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The Philosophy of Social Evolution, Jonathan Birch. Oxford University Press, 2018, xi + 268 pages.

The Philosophy of Social Evolution is an engaging investigation of the intellectual legacy of Bill Hamilton, a central figure in evolutionary biology whose ideas have had a lasting impact far beyond that discipline. The book combines mathematical rigour and accessibility, as many of the more mathematical points can be skipped without too much loss. Birch provides a well-reasoned and even-handed discussion of some controversial topics surrounding social evolution in the first part of the book. Then, he offers suggestions as to how these ideas may be extended and used in areas beyond where they have traditionally been applied, such as public goods games in both microbial and human populations. While this book is foremost a work in philosophy of biology, it should also be of interest to broader audiences, including philosophers of economics, as many of the foundational concepts Birch discusses have found their way into other fields (philosophy, anthropology, economics, sociology, etc.) and some of the extensions proposed (especially those in Chapter 8) are relevant to studying human behaviour.

Chapter 1 provides some examples of social traits, then explains Hamilton's four-part schema which categorizes social behaviours (dividing them into mutually beneficial, selfish, altruistic and spiteful) based on their effects on the reproductive success of the organism and its social partner(s). While the schema is nothing new, Birch argues that the best way to understand the categories is in terms of a trait's recent selective history (e.g. it is an altruistic trait if it was recently selected for its benefits to an organism's social partners, despite having a cost for the altruistic organism itself). He also argues that we should

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think of 'strategies' not as particular actions in a strategic scenario (as a game theorist might think of a strategy), but instead as a pattern of behaviour across many situations and environments (26–7). This pattern of behaviour is more likely to affect ultimate reproductive success, and thus to be the target of selection. To restrict this slightly, we can then think of 'tasks' – benefit- (or harm-) generating mechanisms – as providing context for the actions: a certain action may be beneficial when it comes to one task, but harmful or ineffective when it comes to another (e.g. throwing a spear when hunting a stag versus when there is no stag) (32).

Chapter 2 discusses Hamilton's Rule and its role in explaining social evolution. Hamilton's rule says, basically, that we expect a behaviour to be favoured by selection when the relatedness-weighted benefit outweighs the cost (when rb > c). In the 'general' form of Hamilton's rule (HRG), b and c are population statistics (regression coefficients) and should be thought of as capturing differential fitness effects for the character value of interest, rather than, e.g., payoffs or costs/benefits from a particular interaction (45). The predictive and explanatory value of such a rule has been questioned, but Birch argues that we should think of HRG as a unifying principle for the study of social evolution in the sense that it provides an organizing framework for classifying explanations of social behaviours (46-50). While detailed models can provide causal explanations, Hamilton's rule can help us to compare different models (even when they may look very different or start from very different assumptions) and classify them according to what type of explanation they give. For instance, if a model explains the evolution of a trait (e.g. altruism or spite) in terms of its effects on organism's social partners, meaning the 'rb' part of Hamilton's rule is important, then it is an indirect fitness explanation (51). If instead we explain the evolution of a trait in terms of its effect on the organism itself (e.g. direct returns, or reciprocal altruism), then it is the '-c' part of Hamilton's rule that is important and we are providing a direct fitness explanation (55). Hybrid and non-selective explanations are also possible (58-62).

Chapter 3 then defends the usefulness of HRG as an organizing framework rather than as a framework for making predictions. First, Birch makes the point that the sense in which HRG is explanatory rests on this role as an organizing framework: it is not explanatory because it provides the correct causal explanations, but because it deepens our understanding of causes by unifying different processes and so 'one comes to understand something about social evolution one did not understand before' (69). While the categories in Chapter 1 were defined in explicitly causal terms, the cost and benefit terms in HRG are only statistical. Therefore what HRG gives us is not terms that are measureable causal influences, but a way to define classes of causal explanations that are united by their common features. Birch also defends the usefulness of the three part partition into r,

b and *c* over other either more or less fine-grained partitions, arguing that often this is the right grain of analysis, though he also allows that what is most useful can depend on the context (76–82).

