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34 *The competition between paradigms is not the sort of battle that can be resolved by*  
35 *proofs.*

36 T. S. Kuhn

37

### 38 ***Introduction***

39 Despite its status as a cornerstone of modern evolutionary biology,  
40 inclusive fitness theory, conceptualised and formalised by W. D. Hamilton over  
41 50 years ago [1,2], is no stranger to misunderstanding and controversy. In the  
42 21<sup>st</sup> century version of the controversy E. O Wilson, author of *Sociobiology* and  
43 erstwhile supporter of inclusive fitness theory [3], shifted to attacking the  
44 theory, in collaboration with a number of colleagues. The profile of Wilson and  
45 his collaborators, his former support for the theory, and the profile of the venues  
46 in which these attacks were published, moved this controversy from being  
47 confined to technical discussions amongst biologists, and into the limelight; in  
48 2010 the front cover of *Nature* featured the highest profile attack to date by  
49 Wilson, in conjunction with the mathematical biologists Martin Nowak and  
50 Corina Tarnita [4]. These attacks drew extensive responses from the community  
51 of inclusive fitness theory theorists and empiricists (e.g. [5]), and in turn further  
52 critiques, in a cycle that shows little sign of being escaped. In this article, over 10  
53 years after the first high profile attack on inclusive fitness theory by Wilson and  
54 Hölldobler [6], I attempt to provide a personal view on what the disagreements  
55 are about. Critiques of inclusive fitness theory have become increasingly  
56 mathematical in recent years, as have their defences. I suggest that there is  
57 nothing wrong with the mathematics of the critiques, but it is the conceptual  
58 interpretations of these mathematics that are flawed. Hence, if the ongoing  
59 controversy is to be 'put to bed' then the resolution will be conceptual, not  
60 mathematical, in agreement with the quote by Thomas Kuhn reproduced above  
61 ([7], p. 148).

62

### 63 ***What is inclusive fitness theory?***

64 Inclusive fitness theory had its first formal presentation in two papers by  
65 W. D. Hamilton [1,2]. Hamilton's work had two aims, the first and most generally  
66 known being to propose a method of accounting for fitness effects that provided

67 a rigorous explanation for the evolution of social behaviour. This method divides  
68 the inclusive fitness effect of a social trait individual into direct and indirect  
69 fitness components. The direct fitness effects of a trait are the change in fitness  
70 of the bearer that results from the trait's expression, often referred to as the  
71 'cost'  $c$  of the behaviour, although this 'cost' can be negative; direct fitness is  
72 'stripped' of fitness effects received from other bearers of the same trait. Indirect  
73 fitness effects are changes in fitness by recipients of the social behaviour, usually  
74 referred to as 'benefit'  $b$  which can again be negative, weighted by their genetic  
75 relatedness  $r$  to the behaving individual. Baseline fitness due to other traits and  
76 factors completes the description of the individual's total fitness, but since this  
77 does not systematically vary according to whether the trait is borne or not it falls  
78 out of the subsequent analysis. Then asking when a social trait experiences  
79 positive selection yields Hamilton's rule

$$80 \quad rb - c > 0.$$

81 Hamilton's derivation of this result [1] was exact, but under certain simplifying  
82 assumptions. At the same time however, inspired by R. A. Fisher, Hamilton  
83 claimed to have identified inclusive fitness as the quantity that organisms under  
84 natural selection should act as if to maximise. Hamilton's reasoning here was less  
85 formal, and recently inclusive fitness theorists have both advocated and debated  
86 the validity of his maximisation claim (*e.g.* [8–12]). Furthermore, it is important  
87 to note that correct reasoning about inclusive fitness and behaviours requires  
88 consideration of the behavioural options available [13]; for example, a female  
89 honeybee may have higher inclusive fitness as a queen, but when forced into a  
90 worker role through epigenetics resulting from not being fed a diet of royal jelly  
91 during development [14], the only behavioural options available are to raise  
92 sisters, produce males, and police the male reproduction of sisters [15].

93         Perhaps because of some initial opacity in Hamilton's proposal, perhaps  
94 because of simplifying assumptions made but subsequently relaxed, and perhaps  
95 simply because of the volume of the literature that it inspired, Hamilton's  
96 inclusive fitness method of analysing selection on social traits attracted criticism,  
97 the intensity of which has increased in the last ten years as described above.  
98 Since the criticisms I address are all to do with the Hamilton's rule version of  
99 inclusive fitness theory, rather than the inclusive fitness maximisation

100 arguments, I shall refer to ‘inclusive fitness theory’ in the Hamilton’s rule sense  
101 in what follows.

