

William D. Hamilton's Brazilian lectures and his unpublished model regarding Wynne-Edwards's idea of natural selection. With a note on 'pluralism' and different philosophical approaches to evolution

Emanuele Coco¹ 

Received: 28 March 2016 / Accepted: 10 November 2016
© Springer International Publishing AG 2016

Abstract In 1975, the English evolutionist William Donald Hamilton (1936–2000) held in Brazil a series of lectures entitled “Population genetics and social behaviour”. The unpublished notes of these conferences—written by Hamilton and recently discovered at the British Library—offer an opportunity to reflect on some of the author's ideas about evolution. The year of the conference is particularly significant, as it took place shortly after the applications of the Price equation with which Hamilton was able to build a model that included several levels of selection. In this paper I mainly analyse the inaugural lecture in which Hamilton proposes a simple model to disprove the hypothesis supported by the British zoologist C. Vero Wynne-Edwards (1906–1997) regarding mechanisms to prevent “over-exploitation of the food supply” in “the interests of the survival of the group”. The document presented here is of great historical interest. Not only because manuscript offers a model that—since it was intended for teaching purposes—had never before appeared in the published version, but also because of the general index of the lectures that accompanies it. The latter allows us to make some hypothetical considerations on the relationship and differences between kin-selection, group-selection and inclusive fitness that Hamilton wanted to present to the attentive, well-prepared audience of the foreign university that had invited him.

Keywords W.D. Hamilton · V.C. Wynne-Edwards · Altruism · Resources · Pluralism · Philosophy

✉ Emanuele Coco
emanuele.coco@unict.it

¹ Storia della Filosofia, DiSForm, Università di Catania, Via Biblioteca 4, 95124 Catania, Italy

1 Introduction

From the perspective of classical Darwinism, altruism has long been seen as a paradox. When an animal “increases the fitness of another at the expense of his own fitness, he can be said to have performed an act of *altruism*” (Wilson 1975, p. 117). It assigns resources (energy, food, etc.) for the benefit of the others. As a result, its reproductive output undergoes a decline. Herein lies the paradox: why does natural selection not eliminate a form of behaviour that is so disadvantageous to the individual?

The problem is even more evident if we take into account forms of radical sacrifice such as abstaining from reproduction. Classical examples concern some kinds of Hymenoptera like wasp, bees and ants. Charles Darwin himself was aware of this difficulty in the framework of his natural selection theory, as he indicated still in the sixth edition of the *Origin* (1872, pp. 226, 230).

The English evolutionist William Donald Hamilton (1936–2000) offered a possible solution to the paradox by introducing a new evolutionary parameter called “inclusive fitness”.¹ In 1964, Hamilton built a mathematical model which revealed some hidden aspects in the dynamics of the evolutionary process of social behaviour (1964). Following the steps of the founders of population genetics—Ronald Aylmer Fisher (1890–1962), John Burdon Sanderson Haldane (1892–1964) and Sewall Wright (1889–1988)—he applied his mathematical analysis on the individual and on his gain in genetic terms. The inclusive fitness approach showed that a subject can increase his fitness not only through his offspring but also through the offspring of his relatives. In this perspective the altruistic behaviour becomes a way by which the altruist is able to increase his own gain—an idea that has had many additional developments and objections.²

¹ Hamilton suggests seeing inclusive fitness as “the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual’s social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitness of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects: unity for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins, ... and finally zero for all neighbours whose relationship can be considered negligibly small” (1964). On this subject see also what Hamilton anticipated briefly (Hamilton 1963) while waiting for the release of his long article. The meaning of this parameter has not always been understood properly, as pointed out by Alan Grafen (1982, 1984).

² John Maynard-Smith (1964)—reviewer of the 1964 paper by Hamilton—proposed the term *kin-selection* to refer to the evolutionary force that promotes these kind of characters. The initial idea regarding cost and benefit in helping relatives, however, was outlined by Haldane (1955, 1990 [1932]). For a general historical framework and further bibliographic references, see among others: Dawkins (1976, 1982), De Waal (1996), Dugatkin (2007), Frank (1998); Gardner and Grafen (2009), Gardner and West (2014), Gardner et al. (2011), Ghiselin (1974), Gould and Lloyd (1999); Hull and Ruse (1998), Hull (1980), Jablonka and Lamb (2005), Keller and Lloyd (1992), Keller (1999), Krebs and Davies (1984), Lewontin (1970), Okasha (2001, 2005a), Queller (1991, 1992), Ridley (1993, 1996, 2003), Ruse (1973, 1979), Trivers (1971), West-Eberhard (1975), Wilson (1987), Wilson and Dugatkin (1997), Wilson and Hölldobler (2005), Wilson and Sober (1994), Wilson and Wilson (2007), Wilson D. S. (1975, 1983, 1989) and Wilson E.O. (1975).

In the same years when Hamilton was preparing his solution to the problem of altruism, another school of thought—more interested in the group's perspective—featured in a book written by the English evolutionist Vero Copner Wynne-Edwards (1906–1997) entitled *Animal Dispersion in Relation to Social Behaviour* (1962) and summarized in an article published in *Nature* (1963).

According to Wynne-Edwards, individuals may experience forms of altruism limiting their own personal gain if their behaviour results in a benefit for the community.³ In some cases this is even necessary. The author wrote in this regard: “In a recent book I advanced a general proposition which may be summarized in the following way. (1) Animals, especially in the higher phyla, are variously adapted to control their own population densities. (2) The mechanisms involved work homeostatically, adjusting the population density in relation to fluctuating levels of resources; where the limiting resource is food, as it most frequently is, the homeostatic system prevents the population from increasing to densities that would cause over-exploitation and the depletion of future yields. (3) The mechanisms depend in part on the substitution of conventional prizes, namely, the possession of territories [...]” (Wynne-Edwards 1963, p. 623).

“The greatest benefits of sociality—continued Wynne-Edwards—arise from its capacity to override the advantage of the individual members in the interests of the survival of the group as a whole. The kind of adaptations which make this possible [...] belong to and characterize social groups as entities, rather than their members individually. This in turn seems to entail that natural selection has occurred between social groups as evolutionary units in their own right, favouring the more efficient variants among social systems wherever they have appeared, and furthering their progressive development and adaptation” (*ibid*).

