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Edward O. Wilson and the Organicist Tradition

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Abstract. Edward O. Wilson's recent decision to abandon kin selection theory has sent shockwaves throughout the biological sciences. Over the past two years, more than a hundred biologists have signed letters protesting his reversal. Making sense of Wilson's decision and the controversy it has spawned requires familiarity with the historical record. This entails not only examining the conditions under which kin selection theory first emerged, but also the organicist tradition against which it rebelled. In similar fashion, one must not only examine Wilson's long career, but also those thinkers who influenced him most, especially his intellectual grandfather, William Morton Wheeler (1865–1937). Wilson belongs to a long line of organicists, biologists whose research highlighted integration and coordination, many of whom struggled over the exact same biological riddles that have long defined Wilson's career. Drawing inspiration (and sometimes ideas) from these intellectual forebears, Wilson is confident that he has finally identified the origin of the social impulse.

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E. O. Wilson is at it again. The legendary Harvard biologist (whose affable demeanor belies a serious rebellious streak) finds himself embroiled in yet another academic firestorm. This time around, the furor surrounds his recent disavowal of kin selection, a theory he helped popularize during the 1970s, and one that otherwise continues to enjoy broad support. The debate, which had simmered over the previous few years, reached full boil in August 2010, when Wilson and two of his colleagues, Martin Nowak and Corina Tarnita, published a broadside in the esteemed pages of *Nature* (Nowak et al., 2010). Citing reams of mathematical equations as evidence, the trio wrote that kin selection did not explain the origin of insect eusociality, and was, in fact, superfluous to natural selection.[1] In the two years since the article first appeared in print, more than a hundred biologists have gone on record against Nowak, Tarnita, and Wilson, citing what they consider irrefutable evidence in support of kin selection.[2] The skirmish has generated headlines in the nation's major newspapers and set science blogs abuzz. *Discover* magazine even named Wilson's about-face the third biggest science story of 2010, just behind the worst oil spill of all time and the creation of the first synthetic organism (Weintraub, 2011).

To understand why an otherwise esoteric quibble over insect behavior has aroused such passion, one need only consider what is at stake. After all, kin selection purports to explain one of biology's thorniest riddles: Why would any organism ever assist another when doing so compromises its autonomy and decreases its fitness? According to kin selection, the social impulse is a consequence of genetic proximity. In other words, an organism will act altruistically toward another when doing so improves the likelihood that some of its genes will survive. Kinship is thus an essential prerequisite of eusociality. Although Wilson was not the first person to promote kin selection, he was among its earliest and most ardent supporters. He even granted the theory privileged status when he published a sweeping theory of sociobiology in the mid-1970s, and his early advocacy for kin selection helped facilitate its widespread acceptance. The theory has proven heuristically and empirically fruitful for several decades and is generally treated as standard dogma in the sociobiological literature. As recent as 1994, Wilson proclaimed kin selection the "most important idea" in theoretical sociobiology, adding that "the core of the theory has stood up well" (Wilson, 1994, pp. 315–316).

And that's what is so surprising. The recent paper by Wilson and his colleagues not only rejects kin selection, but does so in grand and decisive fashion. Well, if we're surprised by Wilson's reversal, perhaps we shouldn't be. In fact, several pieces of evidence suggest that we probably should have seen this coming all along. For starters, there's that famous rebellious streak. Although Wilson displays all the gentility one would expect in an Eagle Scout from south Alabama, he has also shown a predilection for contest. Even his critics will admit that the man

[1] Most of the mathematical evidence is contained within a 43-page appendix, available online at the Harvard Program for Evolutionary Dynamics website: http://www.ped.fas.harvard.edu/SI.pdf.

[2] One letter contained more than 130 signatories. Abbot et al., "Inclusive Fitness Theory and Eusociality," *Nature*, vol. 471, no. 7339 (March 24, 2011), pp. E1–E4.

who first lanced swords with James Watson during the "molecular wars" of the 1950s, and who later sparked the highly divisive sociobiology controversy of the 1970s, does his best work when swimming upstream. Still going strong in his eighties, Wilson has shown a willingness to question every axiom of science, including, apparently, the ones he helped draft.