102

### 103 ***Critiques of inclusive fitness theory, and their responses***

104 Various summaries of the recurrent or recent misunderstandings of  
105 inclusive fitness theory exist (see for example [16–19]). Here I briefly break  
106 down the development of some of the main arguments against inclusive fitness  
107 theory over the last 10 years, and summarise their responses. Having provided a  
108 brief introduction to inclusive fitness theory above, I assume a passing  
109 familiarity with the basic concepts of multilevel (or ‘trait group’) selection  
110 theory, in which social behaviours are favoured when between-group selection  
111 outweighs within-group selection.

112 The first criticism, originally publicised by Wilson and Hölldobler [6], is  
113 that inclusive fitness theory models of the evolution of social behaviour in  
114 colonies are less general than models of competition between colonies.  
115 Commentators at the time [20] noted that this ‘new’ form of model appeared to  
116 be inclusive fitness theory in disguise; the critique that inclusive fitness theory is  
117 less general than multilevel selection theory has been repeated subsequently  
118 (e.g. [4]), despite the long-standing result that inclusive fitness and multilevel  
119 selection analyses are different partitionings of fitness and therefore always  
120 agree on the direction of selection (see [16] for a summary), and despite the  
121 longstanding existence of methods for generalising Hamilton’s rule beyond the  
122 simple additive social interactions he originally considered [21].

123 In support of the arguments that inclusive fitness theory could not explain  
124 the evolution of reproductive division of labour in colonies, Nowak, Tarnita and  
125 Wilson presented a mathematical model in which they claimed the evolution of  
126 costly helping was not correlated with within-colony relatedness, as predicted  
127 by Hamilton’s rule [4]. However a subsequent more thorough analysis of the  
128 model found that under systematic variation of relatedness Hamilton’s rule  
129 predicted correctly when helping would and would not be favoured [22].

130 A concurrent criticism of inclusive fitness theory, although it was not fully  
131 appreciated at the time [23], is that inclusive fitness is no more than a  
132 conceptually difficult reorganisation of classical Darwinian / Fisherian fitness

133 [4]. A version of this viewpoint has recently been echoed by inclusive fitness  
134 theorists, who focus on a 'gene's eye view' of individual fitness averaged across  
135 time, individuals and states to claim that inclusive fitness is not an extension of  
136 classical Darwinian fitness [24], and that considering it as such is not  
137 conceptually useful. Hamilton clearly conceived of inclusive fitness theory as an  
138 extension to classical fitness [25], and as I have written elsewhere it seems  
139 reasonable to characterise the classical understanding of fitness as indeed being  
140 the fitness an individual would express 'stripped' of all its components due to the  
141 behaviour of others, as first outlined by Hamilton [1]; simply put, Darwin and the  
142 modern synthesists implicitly excluded the social from their formulation of  
143 fitness, with Fisher even going so far as to consider it 'unimportant' ([23], pp. 56-  
144 57)). Regardless of conceptual utility, investigating the history and likely original  
145 definitions of concepts is important in correctly ascribing priority, and useful in  
146 considering how misunderstandings can arise.

147         Other critiques concerned the empirical predictions from inclusive fitness  
148 theory, starting with the 'haplodiploidy hypothesis' that the genetics of the  
149 Hymenoptera facilitate the evolution of costly helping by daughters [4], and then  
150 moving on to sex ratio theory [26] The former critique was in fact not a new  
151 observation, as evidence and theory against the haplodiploidy hypothesis had  
152 already been accumulating, as well as pointing to a replacement theory  
153 (discussed in 'Causality, group adaptations, and major transitions' below) [5];  
154 the extension of the attack to sex ratio theory [26] has since been expertly  
155 addressed by Andrew Bourke [27].

156

### 157 ***Separating concepts and tools***

158         As mentioned in the preceding section, in response to claims that  
159 inclusive fitness has limited applicability, theorists began advocating a  
160 generalisation of Hamilton's rule first proposed by David Queller [21], which  
161 applies the Price equation to derive a version of Hamilton's rule in which fitness  
162 costs and benefits, and relatedness, are all defined in terms of (partial)  
163 regression coefficients (e.g. [16,17,23]).

164         In response to this generalisation, critics of inclusive fitness theory have  
165 also taken aim at this methodology, claiming that it risks confusing correlation

166 with causation [28], as well as making a more general point that applying  
167 statistical models to decompose the selective pressure in exact game theoretic or  
168 population genetic models is pointless [29] (writing in response to [30]).