In other words, the members of a group “must all come to a common agreement or convention [...] and must forego any immediate personal advantage in favour of the long-term benefit of the community as a whole” (1962, p. 7).

In these cited works, Wynne-Edwards defended an idea of evolution focused on the survival of the group. In 1970 Hamilton began to take a new mathematical approach to his models on evolution based on an equation proposed by George Price (1922–1975) equation with which he could also assess the effects of competition between groups (Price 1970, 1972; Hamilton 1970). The new mathematical tool also had other uses; with it, it was possible to analyse the effects of any selection level: individuals, groups, inbreeding, etc.

The use of Price's equation was particularly prolific for the drafting of a study prepared by Hamilton for the conference organised by Robin Fox and Irven DeVore in Oxford in July 1973, and published two years later in a book edited by Fox (1975). In his speech, Hamilton proposed a model in which the effects of selection at the group and at the individual level were both accounted for (Hamilton 1975).⁴ Although there is some difference of opinion on the enthusiasm shown by Hamilton

³ For a detailed analysis of Wynne-Edwards's theories and works see Borrello (2010).

⁴ As early as 1970 Hamilton used Price's equation and made reference to group selection in relation to Price's equation (Hamilton 1970).

regarding group selection, there is no doubt that 1975 (if not 1973) marked a crucial moment in the author's scientific output.⁵

From these premises two questions arise: (1) did the use of Price's equation entail the abandonment of the concept of inclusive fitness previously used? (2) by inserting the effects of group selection in his model, did Hamilton accept Wynne-Edwards's ideas on self-restraint of the individual for the benefit of the community?

In the following pages I will present a previously unpublished text by Hamilton and I will try to discuss these questions.

2 The “Brazilian lectures” by William D. Hamilton 1975

During my research at the Department of Manuscripts at the British Library, I was able to identify and classify four cycles of unpublished lectures (Coco 2008) given by Hamilton in the decade 1965–1975: the years in which he was most interested in the problem of social behaviour linked to spite and altruism. One of these cycles—the “Brazilian lectures”—was prepared by Hamilton for the conferences he was to hold in Ribeirão Preto as a visiting professor.

Between June 1975 and February 1976 the Hamilton family stayed in Brazil at the Faculdade de Medicina di Ribeirão Preto.⁶ A folder in the British Library archives marked “Documents concerning the trip to Brazil, 1975” (Ms ZIX90_1.8.4) recounts, page after page, the story of those months and the necessary preparations for departure. The stay was funded by the Leverhulme Trust and the Conselho Nacional de Pesquisas of Brazil.

Returning to England, Hamilton brought back with him some important results, for example the data with which he was to write the article on spitefulness “Wingless and Fighting Males in Fig Wasps and Other Insects” (Hamilton 1978). But that was not all—he also took away with him the gratifying experience he had had with the students of the Faculdade de Medicina.

Hamilton prepared some handwritten notes for the lectures he was to hold under the title *Population genetics and social behaviour* (Ms ZIX90_19.1). This ‘Brazilian lectures’ manuscript is written in pen, on 34 lined sheets similar to A4. Annotations in the margin confirm the support function for the lectures. Dates are sometimes added on the top of the pages. The text, especially in the final part, tends to thin out until it becomes—in some passages—only an outline on how to intervene orally: “Refer to article [...]. Briefly explain the central diagram [...]. Comment on the situation of the metazoans”. The last of the lectures appears in the index but was not written (or archived). The document opens with a page in which Hamilton had noted

⁵ Indeed, it was a prolific period for the entire evolutionary debate. Consider that, for example, the first edition of “Sociobiology” by Wilson was published in 1975 and “The selfish gene” by Dawkins appeared the following year. With regard to the different opinions about Hamilton's ideas on group selection, see for example: Birch and Okasha (2015), Grafen (2004), Maynard-Smith (1998), Okasha (2001), Ridley (1996, 2003), Sober and Wilson (1998), Trivers (1999).

⁶ Ribeirão Preto is a small town of coffee and sugar cane farmers in the state of San Paulo. It housed the two Faculties of Medicine and Philosophy, Science and Arts in the same campus just outside the city centre.

Table 1 Index of the Brazilian lectures prepared by Hamilton

8/8/75	1. Preview of the courses and its main problems
12/8	2. Basic concepts: fitness, gene frequency, variance e covariance, "altruism"
15/8	3. Natural selection in asocial organisms
19/8	4. Natural selection in social organisms
22/8 Friday	5. Levels of selection: example of meiotic drive
26/8 Tuesday	6. "Group selection" and "Kin selection"
28/8	7. Measurement of kinship
2/9	8. Concept of inclusive fitness
9/9	9. Concept of reproductive value
16/9/75	10. Fisher's principle of the sex ratio
19/9/75	11. Inclusive fitness in haplodiploids
22/9/75 & 23/9/75	12. Inbreeding and genetic drift
	13. Non-Fisherian models of sex ratio
	14. Termites: evolution in rotting wood
	15. Social behaviour in higher animals and man

the subjects to deal with and the dates on which the conferences were held (see Table 1).

Some notes in pen and pencil seem to report brief additions regarding date changes: an arrow and a note indicating 9/9 as the date of the lecture 8 (2/9 is the date on the same line as the title); the same applies in the case of lecture 9 (an arrow indicates the date as 09/16/75, while the title was originally lined up to 9/9), and also in lectures 10 and 11 (dates added: 19/9/75 and 22/9/75). Lessons from 12 to 15 were scheduled under the dates 22 and 23 September, but perhaps they were not held because of changes in the calendar of the previous conferences.

Hamilton had prepared the Brazil seminars well, planning on paper what he was going to explain orally and by drawing a general outline of the topics that he intended to cover.

3 Criticism of Vero Copner Wynne-Edwards's group selection

Hamilton gave the first of his Brazilian lectures (marked "August 8 1975"), beginning with a rebuttal of the idea of self-regulating mechanisms to avoid the exploitation of resources outlined by Vero Copner Wynne-Edwards (1962, 1963, 1964).