Chapter 4 discusses kin selection and group selection. While these are considered equivalent statistical descriptions of the evolution of social behaviours (Birch points out that they are only equivalent when populations are group-structured), the causal processes they describe are distinct. How to causally distinguish between kin and group selection is not always simple, though, and Birch offers his own account of the two processes, taking inspiration from Hamilton and Peter Godfrey-Smith. First, on Birch's reading, Hamilton claimed that the distinction between kin and group selection was important, but was a matter of degree some things might be clearly kin selection while others are clearly group selection, but there are also intermediate cases as well (93-4). Second, Godfrey-Smith distinguished between group and neighbour-structured populations, where organisms interact within sharply bounded groups or where they interact with their nearest neighbours in the absence of any well-defined group structure, respectively (94). Again, this distinction is a matter of degree. Putting these two together, Birch argues for a way of distinguishing the two processes, which he admits is slightly revisionary in that it tells us how we ought to use these two terms: kin selection occurs when relevant interactions occur among genealogical relatives and group selection occurs when there are well-defined social groups (for full definitions of kin and group selection see pages 97 and 99, respectively). He provides examples of selection processes fitting in 'K-G' space, according to how important kin versus group selection (high K vs. high G) is in explaining the evolution of a particular behaviour.

Chapter 5 discusses neighbour-modulated fitness (NMF) and inclusive fitness (IF). In the context of Hamilton's Rule, what distinguishes these two concepts of fitness is the interpretation of *r*: in NMF *r* is thought of as phenotypic correlation leading to an increase in reproductive output, in IF r is thought of as capturing opportunities for indirect reproduction (passing on one's genes through reproduction by genetically similar individuals). Birch clarifies what it takes for these two notions of fitness to be equivalent: actor's control and (weak) additivity (125-9). He argues that while these conditions might often be violated, if we assume weak selection, e.g. that the phenotypic and therefore fitness effect of a mutation is approximately 0, these assumptions will be approximately true (130–1). While assuming weak selection might seem *ad hoc*, Birch argues that in fact many proponents of IF are micromutationists who try to explain complex adaptations in terms of successive small modifications. This leads Birch to expound what he sees as the distinctive role inclusive fitness can play in explaining the evolution of social behaviours: it provides a stable criterion for phenotypic improvement throughout

a process of cumulative adaptation (134–6). Note that this is a more limited role than some claim for the distinctive role of inclusive fitness: that for social evolution, thinking of organisms as maximizing agents (as is often done in adaptationist reasoning) requires us to use inclusive fitness (see e.g. West and Gardner 2013).

These discussions of Hamilton's rule, kin selection and inclusive fitness bring clarity to many of the contemporary discussions among biologists and philosophers studying social evolution. Further, they should be of interest well outside biology and philosophy of biology, as reasoning using these ideas from social evolution is widespread. To take an example from economics: Ken Binmore explains how our assessment of a particular social contract (in terms of fitness) should change when we interact with strangers versus with kin, and claims that taking into account relatedness when thinking about how to value our relative's fitness provides the basis for making the interpersonal comparisons of utility that are required to reason about social contracts using the original position (Binmore 2006: 19). He also discusses experimental results designed to 'test predictions' of Hamilton's rule (Binmore 2005:103-4). According to what Birch has laid out here, we ought not to think about these results in terms of HRG. We might instead think of these experiments as more relevant to a 'special' version of Hamilton's rule (HRS), which is more closely tied to game theory because the cost and benefit terms can be interpreted as payoffs, rather than population statistics (Birch 2013). (We can also perhaps understand why HRG might be more important in biology, where experimenters generally do not have control over the costs and benefits of behaviours.)

We can also fit these types of claims about economic decision making into the evolutionary context, using some of the ideas from Chapter 1. For example, one question that is often raised when connecting economic decision making with biological evolution is how the strategies employed affect fitness, in terms of reproductive success. It seems like cooperating in a prisoners' dilemma or offering an even split in an ultimatum game, for example, might affect our utility at that moment, but are unlikely to affect how many children we will have. However, if we think of selection on strategies as patterns of behaviour, as Birch urges us to do, this connection begins to make more sense - each decision or action alone might not impact fitness much, but a pattern of behaviour over a lifetime could reasonably be expected to do so. This is, of course, not a new point but Birch's discussion of patterns of behaviour, and of their being relative to tasks, provides a nice way to conceptualize and talk about the distinction between strategies in a game and strategies relevant for biological evolution.