169         The link between the partial regression formulation of costs and benefits,  
170 and Hamilton's original presentation in terms of average fitness effects, has  
171 recently been derived afresh by Francois Rousset [31] (but see [32] in section  
172 'Causality, group adaptations, and major transitions'), also criticising the  
173 deliberate misapplication of causal interpretations to correlational models [28]  
174 and the general critique of the statistical approach to analysing social evolution  
175 models (e.g. [29]). Since this approach is fundamentally-rooted in the field of  
176 quantitative genetics [21,33], presumably the critics of the statistical approach to  
177 studying responses to selection also take issue with this well-established and  
178 very productive field. Others have also noted that finding shortcomings in the  
179 mathematical tools used to analyse models in inclusive fitness terms does not  
180 equate to finding shortcomings in the underlying biological concepts that these  
181 tools attempt to describe [16,17,23].

182

### 183 ***Causality, group adaptations, and major transitions***

184         The preceding sections appear to give a gloomy, and well-known, picture  
185 of misunderstandings of inclusive fitness theory, and their associated  
186 correctives. However in parallel with these attacks, and possibly in part because  
187 of them, inclusive fitness theory has over the last few years begun moving in  
188 increasingly fruitful and important directions. Here I highlight developments in  
189 three closely related areas; evaluating causality, determining sufficient  
190 conditions for the evolution of group adaptations, and studying the link between  
191 inclusive fitness theory and major transitions in organismality, particularly from  
192 single cellular life to complex multicellularity, and from subsociality to obligate  
193 eusociality, or superorganismality.

194         Assessing causality is of fundamental interest to evolutionary biologists,  
195 dating back to the ultimate / proximate distinctions of Tinbergen [34] and Mayr  
196 [35]. Hamilton was motivated to develop inclusive fitness theory because of the  
197 apparent gap in the power of neo-Darwinism to explain why self-sacrificing  
198 behaviour should evolve. In the simplest cases, separating direct (own) from

199 indirect (others') fitness effects makes clear what conditions are necessary for a  
200 social behaviour to evolve, and enables it to be classified as either altruism, spite,  
201 mutual benefit, or selfishness [1]. These questions are those that evolutionary  
202 biologists seek to answer on a daily basis when asking 'why did this trait evolve?'  
203 Mathematical biologists considering exact models of evolution may be apt to  
204 forget this [29]; without the decomposition that inclusive fitness provides the  
205 only adaptive explanation to the biologists' question that a mathematical model  
206 may provide is the tautological and insight-free 'because it was favoured by  
207 selection'. Inclusive fitness theory is particularly useful for empirical  
208 evolutionary biology because it facilitates construction of hypotheses about what  
209 might be expected to evolve, naturally taking account of conflicts between  
210 groups, within groups, and even within individuals and genomes; given that  
211 inclusive fitness theory summarises complexity with simple parameters with  
212 well-defined biological meanings, these hypotheses lend themselves well to  
213 empirical validation (e.g. [5,36]).

214         As discussed in 'Separating concepts and tools', the increasingly popular  
215 partial regression approach to deriving Hamilton's rule has been derived from  
216 Hamilton's initial verbal consideration of average fitness effects [31]. Yet Samir  
217 Okasha and Johannes Martens have noted that in non-additive social  
218 interactions, the partial regression definitions of the costs and benefits of  
219 Hamilton's rule do not equal the expected fitness changes from 'mutating' the  
220 genotype of a random member of the population [32]. The solution they follow,  
221 also briefly suggested in [23], is to apply Fisher's 'average effect of a gene  
222 substitution'; Okasha and Martens find that, under a very particular  
223 interpretation of Fisher's argument, it does indeed provide a causal explanation  
224 for the costs and benefits of Hamilton's rule [32].

225         While the evolution of social behaviour within groups due to inclusive  
226 fitness benefits, or equivalently due to between-group competition outweighing  
227 within-group competition, is well understood, the evolutionary process by which  
228 group-level adaptations arise has been far less so [37]. As noted in 'Critiques of  
229 inclusive fitness theory, and their responses', models based on inclusive fitness  
230 and based on group competition necessarily predict the same direction of  
231 evolutionary change. Yet as Okasha notes the two frameworks, despite giving

232 equal evolutionary change predictions, can differ in the causal explanations they  
233 provide [38,39]. By constructing causal graphs of different social scenarios in  
234 which group-level fitness emerges from individual-level fitnesses, and vice-  
235 versa, Okasha found instances in which each framework provided incorrect  
236 causal explanations. Since the evolution of group-level adaptations requires a  
237 transition from group-fitnesses-determined-by-individual-fitnesses to  
238 individual-fitnesses-determined-by-group-fitnesses [40,41], such causal analyses  
239 will be very important in understanding how these adaptations can arise, and be  
240 correctly identified as such. Juusi Lehtonen subsequently showed how multi-  
241 level selection models can be recast using inclusive fitness theory quantities,  
242 making clearer the deep conceptual relationships between the two approaches,  
243 and illustrating this with reference to causal graph models of sperm competition  
244 [42].