The lecture starts with these words⁷:

Since the time of Darwin we have had the idea that natural selection can cause endless evolution of living forms. [...] But since Darwin's time there has been

⁷ Quotations report the original text, including abbreviations, underlined words and rare orthographical inaccuracies.

much confusion about what exactly is meant by a “form” in this argument and this is a point over which we must take great care. (ZIX90_19.1, f2/r)

Hamilton sketches on the page a tree with two branches representing two populations: a “diagram of a bifurcation with one branch (coloured) showing less extinction than another”. He notes on the margin: “Mention disruptive selection but do not go into detail”. Then he writes:

Many biologists seem to think that Darwin was talking about n.s. at the level of this tree. But a minority insist that he was talking about n.s. at the level of differential reproduction of individuals. (ZIX90_19.1, f2/v)

Hamilton then wonders who is right.⁸ He comes up with this answer:

Well, according to what Darwin actually wrote, it is n.s. based on individuals that he described. He never considered the process in terms of competing species, or at least not unless he was satisfied that the character in question was also advantageous in competition between individuals. However, he did occasionally admit that something must have evolved because it was advantageous to a family group rather than an individual. (ZIX90_19.1, f2/v)

At this point he calls Wynne-Edwards into the fray: “The Englishman Wynne-Edwards thought that many species had discovered ways of preventing the over-exploitation of their food supply by spacing themselves out by territory system, and even by refraining from reproduction” (ZIX90_19.1, f 2/v).

“Whether or not he really did have examples that supported his view—maintains Hamilton—the surprising thing is that he saw no conflict between Darwinian theory and his view” (ZIX90_19.1, f 3/r).

Hamilton takes up the same example that Wynne-Edwards used in his 1963 article. Is it possible to imagine that a form of behaviour aimed at the rational consumption of food resources is present in animals in order to avoid over-exploitation of the territory that would result in the destruction of the habitat of the population? Could such behaviour, e.g. eating less to allow future generations to have the same territory, spread?

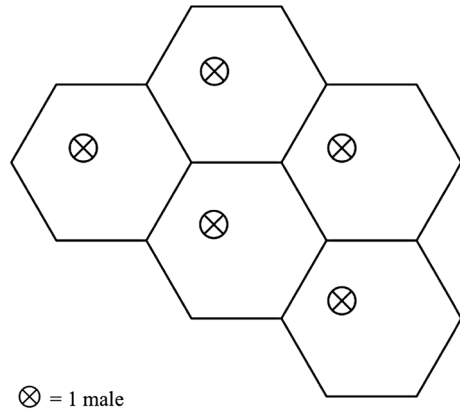
In order to verify this eventuality, he refers to the following model. Suppose we have a population of birds “where total adult population is about 12 pairs”. Each male has a unit of area (represented by a hexagon).⁹ The areas represent the minimum space required to grow a brood (Fig. 1).

We may hypothesise that in each territory a brood of six offspring is produced, but only one male manages to survive to take the place of the father; in due time, the male offspring will reproduce. We may suppose also that “the mean fitness is 1” (the couple manages to produce only one son successfully who is able to reproduce in turn).

⁸ Elliott Sober has convincingly shown Darwin’s gradual acceptance of cases in which selection could act for a collective benefit (2011).

⁹ In his manuscript, Hamilton draws some diagrams to show the arrangement of the animals in the territory hypothesized in his model. The figures here have been designed following the same arrangement of the originals.

Fig. 1 Five areas of minimum space required to grow a brood as hypothesized by Hamilton



“If we also assume that one territory is one unit of area we can say that the efficiency of level use of this system is mean fitness \div territory area = $1 \div 1 = 1$ ” (ZIX90_19.1, f 3/r).

Therefore, the rate of exploitation is given by:

$$\text{Level of exploitation } (t) = \frac{\text{Mean fitness } (\bar{w})}{\text{Units of territory occupied } (a)}$$

In the case considered, $\bar{w} = 1$ (1 nestling) and $a = 1$ (one territory for each couple). Therefore

$$t = \frac{1}{1} = 1$$

Hamilton invites us to hypothesise that “this efficiency is dangerously high”. He traces the scenario of a population of pigeons that devour fruits and seeds: “we might suppose that the birds are pigeons which eat—and in eating destroy—the fruits and the seeds of a particular tree: if they eat the crop too efficiently there may be no tree left to bear fruit in 20 years time. So it would be good for the species, as W-E [Wynne-Edwards] points out, if a less efficient land use by the species could be evolved” (ZIX90_19.1, f 5/r).

The hypothesis of Wynne-Edwards would at this point trust in the self-regulating capacity of animals (an unconscious capacity led through homeostatic mechanisms). The limits to foraging would come about thanks to the presence of an allele B (for rational consumption) that causes less efficiency in the exploitation of a territory. The allele, for example, could induce a sort of *altruism* in some subjects willing—for this reason—to abandon the nesting areas, abstaining therefore from intercourse. Only the individuals lacking the allele would stay in the territory in which it is possible to reproduce. The unconscious and instinctive behaviour of some subjects would allow the group to benefit from control over the number of offspring.¹⁰

¹⁰ It should be observed, however, that while such individuals can be considered to be altruistic (or conscientious), the system works also if they are *timid* or *claustrophobic* without any virtues whatsoever.

Hamilton shows how the system could evolve. He hypothesises that when an individual with the B allele leaves his place free, the territory is occupied by the subject in the neighbouring territory. At this point, the model requires an estimation of the number of nestlings that the new occupant will have. Hamilton imagines that the doubled reproductive surface area does not correspond to twice the number of surviving nestlings. He writes: “the new owner does not double the dimensions of his brood: we may suppose instead that he increases the production of nestlings by 50%” (f 5/r et v). Each couple has—on average—0.5 more nestlings. The level of exploitation is:

$$t = \frac{1 + 0.5}{2} = 0.75$$

It has therefore been reduced, since it has become 0.75 (before it was equal to 1).

Now—continues Hamilton—even if we were to admit a reproductive level compatible with the hypothesis of Wynne-Edwards, the problem arises regarding the behaviour of the new occupant: he may be either type B (altruist) or type A, (non-altruist). At the end, however, seeing that the A types never leave the territory, they will turn out to be advantaged over time. All the territories will soon be occupied by carriers of the A allele and over a few generations, type B will die out: its frequency within the population, entrusted to individuals that are constantly inhibited regarding reproduction will continue to decrease. “So this altruistic mutation cannot easily be used to illustrate Wynne-Edwards’ idea”. He, on the other hand, could reply that the population with low levels of B individuals ends up becoming extinct because of excessive exploitation of resources, while those with a high number of *conscientious* subjects do not. “True—Hamilton replies—, but he still has to explain how the latter comes to have B in high frequency” (ZIX90_19.1, f 5/v).