Having clarified his view on foundational issues in Hamilton's social evolution theory, Birch then discusses some extensions of the basic theory

to other subjects. Chapter 6 discusses microbe sociality. Some microbial behaviour can be thought of as a public goods game: a microbe can, at some cost to itself, produce substances like enzymes or antibiotics, which benefit other microbes in their surrounding area. Birch argues that there are difficulties in using explanations of the evolution of altruism developed for multicellular organisms in trying to explain this sort of microbial behaviour. For one thing, relatedness between interacting microbes is importantly affected by horizontal transmission, where genes are transferred between microbes of the same generation (146). This leads Birch to argue for a diachronic conception of relatedness, where one takes into account the genetic similarity between organisms not just at the time of interaction, but at other stages as well (149–50). Importantly, he argues, increasing relatedness after public goods production has occurred should also aid the evolution of the altruistic behaviour (158). A microbe can increase the reproductive output of others, then make it so that those others pass on the gene for that social behaviour.

Chapter 7 argues that we can see multicellularity as a social phenomenon and provides a hypothesis for the evolution of multicellularity. Since in clonal groups relatedness is (nearly) one, Hamilton explains that high relatedness stabilizes cooperation within multicellular organisms. However, more interesting than how current multicellular organisms function is the question of how they arose in the first place. Birch's explanation rests on two general points. First, following Andrew Bourke, he argues that there is a feedback loop between size of a group (of cells, or of organisms) and specialization of members of the group (175). Second, both size and specialization are mediated by redundancy (178). Both functional versatility (where individuals can switch between different tasks) and redundancy (where there are back-up individuals who can perform a task) are means to robustness of task completion, preventing the task from failing if a few individuals cannot complete their part for whatever reason. As groups increase in size, redundancy becomes more important; if there are enough individuals, having some not contributing all the time is not terribly costly. Birch argues that as groups increase further in size, redundancy – particularly *active* redundancy where there are more individuals than necessary which are specialized for a specific task - becomes even more important (176). (Note that this argument runs whether "individual" is read as "cell" or "organism in a eusocial colony".) He fits all this, and related considerations, into a somewhat complicated feedback loop encompassing his hypothesis for the evolution of multicellularity (fig 7.1, p. 180). He is careful to note that this is a fragile process, and there are many points where it can stall, so we should not be surprised that multicellularity arose so few times in evolutionary history.

Chapter 8 discusses the evolution of 'broad-scope prosocial preferences': the tendency for humans to promote cooperation and

punish failures to cooperate in a variety of types of interactions, including those with strangers (190). Birch makes a fascinating connection between microbial evolution and human cultural evolution, noting the importance of horizontal transmission for both. This motivates him to derive a cultural analogue of Hamilton's rule (202-207) where relatedness should be thought of as measuring correlations between cultural variants, rather than as genetic similarity. With this machinery in place, Birch proposes a cultural relatedness hypothesis: that positive cultural relatedness in extended social networks explains the evolution of broad-scope prosocial preferences (209). He discusses the empirical assumptions of such a hypothesis and distinguishes it from a cultural group selection hypothesis. Importantly, a cultural group selection hypothesis must assume that humans were well-divided into easily delineated groups whereas the cultural relatedness is not committed to this (213). Conversely, the cultural relatedness hypothesis must assume that a certain type of cultural selection occurs (CS_1 , see pages 197–9 for a description and contrast with CS₂) whereas the cultural group selection hypothesis is not committed to a particular type of selection (214).

These ideas, again, have implications beyond their consequences for biology. For instance, understanding behaviour in public goods games is of interest in economics. It is clear that people copy behaviour in these sorts of social situations (see e.g. some results discussed by Henrich and Henrich 2007: 27–30), so if people often play these sorts of games with their cultural kin, it may be worthwhile to focus in on the methods of imitation leading to high cultural relatedness. Further, issues like redundancy, specialization and division of labour are important in many areas of economics – in talking about the organization of societies, issues relevant to small versus large businesses, decisions regarding outsourcing, etc. Thinking in terms of the feedback loops Birch discusses, or making connections to the evolution of multicellularity or eusociality, could be fruitful.

This review has only touched on some of the main issues in the book; there is much more to be found in *The Philosophy of Social Evolution*.

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