What's more, kin selection isn't the only issue on which Wilson has recently reversed course. At the beginning of his professional career, Wilson dismissed the "superorganism" concept, which had dominated entomology during the first half of the twentieth century, as hopelessly outdated. He considered the concept (which regards social insect colonies as true organisms) "of little relevance to the operational aspects of research" and predicted that it would probably never prove useful again (Wilson, 1967, p. 27). Just a few decades later, however, he had changed his mind entirely. By the 1990s, he had decided that the colony was, in fact, a superorganism, and that this unique arrangement was evolutionarily significant. His support for the concept has only increased over the past 20 years, and he is now famously among its foremost champions.

Drawing direct connections between Wilson's dual pivots on kin selection and the superorganism is not always easy. After all, he isn't the only biologist to champion the revival of the superorganism, nor was he the first (Wilson and Sober, 1989; Seeley, 1989; Moritz and Southwick, 1992; Tschinkel, 1999). Even among the 150+ biologists who recently signed letters rebutting Wilson's new position on kin selection, many have comfortably employed the metaphor in their own research (see, for example: Gardner and Grafen, 2009; Strassmann and Queller, 2010). And yet, while Wilson and his detractors both invoke the superorganism, they do so on much different grounds. Supporters of kin selection believe that genetic relatedness provides the initial impetus for sociality, and thus the internal blueprint of the superorganism. In contrast, Wilson and his new allies insist that sociality emerges any time two or more insects coordinate their behavior around a single point (usually a defensible nest with a supply of food), and that natural selection drives the colony's organismic cohesion. Although couched in myrmecological rhetoric, the debate raises serious questions that apply equally well to all social species, humans included. Namely, from whence does our most basic social impulse hail: the genes of which we are comprised, or the environment of which we are a part?

To understand just how closely these two reversals are connected, one must consider Wilson's entire career within its broader historical context. The goal is not to provide a comprehensive review of the kin selection controversy, but rather to determine how and why Wilson has arrived at his current opinions.[3] This requires that one not only examine his initial engagement with kin selection, but also the organicist tradition against which it rebelled. In similar fashion, one must not only examine Wilson's long career, but also those thinkers who influenced him most. Wilson belongs to a long line of organicists, biologists whose research highlighted integration and coordination, many of whom struggled over the exact same biological riddles that have long defined Wilson's career. Now, however, he appears to have made peace with his pedigree. Drawing inspiration (and sometimes ideas) from his intellectual forebears, Wilson is confident that he has finally identified the origin of the social impulse.

Social Insects and the Organicist Tradition, 1850–1950

Our story begins, like so many stories in the biological sciences, with Charles Darwin, the great naturalist who, according to Wilson, ''seems to have anticipated almost every other important idea in evolutionary biology'' (Wilson, 1994, p. 333). As historians of biology are well aware, Darwin recognized that social insects were ''by far the most serious special difficulty'' for his theory of natural selection. Darwin explained that the most advanced social insects contain neuter castes, which serve the colony but make no effort to reproduce. But if they don't leave progeny, he asked, then how do they propagate their (sterile) kind? His answer was suggestive. ''This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end,'' he wrote (Darwin, 1872, p. 230).

[3] For more exhaustive analyses of kin selection theory and its place in the history of evolutionary biology, see: Mark Borrello, *Evolutionary Restraints: the Contentious History of Group Selection* (Chicago: University of Chicago Press, 2010); Oren Harman, *The Price of Altruism: George Price and the Search for the Origins of Kindness* (New York: Norton and Company, 2010); Eliot Sober and David Sloan Wilson, *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Cambridge: Harvard University Press, 1999). For popular accounts of the current controversy, see: Jonah Lehrer, ''Kin and Kind,'' *New Yorker*, March 5, 2012; Howard W. French, ''E. O. Wilson's Theory of Everything,'' *Atlantic* (November, 2011).

Darwin's use of the word "family" instead of group is perhaps significant, for it could suggest an emphasis on relatedness. Accordingly, supporters of kin selection have long hailed Darwin as their intellectual forebear. When discussing the riddle of eusociality, for example, Lee Alan Dugatkin insists that "Darwin resolved this paradox by outlining inclusive fitness theory more than 100 years before Hamilton" (Dugatkin, 1997, p. 5). In similar fashion, Andy Gardner also credits Darwin for his "initial insights on kin selection" (Gardner, 2011, p. 125). Darwin was somewhat inconsistent on this matter, however, and statements made elsewhere could be (and have been) interpreted as support for group selection. Just two paragraphs before the aforementioned quotation about selection targeting the family, Darwin wrote that as long as "it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection" (Darwin, 1872, p. 129). The difference is subtle but important, for the less specific "community" label need not presuppose genetic kinship. Accordingly, supporters of group selection have just as readily claimed Darwin as *their* intellectual forebear. Historian Mark Borrello believes "it is apparent that Darwin believed there was some possibility for his mechanism to function above the level of the individual" (Borrello, 2005, p. 45). Others have also credited Darwin with intuiting multilevel selection. "Group selection… was first proposed by Darwin, who observed that social adaptations frequently are not locally advantageous," note biologists Omar Tonsi Eldakar and David Sloan Wilson (2011, p. 1523).