4 An alternative model

Hamilton proposes a possible alternative system through which the density of the population and the level of foraging may be limited, and in doing this he takes into consideration the fighting ability.

Suppose that the system of attribution of territories described above (each pair of birds has a territory equal to a surface unit) can be modified by the emergence of an allele C, which makes some males more aggressive and therefore able to conquer larger reproductive territories. This may be “another way in which reduced density and reduced efficiency of land use could be achieved without any assumption of ‘altruism’” (ZIX90_19.1, f 6/r).

Footnote 10 continued

The functioning of the hypothesis does not change. It is not, therefore, a case of being good or bad, altruists or snobs: the simple homeostatic mechanism due to the presence of the mutated allele B induces an instinctive tendency to abandon reproductive territory when it is over-exploited. Thanks to the mutation, the group benefits of a number of subjects (those of type B) that will be induced to abandon the territory when the size of the population reaches high levels.

One could realistically assume that a *C* mutation instils such a degree of aggressiveness in male carriers that it allows them to conquer areas of territory that are twice the normal size. However, this is verified only if the neighbours are non-aggressive types; otherwise it would be necessary to engage in combat with an equally fiery male, and therefore one would have only 50% of probability of winning or losing. So there are two possible cases:

- C* male vs normal male: has 100% probability of conquering a double territory
- C* male vs. *C* male: has 50% probability of conquering a double territory

Also in this case, as in the previous one, we may assume that the increase of fitness following the conquest of space is 0.5. That is, the couple have on average 50% more nestlings if they have double territory. Assuming that this basic number of nestlings is equal to a hypothetical value *b*, the level of exploitation (level of use) will be lower than the previous value:

$$\text{Level of use } (t) = \frac{1 + 0.5}{2} b = \frac{3}{4} b$$

Hamilton asks therefore “will the *C* allele spread?”.

In order to calculate the possible propagation of *C*, he builds a geometric system, analogous to the one set out below (Fig. 1), assuming that out of 12 individual adults, 7 possess allele *C*. The genetic frequency of the mutant before manifesting the aggressive behaviour *f*(*C*) is therefore 7/12 = 0.583. When the moment of reproduction arrives, the seven males start to fight (among themselves and against the non-aggressive types) and chase some individuals away (Fig. 2). After the fights, the following remain: five aggressive males, each with double territory, and two normal males with single reproductive areas. Then they reproduce. Assuming that those who have conquered a double territory have a number of nestlings that is equal to the basic unit multiplied by the level of exploitation (*t* = 0.75), we could calculate the genetic frequency of the *C* allele in the broods. This is 0.652, which is higher than in the population of parents before the fighting (Table 2).

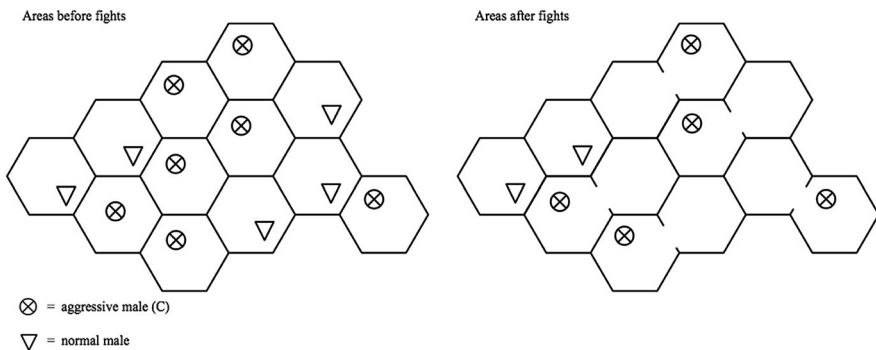


Fig. 2 Situation of territories following fighting as described by Hamilton

Table 2 Frequencies of the C allele

Frequency of C (parents) = $\frac{\text{Individuals C}}{\text{Individuals A} + \text{Individuals C}}$ Frequency of C (offsprings) = $\frac{\text{Individuals C} \times \text{reproductive efficiency of C types}}{(\text{Individuals A} \times \text{reproductive efficiency of A types}) + (\text{Individuals C} \times \text{reproductive efficiency of C types})}$	Frequency of C (parents) $= f(C) = \frac{7}{(5 + 7)} = 0.583$
Frequency of C (offsprings) $= f'(C) = \frac{5 \times 0.75}{2 + (5 \times 0.75)} = 0.652$	

It should be noted that the model represents a simplified situation. In fact, the calculation of the frequency of the C allele takes into account neither the mothers' alleles nor the ploidy of the species. A rigorous calculation should verify, respectively, whether the C allele is present in the mothers or not, the level of probability that it will be found in the gametes, or the effects of dominance.

Hamilton makes reference to these aspects, even if he does not develop them further. He writes: "Let us also write that if instead of speaking of mutations on the Y chromosome [...] we got a diploid pattern of inheritance" (ZIX90_19.1, f 8/v). In this case "we would have the possibility to get another level of selection: that of the diploid pair" (*ibid.*).

Anyway, in the context of a simplified system the model works. Moreover, since the frequency of C in the population before the reproductive cycle was 0.583 and in broods is equal to 0.652, it shows that there has been an increase of the C allele.

Hamilton concludes:

So here we have a way in which a lower density of population can be achieved by something that is rather the opposite of altruistic behaviour by the males. It may be suggested that some of the phenomena which Wynne-Edwards cites as if they had altruistic component really rest on a foundation of selfish behaviour much as I have described here. (ZIX90_19.1, f 8/r)

In other words, the reduced efficiency in the exploitation of resources does not coincide with a reduction of the advantages obtained by the individual. In the model shown, what permits a regulation in the number of subjects that reproduce is the tendency to maximise the individual output. The most aggressive male behaves in such a way by virtue of the fact that his *direct* fitness has an increase of 50%. In this scenario, paradoxically, what allows to avoid the over-exploitation of the resources is the individualistic behaviour of the aggressive types. Moreover, unlike what happened in the system based on altruists, the model based on aggressiveness is evolutionarily stable because it tends to increase the frequency of C over time and therefore it makes the hypothetical behaviour due to the presence of C more and more common within the group *ceteris paribus*.

