well-mixed populations, then the same would be true of additive

118 genetic variance.

119

120 Goodnight's concern with the breeding-value approach seems to be that the

121 regression terms depend upon context. A gene's average effect with regards to a

122 phenotype of interest may depend on its interactions with other genes and with

123 factors such as climate such that, in subsequent generations, when the gene may

124 find itself incorporated into different genotypes and experiencing different

125 climates, its average effect is liable to change. Consequently, the same genotype
126 is liable to have different breeding values in different generations.

127

128 It is true that such changes in breeding value are not explicitly represented in my
129 equations. However, they are allowed for, in the sense that the equations remain
130 valid irrespective of such changes occurring. The reason that they do not feature
131 in the equations is that my aim was to describe only the action of natural
132 selection, and these changes in breeding value are not part of natural selection,
133 but instead represent a distinctly non-Darwinian factor in evolution. In the
134 context of Price's (1970, 1972a) theorem, such changes accrue to the
135 "transmission" term. In the context of Fisher's fundamental theorem, such
136 changes contribute to the "deterioration of the environment" (Fisher 1930, 1941;
137 Price 1972b). I discussed both transmission and environmental deterioration as
138 part of the explication of my theoretical synthesis, making clear that these are
139 conceptually distinct from the action of MLS.

140

141 The careful separation of selection and transmission effects is not merely a
142 matter of convention, but actually necessary from an adaptationist standpoint. It
143 is only natural selection, and not transmission factors – such as spontaneous,
144 random mutation and fluctuating average effects – that gives rise to adaptive
145 design (e.g. Gardner 2009; Gardner & Welch 2011). It is this unique role of
146 natural selection that motivated the focus of Fisher's (1930) *The genetical theory*
147 *of natural selection*, and his opening sentence: "Natural Selection is not
148 Evolution". Fisher's fundamental contributions to Darwinian theory, and the
149 contributions of others who have worked within his genetical framework, will

150 continue to be misunderstood for as long as the concepts of natural selection and
151 evolution are conflated.

152

153 **Multilevel selection and covariance**

154

155 Goodnight suggests my theoretical synthesis is also flawed on account of it being
156 framed within the Price-Hamilton approach to MLS (Price 1972a; Hamilton
157 1975). In particular, he points out that the Price-Hamilton formalism may detect
158 the operation of group selection even for nonsocial behaviours, and he suggests
159 that an alternative, contextual-analysis approach provides the correct means of
160 capturing the action of MLS. I believe that both the Price-Hamilton and
161 contextual-analysis approaches yield useful insights, but that it is the former
162 rather than the latter that properly engages with the ideas of selection and
163 adaptation at the group level. Moreover, I believe it is desirable – rather than
164 problematic – that the Price-Hamilton approach is able to diagnose the operation
165 of group selection beyond the realm of social behaviour.

166

167 Price's (1970, 1972a) selection-covariance theorem provides a very general
168 framework for thinking about selection in any context and in any medium. In the
169 context of evolutionary biology, it defines the action of natural selection in terms
170 of a partial change in the average value of a genetical trait, and it reveals that this
171 change is equal to the covariance, taken across all the individuals in the
172 population, between the individual's genetical trait and her relative fitness. It is
173 intuitive, then, that group selection should be defined analogously, as the
174 covariance, taken across all the groups in the population, between the group's

175 genetical trait and the group's fitness. This is exactly the Price-Hamilton
176 approach to MLS. This approach conceives of the group itself as the unit of group
177 selection, it assigns the group its own fitness, and it views group selection as
178 being driven by the differential fitness of groups per se. Importantly, by focusing
179 on the group's fitness, it directly connects with ideas of adaptation "for the good
180 of the group".

181

182 In contrast, whilst contextual analysis is also rooted in Price's covariance
183 definition of natural selection, it instead conceives of group selection in terms of
184 the impact that the individual's social environment has on that individual's
185 fitness. Accordingly, it conceptualises the individual as the unit of group
186 selection, and it views group selection as being driven by the differential fitness
187 of individuals per se, rather than the differential fitness of groups. This is how
188 contextual analysis is able to diagnose the action of group selection in the context
189 of soft selection, e.g. despite all groups having equal fitness. Put another way:
190 whereas the Price-Hamilton approach isolates the part of natural selection that
191 corresponds with the adaptation of groups, contextual analysis isolates the part
192 of natural selection that corresponds with the adaptation of individuals to their
193 particular group contexts. Both are useful approaches for studying selection but,
194 I'd argue, only one is properly engaging with the concept of group selection.