Wilson's indebtedness to Darwin will shock no one, but his reverence for Darwin's oft-maligned contemporary, Herbert Spencer, probably should. Even though Spencer was the most widely read philosopher in the United States during the latter half of the nineteenth century, the past hundred years or so have not been kind to him. The two fields in which he achieved most of his fame today seldom mention his name. In sociology, Spencer's affiliation with social Darwinism has rendered his entire philosophy unpalatable to generations of practitioners (Hofstadter, 1944). In biology, he is remembered, in large part, for his decision to back the wrong horse when debating acquired characteristics with August Weismann. These facts have rendered him a "pariah" among both biologists and social scientists, "a virtual non-person" (Corning, 2005, p. 202). And yet, despite this widespread disregard, E. O. Wilson has a framed picture of Spencer in his office (Ruse, 2004).

Unlike Darwin, who emphasized competition and the struggle for survival, Spencer belonged to what might be called the organicist tradition in science, one that prioritizes integration, coordination, and equilibrium.[4] Unlike neo-reductionists, who would explain all biological phenomena via chemistry and physics, Spencer instead viewed evolution as a hierarchical process, from cells to societies (Ruse, 2004). He expounded on these ideas in early 1860 (just months after Darwin had published the first edition of the *Origin*), when he drafted a now-famous essay comparing human society to an organism. Spencer acknowledged that others, including Plato and John Stuart Mill, had compared society to an organism, but they had always stipulated it was a *human* organism. Spencer applied the metaphor more broadly, explaining that human society resembled *all* individual organisms in three conspicuous ways: they commence as small aggregations and soon augment in mass thereafter; they move inexorably from a state of simplicity and homogeneity to one of greater complexity and heterogeneity; and they are, perhaps most importantly, comprised of mutually dependent parts (Spencer, 1860).

Although Spencer made no mention of insects in his essay on the social organism, his interest in sociality naturally led him their way. In *Principles of Sociology*, he wrote that social insects provide the most striking examples of nonhuman "super-organic" phenomena. Working together, Spencer remarked, individual ants yield "products of size and complexity far beyond any that would be possible in the absence of united efforts." What is more, just as this tendency toward specialization and individuation rendered human society an organism, so too did the insects' self-organized integration render the insect colony an organism. "The growths and developments of these social aggregates have analogies with the growths and developments of the individual aggregates," he wrote. Finally, he appears to have anticipated Weismann's germ/soma dichotomy when he compared the colony's queen to an organism's germ line: "Just as the germ of a wasp evolves into a complete individual; so does the adult queen-wasp, the germ of a wasp-society, evolve into a multitude of individuals with definitely-adjusted arrangements and activities" (Spencer, 1881, pp. 4–5).

Although Spencer allowed that "super-organic evolution" was manifest among the social insects, it was their very kinship to one

[4] For the best analyses of the organicist tradition in the history of science, see: Michael Ruse, *The Gaia Hypothesis: Science on a Pagan Planet* (Chicago: Chicago University Press, 2013); Carolyn Merchant, *Death of Nature: Women, Ecology, and the Scientific Revolution* (New York: Harper Collins, 1980). I thank Dr. Ruse for sharing an advance copy of his manuscript with me.

another that prompted him to declare that insect colonies are *not* true social aggregates. ‘‘Each of them is in reality a large family,’’ he explained. ‘‘It is not a union among like individuals substantially independent of one another in parentage, and approximately equal in their capacities; but it is a union among the offspring of one mother, carried on, in some cases, for a single generation and in some cases for more.’’ He therefore distinguished insect sociality (which he deemed *merely* familial) from human sociality (which transcended kinship). In his opinion, the human ability to coordinate with others beyond one’s immediate family constituted ‘‘a form of Super-organic Evolution which so immensely transcends all others in extent, in complication, in importance, as to make them relatively insignificant’’ (Spencer, 1881, pp. 6–7).