5 Considerations concerning the index of the Brazilian's notes and the first lecture

The document presented here provides a historical record of high value. It provides answers to questions posed in the introduction and provides indications of some additional aspects for discussion. I have listed below some indications which I believe can be drawn from the manuscript.

5.1 Hamilton and Wynne-Edwards's idea of ways of preventing the over-exploitation of food supply

The first aspect that we may draw from the document is Hamilton's position—at least until 1975—regarding Wynne-Edwards's idea of group selection. The manuscript presented here describes an explanatory model which illustrates a way chosen by Hamilton to refute the altruistic argument of self-restraint. Even if it was written just for the seminars, the model hangs on different mathematical tools from those used by Hamilton in his published articles, and shows a simpler method to disprove the thesis held by Wynne-Edwards.¹¹

5.2 Hamilton's teaching ability

Jeremy Leighton John—to whom I am grateful for his precious help in my search for documents in the British Library—told me of the criticisms leveled at Hamilton by his Imperial College students because of the lack of clarity of some of his lessons. This information, moreover, is indicated by Hamilton himself in his memoirs: “during the classes most students would be good-humouredly chatting or perhaps deep in their morning newspapers. And towards the end of the course I knew they would have another topic: they would be discussing who was to lead this year's delegation to the professor to complain about the irrelevance and incomprehensibility of the lectures I was giving”. (Hamilton 1996, p. 425).¹²

In spite of the complaints he received during his first experience of teaching, Hamilton was neither indifferent nor uncaring towards his students. The index of the manuscript presented here also shows this. It demonstrates the careful logic used by Hamilton to explain the history of the key research around the evolution of social behaviour. He knew the subjects well. He had worked on them for years and did not need a reminder or texts to follow. Yet he probably wanted to order them in written form to be sure that his lessons would be clear and comprehensible to everyone. Nor were they limited to basics. He aimed to enrich his seminars by updating them to the boundaries of contemporary research, including his own articles and Price's equation.

¹¹ It is worth noting that the model is presented here for its historical interest and not to defend a theoretical position regarding levels of selection. This debate is still going on, and I believe that the position of Hamilton in 1975 adds little to the current development of models whose validity should be tested by their mathematical coherence, degree of realism in the natural environment and by any possible empirical evidence.

¹² Regarding these teaching difficulties, see also Grafen (2004, p.120) and Segerstråle (2013, p. 189).

One might think that such careful attention was due to the exceptional nature of the event, a series of lessons to be held abroad. Of course, the opportunity may have influenced the care with which Hamilton prepared his lessons and the level to which he updated them. However, I found another manuscript (Coco 2008) that aims to explain the operation of Price's equation to students of Imperial College; this shows that Hamilton paid similar attention to his lessons in his normal academic courses. That text begins with these words: "These notes are intended to help you to understand the basic process of biological evolution. Do not glance at the following pages and decide that such mathematics are not for you. If there seems to be a lot of algebra it is because it is given in very pedestrian fashion to make it easy to follow" (Hamilton, Ms ZIX90_6.6.1).

So, in England as in Brazil, he wanted to share with his students the excitement and the intellectual stimulation that the last discoveries in the study of evolution could arouse. Of course, criticism in the early days of his academic career had shown him that mathematics could mislead. However, this was not a reason to eliminate these topics from his lessons. All he had to do was lead the audience by the hand so they would not be scared. It was probably with this intention that Hamilton had also prepared the index of his Brazilian lessons.

5.3 Kin-selection, inclusive fitness and group selection

The index of the Brazilian lectures suggests another aspect. Let us start with this consideration: Hamilton decided to begin his lectures with a strong rejection of the group-benefit idea of Wynne-Edwards in a period in which his last published paper was about a model he had used to take group selection into account—the one included in the book edited by Fox (see Sect. 1).

Hamilton's attention to group selection has sometimes been underestimated. The article that came out in 1975 was nearly ignored. This is perhaps due to the fact that he extended it to humans—as Hamilton himself complains (1996, p. 324)—perhaps because many scholars who were enthusiastic about inclusive fitness or kin-selection did not have the same enthusiasm for group selection. In this regard Segerstråle pointed out that "It seems that colleagues just continued seeing kin selection as opposed to group selection, and treating kin selection as an alternative name for inclusive fitness. People are typically not aware of 'Hamilton II'—the group selectionist" (2013, p. 154).

So, why did Hamilton attack Wynne-Edwards just when he was considering group selection as one of the forces that act in the evolutionary process? The answer—I think—is suggested by the index of the notes for the Brazilian lectures. In fact, the index presents the general structure that Hamilton had decided on for his summer cycle of lectures. It followed a time logic linked to the history of his researches and, to my mind, also a sequence articulated by a progressive degrees of importance that each topic had for Hamilton in understanding the evolution of social behaviour. If we accept this key of interpretation, we should not be surprised at the choice of presenting a rejection of Wynne-Edwards as a starting point. A similar criticism had marked the beginning of Hamilton's career, albeit indirectly, as we shall see shortly.

In 1962, the publisher Oliver and Boyd of Edinburgh released *Animal dispersion in Relation to Social Behaviour* by Wynne-Edwards. The main points of the book were summarized in an article (1963). John Maynard Smith (1920–2004) replied critically with a letter to the journal in which he introduced the term ‘kin-selection’ (that he had coined), and the concept of inclusive fitness (1964). The article in which Hamilton presented his new mathematical parameter had not come out yet. The referee of the paper (anonymous, as is the norm) had requested some important corrections including dividing the text into two parts. This was to cause some delay in its publication. However, Maynard Smith was aware of Hamilton’s idea as he was the secret referee who had requested the modifications (Segerstråle 2000, p. 63).