195

196 It is true that the Price-Hamilton approach may diagnose the operation of group
197 selection in some scenarios that do not involve social behaviour. For example, if
198 some individuals have better eyesight, and if some groups – by chance – have
199 more better-sighted individuals than others, then a portion of the action of

200 natural selection for improved eyesight will occur at the between-group level.
201 However, although this point has been much discussed in the literature for the
202 last ~30 years, there does not appear to be any consensus on whether it is
203 actually fatal to the Price-Hamilton approach.
204
205 My own view is that, far from being fatal, this diagnosis of group selection
206 beyond the realm of social behaviour is actually desirable (Gardner & Grafen
207 2009). The MLS partition of natural selection into its within-group and between-
208 group components is not supposed to delineate the boundary between the social
209 and nonsocial realms: that is the job of the kin-selection partition of natural
210 selection into its direct-fitness and indirect-fitness effects (Gardner et al 2011).
211 Moreover, it would be a mistake to view within-group selection as the sole driver
212 of individual-level adaptations, including good eyesight: rather, it is the total
213 action of natural selection, acting both within and between groups, that leads
214 individuals to become adapted to maximize their inclusive fitness (Gardner &
215 Grafen 2009). Instead, the conceptual significance of the MLS partition is that it
216 separates natural selection into the component that is responsible for group-
217 level adaptation (i.e. between-group selection) and the component that acts to
218 undermine the adaptive integrity of groups (i.e. within-group selection; Gardner
219 & Grafen 2009).
220
221 If natural selection is acting – wholly or in part – at the within-group level, then
222 traits will not be favoured to maximize group fitness and any adaptive rationale
223 will need to be sought at a lower level. But if natural selection is acting only at
224 the between-group level – e.g., if groupmates are genetically-identical clones –

225 then adaptations will evolve for the good of the group (Gardner & Grafen 2009).
226 Note that, in scenarios permitting a group-adaptationist interpretation, one is
227 free to interpret good eyesight either as an individual-level adaptation for
228 maximizing the individual's inclusive fitness or a group-level adaptation for
229 maximizing the group's inclusive fitness. This is analogous to how one can view a
230 macrophage engulfing a bacterium as either a cell maximizing its own inclusive
231 fitness or part of a larger suite of adaptations employed by a multicellular animal
232 for maximizing her inclusive fitness (Gardner 2014). Adaptationism is a scientific
233 tool that uses optimization thinking to formulate testable predictions (Parker &
234 Maynard Smith 1990) and, if the interests of individual and group are aligned,
235 then it is empirically vacuous to debate whether it is the individual or the group
236 that has been optimized.

237

238 **Multilevel selection in class-structured populations**

239

240 Turning to the specific issue of class structure, Goodnight suggests my approach
241 to MLS in this context is flawed on both conceptual and technical grounds. In
242 particular, he suggests that I have erroneously assigned fitness to only one level
243 of biological organization – the individual – and he provides a contextual-
244 analysis treatment of MLS in parasitoid wasps that he claims is superior to my
245 Price-Hamilton approach. Here, I suggest there there has been a
246 misunderstanding of the concept of reproductive value and its role in theory of
247 natural selection, and I show that the contextual-analysis treatment is
248 mathematically, biologically and conceptually invalid as an alternative to the
249 Price-Hamilton approach.

250

251 The concept of reproductive value is of crucial importance in the context of class-
252 structured populations. If individuals differ in ways that are not strictly genetical,
253 then they cannot be considered equivalent from a natural-selection perspective,
254 and must be subdivided into separate classes. One aspect of the problem of class
255 structure is that not all offspring are equal, such that a simple count of offspring
256 number may not provide an adequate measure of an individual's Darwinian
257 success. A vivid example is provided by sex allocation, in which parents decide
258 the sex, rather than the number, of their offspring (Darwin 1871; Fisher 1930).
259 Accordingly, a proper measure of Darwinian success is provided by the
260 individual's reproductive value, i.e. her expected, asymptotic, relative
261 contribution of genes to future generations, and each class of individual
262 contributes to the overall action of natural selection in proportion to its
263 reproductive value (Fisher 1930). Taylor (1996) provides an introductory-level
264 overview of the mathematics of reproductive value.