When Spencer clashed with August Weismann in the early 1890s, social insects were again front-and-center. The controversy, which Osborn (1894) ranked among the three biggest in the history of evolutionary thought, pitted inheritance of acquired characteristics (favored by Spencer) against natural selection (favored by Weismann). The two eminent scholars lobbed a series of sometimes catty articles back and forth at one another in the pages of the *Contemporary Review*. Weismann was the first to invoke the social insects. He pointed out that neuter insects (representing the soma) cannot transmit their acquired characteristics to the queen (the germ line), nor to future generations (Weismann, 1893a). In response, Spencer hastened to point out that caste differentiation did not emerge *ex nihilo*, but rather through a process, from simpler to more complex. Thus, in order to understand insect castes one must account for the conditions under which they first arose. Spencer suggested that, from a pre-social state, insect castes might be explained just as easily by ‘‘arrested nutrition’’ (Spencer, 1893c, p. 900). They thus disagreed on the means by which the insect castes achieved their adaptive characteristics. Spencer assumed the internalist position, inasmuch as he believed that an organism’s adaptive capacity was latent within the organism itself. Weismann, on the other hand, assumed the externalist position, insisting that natural selection shaped the organism.

Although much has been made of the controversy, it is equally enlightening to consider the points on which they agreed. It is important to note, for example, that Spencer did not reject all instances of natural selection outright. He acknowledged that *The Origin of Species* had convinced him that acquired characteristics could not explain everything (Spencer, 1894, p. 690). What is more, he acknowledged that natural selection targets the entire colony, and not just its individual members. "The only way in which natural selection here comes into play is in the better survival of the families of those queens which made as many cells, and laid as many eggs, as resulted in the best number of half-fed larvae, producing workers; since by a rapid multiplication of workers the family is advantaged, and the ultimate production of more queens surviving into the next year ensured," he once observed (Spencer, 1893c, p. 898). Though Weismann rejected Spencer's arrested-nutrition explanation, he agreed with his rival that natural selection targets the entire colony. "In respect of selection," he wrote, "the whole state behaves as a single animal; the state is selected, not the single individual; and the various forms behave exactly like the parts of one individual in the course of ordinary selection" (Weismann, 1893a, pp. 326–327).

Like other naturalists who came of age during the late nineteenth century, Charles Otis Whitman (E. O. Wilson's intellectual great-grandfather) was a devout acolyte of Herbert Spencer, whose writings he frequently quoted. In an address to fellow biologists at Woods Hole Marine Biological Laboratory during the summer of 1890, Whitman adopted and inverted Spencer's society-as-organism metaphor. "On the same grounds that the sociologist affirms that a society is an organism, the biologists declares that an organism is a society," he announced. In this case, it was a society of cells. In Whitman's mind, this revelation struck at the "very foundation of organic and social existence." He believed that life manifested similar patterns at different levels, and that the most characteristic traits of social evolution were (a) increased division of labor and (b) increased union of laborers. Significantly, Whitman credited Spencer with articulating the notion best. "As Herbert Spencer long ago pointed out in his *Social Statistics*, 'progress is toward complete separateness and complete union,' and 'the higher individuation is joined with the greatest mutual dependence'" (Whitman, 1891, pp. 1–2, 6).

Despite his assertion that each organism was a society of cells, Whitman did not believe that it was *merely* a society of cells. He distinguished himself from those who would reduce all biological phenomena to a single level. The cell had become the "alpha and the omega" of morphological and physiological research, he informed colleagues during an address at the 1893 Columbian Exposition in Chicago. "It has come to signify in the organic world what the atom and molecule signify in the physical world," he added (Whitman, 1894, p. 105). But Whitman worried that reducing all vital phenomena to the action of cells obscured other forces at work. He cited ontogenetic development as evidence that cells were subject to a higher individuality for which cell theory could not exclusively account. Though lacking our current vocabulary, Whitman clearly intuited the importance of higher-level evolutionary dynamics. "Comparative embryology reminds us at every turn that the organism dominates cell formation, using for the same purpose one, several, or many cells, massing its material and directing its movements, and shaping its organs, as if cells did not exist, or as if they existed only in complete subordination to its will," he wrote (Whitman, 1894, p. 119).