Maynard-Smith wrote to *Nature*: “There is no need to invoke group selection to explain the evolution of the individual breeding territories, or the adjustment of territory size to food supply or to variations in the habitat. [...] It is possible to distinguish two rather different processes, both of which could cause the evolution of characteristics which favour the survival, not of the individual, but of other members of the species. These processes I will call kin selection and group selection, respectively. Kin selection has been discussed by Haldane and by Hamilton” (1964, p. 1145). Maynard Smith presented his concept of kin-selection emphasizing that the theoretical bases to support its effectiveness had been backed by Haldane in 1955 “and more recently” by Hamilton.

So the rejection of Wynne-Edwards’s positions was the first time that the scientific world had encountered Hamilton’s point of view on the problem of social behaviour. Perhaps Hamilton wanted to retrace this process, that was historical besides being logical and theoretical, by beginning his lessons for the Brazilian students with the same subject.

However, the index not only suggests a historical trend. I think we can glimpse an important arrangement also in the order of the topics covered—a scale that reflects the theoretical positions and maybe some “emotional” reasons.

Let us examine the structure. After the first lesson, there are some basic concepts required to understand Price’s equation (“basic concepts” and related topics), then group selection and kin-selection (dealt with in the same class). Only later was inclusive fitness dealt with. This concluded the section on altruism. The remaining classes concerned connected topics: some insights that could be drawn using Price’s equation and inclusive fitness; some possible empirical evidence; some final thoughts on “Social behaviour in higher animals and man”.

I think we may assume that what Hamilton cared about as he prepared his lessons for Brazil was to emphasize the distinction between his “inclusive fitness” and the “kin-selection” of Maynard Smith.¹³ There were two reasons making this distinction so important. The first was due to the recent model developed by Hamilton in which he—using Price’s equation—had seen the possible effects of group selection (enabling an assimilation between kin-selection and group selection under certain conditions); the other was due to some unease that he felt towards

¹³ Consider in this regard that, after exposing inclusive fitness, and be thus concluded the arguments in favour of this distinction, Hamilton dedicates only two and a half pages (of 34 total) for the remaining four lectures, the last of which was not even drafted.

Maynard Smith because of the way he had presented the idea of kin-selection and inclusive fitness.

Ullica Segerstråle reported in depth the story, quoting in full a letter of 19 October 1972 that Price wrote to Maynard Smith. Price wrote: “the point is that he [Hamilton] thinks that you wronged him on the matter of ‘kin selection’. His account of the matter is that you refereed his 1964 paper for the *Journal of Theoretical Biology*, and required a major revision (changing it from one paper to two) that caused a 9-month delay in publication and meanwhile you sent Nature a letter with the term ‘kin selection’ that has received much of the credit for the idea. In your paper on alarm calls (a paper published 1965 in *Animal Behaviour*) you don’t cite Hamilton at all and in the paper you just sent me (the draft of their joint paper on the logic of animal conflict for Nature) you again don’t cite him on kin selection (though you do cite him on group selection and on genetic strategy). Especially undesirable is that you cite not only yourself but Levins on kin selection. This is just adding fuel to the fire” (Segerstråle 2013, p. 149).

It is likely that in imagining the plan of his lessons Hamilton wanted to emphasize the distinction between his idea of inclusive fitness and the concept of kin selection—explaining the reasons that led him to prefer the former to the latter.

Moreover, two more years later (October 1977) he was to return to the question publicly, using the occasion of his tardy review of “Sociobiology” by Wilson. He wrote: “In my opinion the present confused situation could be best tidied by using the term ‘kin-group selection’ for the area of overlap of the two common terms, covering all those cases where there are identifiable groups on the ground whose members are kin. [...] Then, alongside the term ‘kin-group selection’, a term such as ‘nepotism’ could be used for the remaining part of the present kin selection concept, covering those cases where interactions are too ephemeral or too interwoven for an epithet of ‘group’ to be really appropriate. Finally for the remaining cases where kinship is not involved, we could have ‘reciprocant selection’, ‘assortative selection’ (or equivalent more felicitous terms if these can be produced), and perhaps others as well. [...] It cannot be too strongly emphasized, however, that all such terminology is just differentiating natural selection of replicating molecules according to the various kinds of assemblage into which they are formed or form themselves. In my opinion (doubtless very biased) the best general guide to which way the cat of adaptation will jump is provided by the concept of inclusive fitness” (Hamilton 1977).

6 A note on pluralism and different ‘philosophical’ approaches to evolution

Samir Okasha has correctly claimed that “Maynard Smith remained firmly wedded to the gene’s eye approach, while both Williams and Hamilton expressed sympathy for ‘hierarchical’ approaches to evolution, though for quite different reasons” (Okasha 2005b, p. 996). Besides, he claimed that “Maynard Smith was sympathetic to pluralism, though had reservations. He agreed that a single evolutionary process could often be modelled, or mathematically described, in alternative ways, and that

the choice between the alternatives was heuristic, not factual (cf. Maynard Smith 1987, 2002). However, unsurprisingly, he also admitted to a general bias in favour of lower-level descriptions where possible. Thus in the inclusive fitness versus gene's eye case, he argued that the gene's eye approach was 'both mathematically simpler and causally more appropriate'.¹⁴

I think that like Maynard-Smith, Hamilton as well adopted a pluralist philosophy. Nevertheless he remained close to his approach through "inclusive fitness" which, though it could not boast the mathematical simplicity that Maynard Smith saw in the "gene's eye approach", had the merit of being more general. In his 1975 paper—after using Price's equation—he wrote: "The usefulness of the 'inclusive fitness' approach to social behaviour (i.e. an approach using criteria like $(b_{AB}K - k) > 0$) is that it is more general than the 'group selection', 'kin selection', or 'reciprocal altruism' approaches and so provides an overview even where regression coefficients and fitness effects are not easy to estimate or specify" (Hamilton 1975, then in Hamilton 1996, pp. 336–337).

This philosophical position could be found in his published writings and also in the index of the Brazilian lectures. The structure of the index seems to suggest that Hamilton was convinced of a considerable difference between the concepts of kin selection and inclusive fitness. Not surprisingly—after talking about over-exploitation of resources, kin selection, group selection and the other phenomena related to these processes—he wished to conclude the theoretical aspects of his Brazil lectures with his discovery: inclusive fitness.