265

266 As an illustrative application of my theoretical and conceptual synthesis, I
267 discussed the relationship between non-transmissible cancer and MLS. Although
268 cancer has often been conceptualized as involving a tension between different
269 levels of selection – i.e. favoured at a within-individual level and disfavoured at a
270 between-individual level – I pointed out that the proliferation of cancer cells
271 cannot be conceptualized in terms of MLS, in the strict sense of the genetical
272 theory, because cancer cells – and somatic cells in general – have no
273 reproductive value. But Goodnight suggests that my logic is faulty: he argues that
274 since cancerous cells have the capacity to proliferate and exhibit heredity, their

275 proliferation does represent within-individual selection, and that my conclusion
276 had stemmed from me assigning fitness only at the level of individual organisms.
277
278 However, this is incorrect: I did not assign zero reproductive value to cancer cells
279 because they are cells and not individuals, but rather because they are cells
280 whose lineages perish with the death of the individual organism, such that their
281 expected, asymptotic, relative contribution of genes to future generation is zero.
282 Even if reproductive value is assigned only to cells and not to whole organisms,
283 all of the reproductive value in the population belongs to germline cells whilst
284 somatic cells have zero reproductive value. Thus, according to Fisher's
285 proportionality principle, the proliferation of cancerous cells within somatic
286 tissues cannot be part of MLS, in the strict sense of the genetical theory – though
287 it may induce differential reproductive value of germline cells, at a between-
288 organism level, selectively favouring the evolution of anti-cancer adaptations.
289
290 The role of reproductive value in modulating a class's contribution to the overall
291 action of natural selection is captured mathematically by Price's (1970) equation
292 for class-structured populations – specifically, Price's equation (5) and my
293 equation (4). This describes a separate selection covariance for each class in the
294 population, and adds them together to yield the total action of natural selection,
295 with each class's contribution being weighted by its reproductive value (such
296 that a class with no reproductive value makes no contribution at all). As part of
297 my theoretical synthesis, I combined this equation with Price's (1972a) equation
298 for MLS – specifically, Price's equation (A17) and my equation (5). This provided
299 a statement of MLS for class-structured populations – specifically, my equation

300 (7). This equation takes each class's separate contribution to the total action of
301 natural selection, and separates its within-group and between-group
302 components, such that the total action of group selection is defined as a class-
303 reproductive-value-weighted sum of the between-group selection terms for each
304 class.

305

306 In my study, I pointed out that this formulation presents some conceptual
307 problems for the idea of the social group as a unit of selection. In particular,
308 whilst in some scenarios the sum of between-group-selection terms can be
309 brought together as a single selection covariance, with the social group acting as
310 the unit of selection, more generally the social group remains fragmented into its
311 separate pure-class subgroups, and it is these that are considered the units of
312 group selection, rather than the whole social group. To illustrate the problem, I
313 considered the following scenario:

For example, a parasitoid wasp might oviposit a single unfertilized (i.e. male) egg and a single fertilized (i.e. female) egg into a caterpillar, within which these siblings develop and compete for resources, and this yields both a clearly defined social group of more than one individual and also ample scope for kin selection. Yet, it is unclear whether group selection can occur, except in the trivial sense that a single individual can be considered a group of size 1, owing to difficulties in bringing the separate selection covariances

314 for male subgroups and for female subgroups together into
315 a single selection covariance.
316
317 Goodnight suggests that this Price-Hamilton approach is simply flawed, and
318 instead provides a treatment of the parasitoid wasp scenario using his preferred
319 contextual-analysis approach. He states that the response to selection for
320 arbitrary individual-level and group-level traits is given by $R = \frac{1}{2} (G P_F^{-1} S_F + G$
321 $P_M^{-1} S_M)$, where: P_F and P_M are 3×3 phenotypic covariance matrices describing
322 female, male and group traits in females and males, respectively; G is the
323 corresponding 3×3 genetic covariance matrix; and S_F and S_M are vectors of order
324 3 describing the selection differentials in females and males, respectively. This is
325 a modified version of Lande's (1980) classic result.
326
327 However, this contextual-analysis treatment is problematic in several respects.
328 Firstly, it is mathematically invalid because the phenotypic covariance matrices,
329 being singular, are uninvertable, so the right hand side of the equation is actually
330 undefined: this is the linear-algebraic equivalent of a division-by-zero error. To
331 be clear, this error is present only in Goodnight's treatment, and not in Lande's
332 formulation. Secondly, the contextual-analysis treatment is biologically invalid
333 because it assumes a diploid mode of inheritance, which is incompatible with the
334 haplodiploid mode of inheritance exhibited by parasitoid wasps (both in reality
335 and in the hypothetical scenario outlined above). Lande's article does contain a
336 result for haplodiploidy, in the Appendix, that might serve as the basis for a re-
337 worked contextual-analysis treatment. Thirdly, the contextual-analysis
338 treatment hinges upon particular, ad hoc assumptions – such as Gaussian

339 variance – that may yield a more or less reasonable approximation in the context
340 of particular applications, but which fundamentally limit its wider generality.
341 This contrasts with the Price-Hamilton approach to MLS, which emerges from
342 purely notational definitions as an exact mathematical identity, and enjoys the
343 fullest generality of mathematical and empirical application.

344

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346

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350

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