Although Whitman did not invoke social insects when describing his organism-as-society analogy, the relevance was not lost on his most accomplished student (and E. O. Wilson's intellectual grandfather), William Morton Wheeler. Interested in the natural world from a very early age, Wheeler began his apprenticeship under Whitman at the Allis Laboratory in Milwaukee in 1886, and followed his mentor across the academic landscape for a decade thereafter. When Whitman was named professor at Clark University in 1889, Wheeler followed him there to pursue doctoral studies. When Whitman was named the first director of the biological station at Woods Hole in 1891, Wheeler began spending his summers on the Massachusetts coast as well. And finally, when Whitman was named professor of zoology at the University of Chicago in 1892, he brought Wheeler along to serve as an instructor (Evans and Evans, 1970, pp. 99–104).

Wheeler taught embryology at the University of Chicago for several years before accepting a position at the University of Texas in 1900. It was on a river bank outside of Austin that he first chanced across a line of marching army ants. Fascinated by their coordinated behavior, he resolved to devote the rest of his career to these creatures. "I had at last found a group of organisms that would repay no end of study," he later recalled (Wheeler, 1918, p. 295). What's more, he had identified a scientific field that was scarcely inhabited. By his own estimation, there were no other professional myrmecologists in the United States at the turn of the century (Evans and Evans, 1970, p. 127). According to historian Charlotte Sleigh, the field was little more than "a rather Victorian network of letter writing and specimen swapping" (Sleigh, 2007, p. 40). Wheeler wasted little time establishing his name, publishing more than thirty papers on ants between 1900 and 1903. As his output grew, so too did his reputation. In 1903, he accepted a position as curator of invertebrates at the American Museum of Natural History in Manhattan, and in 1907, he was named professor of economic entomology at Harvard, where he remained for the rest of his life. His early efforts culminated in 1910, when he published *Ants: the Structure, Development and Behavior*, a massive tome that cemented his reputation as the nation's foremost entomologist (Wheeler, 1910).

Wheeler acknowledged a striking similarity between ant colonies and multicellular organisms, and elaborated on the idea one year later in a special issue of the *Journal of Morphology* dedicated to the memory of the recently deceased Charles Otis Whitman. The topic could scarcely be more appropriate. Much as Whitman had inverted Spencer's metaphor and applied it to cell republics, so too did Wheeler adopt Spencer's metaphor and apply it to insect societies. He insisted that the similarities between a metazoan organism and an ant colony were more than incidental, and legitimated his claim by referencing individual organisms at other levels. "Like the cell or the person," he wrote, the "(ant colony) behaves as a unitary whole, maintaining its identity in space, resisting dissolution and, as a general rule, any fusion with other colonies of the same or alien species." What is more, because colonies were reproductively differentiated, they also adhered to Weismann's concept of the organism. "The mother queen and the virgin males and females represent the germ-plasm," he wrote, "while the normally sterile females, or workers and soldiers, in all their developmental stages, represent the soma." Finally, he added that the ant colony, like any organism, exhibited both ontogenetic and phylogenetic development (Wheeler, 1911, pp. 310–312).

Published in the same year that Henri Bergson's *Creative Evolution* was first translated into English, Wheeler showed little patience for vitalistic interpretations of life. Calling them "useless," he dismissed Bergson's *élan vital* and Hans Driesch's *entelechy* with belittling eloquence. "I believe that we ought not to let it [vitalism] play about in our laboratories," he remarked, adding that he was "quite willing to see it spanked and sent back to the metaphysical household" (Wheeler, 1911, p. 324). Alas, rejecting vitalism left Wheeler with no explanation for the curious bonds that united social insects, and he could do little more than cite Solomon's timeless observation that ant coordination relies on "neither guide, (nor) overseer, nor ruler" (Wheeler, 1911, p. 320). He remained at a loss until 1918, when he observed a peculiar phenomenon. Among many social insects, colony members shared fluids and foodstuffs with one another through a process he termed *trophallaxis*. Wheeler became convinced that this process of reciprocal exchange was "the source of the social habit in wasps, ants and termites" (Wheeler, 1918, p. 323). Serving as a material binding agent among the colony's constituent parts, trophallaxis also reified his organismic analogy. The circulating liquids unified the colony, "just as the cells of the body of a higher animal are bound together as a syntrophic whole by means of the circulating blood" (Wheeler, 1923, p. 260).