7 Conclusions

The manuscript presented here is of great historical value. While not substantially changing the current status of the debate on altruism and levels of selection, it presents—from a historical perspective—the general idea of the relationships between genetics and social behaviour that Hamilton wanted to illustrate in the course of his lectures in Brazil. The first of these lessons—the one shown here in full—also offers an interesting unpublished model: although it is a more a mathematical example for teaching purposes than a proper model, it shows a clear approach made by Hamilton to refute the idea of self-restraint in the use of resources claimed by Wynne Edwards, without resorting to abstract or complex mathematics. The document thus enables us to answer some questions as we have seen.

¹⁴ The distinction between different "philosophical" approaches is so illustrated by Maynard-Smith: "First, a 'gestalt switch' between two models can be helpful. For example, the effect of genetic relatedness can be modelled either by ascribing an 'inclusive fitness' to individuals (Hamilton 1964), or, as sketched by Hamilton (1963) and made more explicit by Dawkins (1976), by a gene-centred approach: note that, in this example, the individual is the 'higher level' entity and the gene the 'lower level' one. I confess that in this case I find the gene-centred approach both mathematically simpler and causally more appropriate, but this may merely reflect the fact that I prefer microscopic to holistic models: Maxwell–Boltzmann to classical thermodynamics, and Dawkins to Price's equation" (Maynard-Smith 2002, p. 523).

Today, after forty years, many advances have been made and the debate on the evolution of social behaviour has been enriched. New formulations of group selection have been put forward using new aspects and old issues. For example: the distinction between inter-demic and intra-demic groups, the distinctions between models (if they are “semantic” or “real”), the re-reading of the game theory in terms of competition between groups of couples, the need to include or not a group-level heritability in the models, and the distinctions between the reasons in favour of a “contextual approach” or the Price’s equation. At the same time, evolutionistic reflection has also added material relative to other levels of selection: much has been done to test cultural evolution and its dependence/independence on the genetic blueprint, the psychological dimension, epigenetic phenomena and neuronal plasticity.

But on that day long ago when Hamilton found himself talking in Brazil, some of these aspects were not yet well known. Nevertheless, on that day, he had chosen a simple and concrete model of evolution to speak to his audience, “finding a method—as Condorcet said—to calculate the movements of a star that we have never seen”.

Acknowledgements I would like to thank, for their support or suggestions, Maurice Aymard (EHES, Paris), Pietro Corsi (University of Oxford), Robin Fox (Rutgers University), Jean Gayon (Institute for the History and Philosophy of Science and Technology, Paris), Jeremy Leighton John (British Library), Michael Ruse (Florida State University), Robert Trivers (Rutgers University), Francesco Coniglione (University of Catania), Francesco Dessi-Fulgheri and Laura Beani (University of Florence). I am also grateful to the Editor-in-Chief of HPLS and to the secret referees for their useful comments. This paper has been possible thanks to a Mary Curie Fellowship at École des Hautes Études en Sciences Sociales (EHES, Paris)—grant agreement PIEF-GA-2009-236567.

References

- Birch, J., & Okasha, S. (2015). Kin selection and its critics. *BioScience*, 65(1), 22–32.
- Borrello, M. (2010). *Evolutionary restraints: the contentious history of group selection*. Chicago: University of Chicago Press.
- Coco, E. (2008). *Egoisti malvagi e generosi. storia naturale dell'altruismo*. Milano: Bruno Mondadori.
- Darwin, C. (1872). *On the origin of species by means and natural selection* (6th ed.). London: John Murray.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Dawkins, R. (1982). *The extended phenotype. the gene as unit of selection*. Oxford and San Francisco: Freeman.
- De Waal, F. (1996). *Good natured: the origins of right and wrong in humans and other animals*. Cambridge, MA: Harvard University Press.
- Dugatkin, L. A. (2007). Inclusive fitness theory from Darwin to Hamilton. *Genetics*, 176, 1375–1380.
- Fox, R. (Ed.). (1975). *Biosocial anthropology*. New York: John Wiley and Sons.
- Frank, S. A. (1998). *The foundations of social evolution*. Princeton: Princeton University Press.
- Gardner, A., & Grafen, A. (2009). Capturing the superorganism: a formal theory of group adaptation. *Journal of Evolutionary Biology*, 22, 659–671.
- Gardner, A., & West, S. A. (Eds.). (2014). *Theme Issue 'Inclusive fitness: 50 years on' compiled and edited by Andy Gardner and Stuart A. West*, *Philosophical transactions of the royal society B* (Vol. 369). doi:10.1098/rstb.2013.0356.
- Gardner, A., West, S. A., & Wild, G. (2011). The genetical theory of kin selection. *Journal of Evolutionary Biology*, 24, 1020–1043.
- Ghiselin, M. T. (1974). *The economy of nature and the evolution of sex*. Berkeley: University of California Press.