245         As alluded to above, identification of group adaptations has a long and  
246 contentious history [37,43,44]. Jonathan Pruitt and Charles Goodnight recently  
247 claimed to have collected evidence that adaptive changes in aggressiveness  
248 phenotype ratio in colonies of social spiders, in response to varying colony size  
249 and environmental conditions, arise due to group-level selection and constitute  
250 group-level adaptations [45]. Various authors have pointed out the need to  
251 account for the potential for individual-level selection within groups conflicting  
252 with selection between groups [46–48]. Recently Jay Biernaskie and Kevin  
253 Foster presented ecologically-motivated models incorporating within-group  
254 competition; these models give improved fits to Pruitt and Goodnight’s data,  
255 concluding that the ‘group-level’ adaptive trait identified by those authors is  
256 actually explained by individual-level within-group selection [49].

257         Arguably the most significant of group adaptations are those in which a  
258 new level of evolutionary individual emerges; in understanding these scenarios,  
259 dubbed major evolutionary transitions [50], inclusive fitness theory is  
260 increasingly proving its worth. While the inclusive fitness theory community has  
261 accumulated evidence and theory to undermine the ‘haplodiploidy hypothesis’  
262 (see ‘Critiques of inclusive fitness theory, and their responses’), inclusive fitness  
263 theory has been crucial in providing a new framework, the ‘monogamy  
264 hypothesis’ [51] that has explanatory power for transitions to (and from)

265 reproductive helping by offspring, in social insects [52] and in cooperatively  
266 breeding birds [53], for example; this approach has also been adapted to  
267 consider the evolution of multicellularity [54]. Wilson's collaborator Martin  
268 Nowak, and colleagues, have recently presented a population genetical model  
269 claimed to show that monogamy is not necessary for the evolution of  
270 reproductive division of labour under haplodiploidy, which they take to be a  
271 refutation of the monogamy hypothesis [55]; while it is beyond the scope of this  
272 Opinion to address this model in any detail, others question whether the result  
273 may be little more than a mathematical curiosity [56], and given that previous  
274 detailed models claiming to show no role for relatedness in the evolution of  
275 eusociality [4] have subsequently been re-analysed to show its central  
276 importance [22], as described above, the model of [55] will merits analysis from  
277 an inclusive fitness perspective. In fact, Nick Davies and Andy Gardner do  
278 precisely this, and do indeed show that the disconnect between monogamy and  
279 the evolution of reproductive division of labour is indeed a mathematical artefact  
280 of the assumptions made in the model [57]. There is also the issue of whether  
281 this result, if it were correct, really addresses the monogamy hypothesis, as  
282 discussed below.

283         Recently, focussing on social insects, Jacobus Boomsma and Richard  
284 Gawne have reviewed the literature on the 'superorganism concept' from its  
285 earliest statements at the turn of the 20<sup>th</sup> century through to its present day  
286 presentation and usage. Boomsma and Gawne [58] note that the historical  
287 conception of superorganismality, as requiring an irreversible group-level  
288 adaptation in the form of a distinct non-reproductive caste, dates back to  
289 Wheeler, Huxley and Fisher, but that this strict criterion was subsequently  
290 diluted by weaker and biologically-ungrounded definitions of eusociality, and in  
291 particular by the rise to prominence of E. O Wilson's definition of the  
292 superorganism. By linking with the monogamy hypothesis Boomsma and Gawne  
293 highlight the importance of inclusive fitness theory and irreversible  
294 commitments to caste formation, in the form of germ/soma segregation, in  
295 explaining the major transitions to complex eusociality and multicellularity, and  
296 the genuine group-level adaptations they exhibit. It is worth briefly noting that in  
297 criticising the monogamy hypothesis, Nowak and colleagues [55] use the less

298 specific definition of eusociality as reproductive division of labour, rather than  
299 irreversible commitment to a sterile caste. Sterility of workers can be reversed  
300 over evolutionary time in their model, and indeed the original transition to  
301 workers foregoing mating, and hence by necessity foregoing production of  
302 daughters, is not even considered; thus their model is not well-motivated as a  
303 critique of the monogamy hypothesis, which seeks to explain eusociality *sensu*  
304 *stricto* [58].