- Gould, S. J., & Lloyd, E. A. (1999). Individuality and adaptation across levels of selection: How shall we name and generalize the unit of Darwinism? *Proceedings of the National Academy of Sciences USA*, 96(21), 11904–11909.
- Grafen, A. (1982). How not to measure inclusive fitness. *Nature*, 298, 425–426.
- Grafen, A. (1984). Natural selection, kin selection and group selection. In J. Krebs & N. B. Davies (Eds.), *Behavioural ecology* (pp. 62–84). Oxford: Blackwell Scientific.
- Grafen, A. (2004). William Donald Hamilton 1 August 1936—7 March 2000. *Biographical Memoirs of Fellows of the Royal Society*, 50, 109–132.
- Haldane, J. B. S. (1955). Population genetics. *New Biology*, 18, 34–51.
- Haldane, J. B. S. (1990 [1932]). *The Causes of Evolution*. Princeton: Princeton University Press.
- Hamilton, W. D. (1963). The evolution of altruistic behaviour. *The American Naturalist*, 97, 354–356.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. Part I & II. *Journal of Theoretical Biology*, 7, 1–52.
- Hamilton, W. D. (1970). Selfish and spiteful behaviour in an evolutionary model. *Nature*, 228(5277), 1218–1220.
- Hamilton, W. D. (1975). Innate social aptitudes of man: an approach from evolutionary genetics. In R. Fox (Ed.), *Biosocial anthropology* (pp. 133–157). New York: Wiley.
- Hamilton, W. D. (1977). Review of E.O. Wilson (1975). Sociobiology. The new synthesis. *Journal of Animal Ecology*, 46(3), 975–977.
- Hamilton, W. D. (1978). Wingless and fighting males in fig wasp and other insects. In M. S. Blum & N. A. Blum (Eds.), *Reproductive competition mate choice and sexual selection in insects* (pp. 167–220). New York: Academic Press.
- Hamilton, W. D. (1996). *Narrow roads of gene land. Evolution of social behaviour* (Vol. 1). New York: W. H. Freeman.
- Hamilton, W. D. (Ms). ZIX90_1.8.4. Folder. “Documents concerning the trip to Brazil, 1975”. London: British Library, Hamilton Archive.
- Hamilton, W. D. (Ms). ZIX90_19.1 “Population genetics and social behaviour”. London: British Library, Hamilton Archive.
- Hamilton, W. D. (Ms). ZIX90_6.6.1. “Elementary Theory of Natural Selection”. London: British Library, Hamilton Archive.
- Hull, D. L. (1980). Individuality and selection. *Annual Review of Ecology and Systematics*, 11, 311–332.
- Hull, D. L., & Ruse, M. (1998). *The philosophy of biology*. Oxford: Oxford University Press.
- Jablonka, E., & Lamb, M. (2005). *Evolution in four dimensions*. Cambridge, MA: MIT Press.
- Keller, L. (Ed.). (1999). *Levels of selection in evolution*. Princeton: Princeton University Press.
- Keller, E. F., & Lloyd, E. A. (Eds.). (1992). *Keywords in evolutionary biology*. Cambridge, MA: Harvard University Press.
- Krebs, J., & Davies, N. B. (Eds.). (1984). *Behavioural ecology*. Oxford: Blackwell Scientific.
- Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics*, 1, 1–18.
- Maynard-Smith, J. (1964). Group selection and kin selection. *Nature*, 201(4924), 1145–1146.
- Maynard-Smith, J. (1987). How to model evolution. In J. Dupré (Ed.), *The latest on the best: Essays on evolution and optimality* (pp. 119–131). Cambridge, MA: MIT Press.
- Maynard-Smith, J. (1998). Review of unto others: The evolution and psychology of unselfish behaviour. *Nature*, 393, 639–640.
- Maynard-Smith, J. (2002). Commentary on Kerr and Godfrey-Smith. *Biology & Philosophy*, 17(4), 523–527.
- Okasha, S. (2001). Why won't the group selection controversy go away? *The British Journal for the Philosophy of Science*, 52(1), 25–50.
- Okasha, S. (2005a). Altruism, group selection and correlated interaction. *The British Journal for the Philosophy of Science*, 56(4), 703–725.
- Okasha, S. (2005b). Maynard Smith on the levels of selection question. *Biology and Philosophy*, 20(5), 989–1010.
- Price, G. R. (1970). Selection and covariance. *Nature*, 227(August 1), 520–521.
- Price, G. R. (1972). Extension of covariance selection mathematics. *Annals of Human Genetics*, 35, 485–490.
- Queller, D. C. (1991). Group selection and kin selection. *Trends in Ecology & Evolution*, 6(2), 64–65.
- Queller, D. C. (1992). Quantitative genetics, kin selection, and group selection. *American Naturalist*, 3(139), 540–558.

- Ridley, M. (1993). *The red queen: sex and the evolution of human nature*. New York: Viking—Penguin Books.
- Ridley, M. (1996). *The origins of virtue*. London: Viking—Penguin Books.
- Ridley, M. (2003). *Nature via nurture: genes, experience and what makes us human*. London: HarperCollins.
- Ruse, M. (1973). *The philosophy of biology*. London: Hutchinson.
- Ruse, M. (1979). *Sociobiology sense or nonsense?*. Dordrecht: D. Reidel.
- Segerstråle, U. (2000). *Defenders of the truth: The sociobiology debate*. Oxford: Oxford University Press.
- Segerstråle, U. (2013). *Nature's oracle: The life and work of W. D. Hamilton*. Oxford: Oxford University Press.
- Sober, E. (2011). *Did Darwin write the origin backwards? philosophical essays on Darwin's theory*. Amherst, NY: Prometheus Books.
- Sober, E., & Wilson, D. S. (1998). *Unto others: The evolution and psychology of unselfish behaviour*. Cambridge, MA: Harvard University Press.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46(1), 35–57.
- Trivers, R. L. (1999). As They would do to you. review of Elliott Sober and David Sloan Wilson's "Unto Others". *The Skeptic*, 6(4), 62–72.
- West-Eberhard, M. J. (1975). The evolution of social behaviour by kin selection. *Quarterly Review of Biology*, 50(1), 1–33.
- Wilson, D. S. (1975a). A theory of group selection. *Proceedings of the National Academy of Science USA*, 72(1), 143–146.
- Wilson, E. O. (1975b). *Sociobiology: The new synthesis*. Cambridge, MA: Harvard University Press.
- Wilson, D. S. (1983). The group selection controversy: History and current status. *Annual Review of Ecology and Systematics*, 14, 159–187.
- Wilson, D. S. (1987). Altruism in Mendelian populations derived from sibling groups: The haystack model revisited. *Evolution*, 41(5), 1059–1070.
- Wilson, D. S. (1989). Levels of selection: an alternative to individualism in biology and the human sciences. *Social Networks*, 11, 257–272.
- Wilson, D. S., & Dugatkin, L. A. (1997). Group selection and assortative interactions. *American Naturalist*, 149, 336–351.
- Wilson, E. O., & Holldobler, B. (2005). Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences USA*, 102, 13367–13371.
- Wilson, D. S., & Sober, E. (1994). Reintroducing group selection to the human behavioural sciences. *Behavioural and Brain Sciences*, 17(4), 585–654.
- Wilson, D. S., & Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology*, 82(4), 327–348.
- Wynne-Edwards, V. C. (1963). Intergroup selection in the evolution of social systems. *Nature*, 200(4907), 623–626.
- Wynne-Edwards, V. C. (1964). Group selection and kin selection. *Nature*, 201(4924), 1147.
- Wynne-Edwards, V. C. (1967 [1962]). *Animal Dispersion in Relation to Social Behaviour*. Edinburgh and London: Oliver & Boyd.