305

### 306 **Conclusions**

307 Most of the critiques of inclusive fitness theory mentioned above ('Critiques of  
308 inclusive fitness theory, and their responses') would be uncontroversial, and  
309 potentially useful, if presented as investigations into the subtleties of inclusive  
310 fitness theory, rather than debunkings of it; as discussed above, they may well  
311 claim to have inspired further research into the subtleties and application of  
312 inclusive fitness theory. Of course iconoclasm provokes attention, and fame is  
313 usually attached to the protagonists in 'revolutionary science' than the  
314 practitioners of 'normal mode' science [7], so we may never be free of attempts  
315 to dethrone Hamilton, or the modern synthesists, or even Darwin. However the  
316 theory of evolution through natural selection, and its expositions and  
317 refinements, have withstood sustained assault for over 150 years, and there is  
318 now little reason to expect fatal flaws to be discovered in the future. One thing  
319 that may mark out the recent controversy as a sociological phenomenon are the  
320 shifting arguments of the critics of inclusive fitness theory (see 'Critiques of  
321 inclusive fitness theory, and their responses'), which are more typical of the  
322 defence of a particular world-view than a genuine search for scientific  
323 understanding. These may also be symptomatic of differences in the viewpoints  
324 of Wilson and his various collaborators. Furthermore, David Queller has shown  
325 how understanding the historical development of inclusive fitness theory and its  
326 application may help to understand recurrent criticisms [59]. To echo Darwin's  
327 words, however, "I look with confidence to the future, to young and rising  
328 naturalists, who will be able to view both sides of this question with  
329 impartiality." ([60], quoted in [7], p. 151)

330

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334

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460  
461 **Reference Annotations**

- 462 • Liao, Rong and Queller (2015) - \*\* In this modelling paper the authors  
463 present a fuller examination of the model of the evolution of ‘eusociality’  
464 presented by Nowak, Tarnita and Wilson. They find that while the model  
465 is correct, an overly restrictive set of assumptions led to Nowak et al.’s  
466 claims that it was inconsistent with inclusive fitness theory. Relaxing  
467 these assumptions Liao et al. find that the model actually confirms  
468 predictions from inclusive fitness theory.
- 469 • Marshall (2015) - \* This monograph attempts to provide an accessible  
470 introduction to how inclusive fitness theory works, and how to interpret

471 the controversies surrounding it; a particular focus on causality, for  
472 example explaining competing classifications of the same social  
473 behaviour, is held.

- 474 • Bourke (2015) - \*\* In this review Bourke addresses recent criticisms of  
475 sex-ratio predictions derived from inclusive fitness theory, by Wilson and  
476 Nowak. With reference to classical sex ratio theory and empirical data  
477 Bourke shows how Wilson and Nowak's thesis fails to explain  
478 experimental observations that match standard predictions of inclusive  
479 fitness theory.
- 480 • Okasha (2015) - \*\* In this modelling paper Okasha uses causal graphs to  
481 examine conditions under which inclusive fitness and multilevel selection  
482 partitions are more or less 'causally apt' as descriptions of evolutionary  
483 change, despite the fact that both approaches predict the same gene  
484 frequency change under selection. Examples are presented in which each  
485 partition provides the more appropriate causal representation.
- 486 • Davies and Gardner (2016) - \* This article reviews the mathematical  
487 assumptions in the model of the evolution of worker sterility by Olejarz et  
488 al. (2015), showing that main results of that model arise from assuming  
489 genes of large effect. When these assumptions are relaxed the model  
490 shows monogamy promotes raising of siblings in social insect colonies, as  
491 predicted by inclusive fitness theory.
- 492 • Boomsma and Gawne (2016) - \*\* In this review the authors forensically  
493 investigate the history and conceptual content of the superorganism  
494 concept, from its origin in the early 20<sup>th</sup> century to its present day form.  
495 With reference to inclusive fitness theory and the major transitions to  
496 obligate eusociality and multicellularity, the authors show that the  
497 original presentation of superorganismality was biologically sound and  
498 useful, but subsequent presentations of the idea have diluted its biological  
499 meaning.
- 500 • Lehtonen (2016) - \* In this article Lehtonen shows how inclusive fitness  
501 quantities (the  $r$ ,  $b$  and  $c$  of Hamilton's rule, equation in main text) can  
502 appear explicitly in multi-level selection analyses. Lehtonen illustrates the  
503 utility of recognising the 'kin selection' components of multilevel selection

504 with reference to causal graph models, and the popular 'evolutionary  
505 stable strategy' approach to building inclusive fitness models.