Although Wheeler consistently referred to the colony as an "organism" throughout the 1910s, he began using the "superorganism" label with greater frequency during the 1920s. He first applied the label to a termite colony in a humorous essay written from the perspective of a termite king (Wheeler, 1920). Over the next several years, he also began applying the label to ant colonies, and in his own authorial voice (Wheeler, 1923, 1928b). By 1928, Wheeler's description of the superorganism had changed in one subtle but important way. He still cited all the familiar comparisons based on reproductive differentiation and ontogenetic growth, but he also placed a greater emphasis on the colony's individuality. "The insect colony or society may be regarded as a super-organism and hence as a living whole bent on preserving its moving equilibrium and its integrity," he wrote in *Social Insects* (Wheeler, 1928b, pp. 230–231).

The increased emphasis on the colony's holistic nature reflected the spirit of an age. Throughout the interwar period, scientists and scholars across the globe endorsed a variety of organicist philosophies. Among Wheeler's colleagues at Harvard, Henderson (1917), Parker (1924), Whitehead (1925), and Cannon (1932) all developed explicitly organicist interpretations of life. Meanwhile, numerous scholars across the globe, including Spaulding (1918), Alexander (1920), Sellars (1922), Morgan (1923), Broad (1925), and Smuts (1926) offered similar theories that were also squarely within the organicist tradition. Emboldened by their success, Wheeler soon became the nation's foremost advocate for the theory of emergent evolution, a sweeping interpretation of evolution that encompassed every level of the biological hierarchy, and which prioritized coordination and integration. He believed that insect eusociality was but one extreme manifestation of a deeper social impulse that suffused all living things, from sub-cellular "biophors" to multi-species biocoenoses. "There is something fundamentally social in living things," he observed, adding that "closer scrutiny shows that this must be a characteristic of all life." From the microscopic to the macroscopic, organic entities at every level of the biological hierarchy were "endowed with an irresistible tendency to cohere and organize themselves into more and more complex emergent wholes" (Wheeler, 1926, pp. 437–438). Though Wheeler referred to the grades of emergence as "levels," he regretted that the word failed to capture the dynamism latent in the evolutionary process. "These sections have been called levels," he wrote. "The word is not very apt since it conveys a spatial and static metaphor, whereas emergents must be regarded as intensively manifold spaciotemporal events" (Wheeler, 1928, p. 22).

It is difficult to say whether Wheeler would have supported kin selection theory if he were alive today. His devotion to trophallaxis would seem to indicate his belief that the colony's peculiarities owe more to internal (material) factors than external (immaterial) selective pressure. What is more, he defended trophallaxis on explicitly individualistic grounds. "A decidedly egoistic appetite, and not a purely altruistic maternal anxiety for the welfare of the young, constitutes the potent 'drive' that initiates and sustains the intimate relations of the adult ants to the larvae," he once remarked (Wheeler, 1923, p. 172). Accordingly, historian Sandra Mitchell places Wheeler alongside other Darwinian critics, "those concerned with internal processes, like embryogenesis and other developmental considerations… against a strictly external selectionist interpretation of Darwin" (Mitchell, 1995, p. 240). Supporting Mitchell's interpretation, Wheeler remarked as late as 1928 that only members of the same species were capable of "true societies" (Wheeler, 1928a, p. 31). This statement suggests that he believed genetic proximity played some role in sociality, a fact that modern supporters of kin selection would no doubt cheer.

Wheeler contained multitudes, however, and he sometimes contradicted himself. Recall, for example, that he labeled the multi-species biocoenosis a "true organism" throughout his entire career (Wheeler, 1911). What is more, he regarded the social bonds between members of the same species as indistinguishable from those between members of dissimilar species, and suggested that the term *symbiosis* applies equally well to both homogenous and heterogeneous partnerships (Wheeler, 1923, p. 195). Moreover, he noted that it was not uncommon for "alien organisms" of different species to fall into the insect colony's trophallactic vortex. In Wheeler's estimation, this "tendency to consociation with strange organisms" rendered the mixed colony a "super-superorganism," or a superorganism of the second degree (Wheeler, 1926, p. 437). It is difficult to reconcile these statements with kin selection, in which familial bonds provide the initial impetus for sociality.

Wheeler trained many graduate students during his long tenure at Harvard, one of whom, Frank M. Carpenter (1902–1994), remained at Harvard and would later serve as E. O. Wilson's doctoral advisor. Despite his affiliation with both Wheeler and Wilson, Carpenter provides something of an anomalous link in this chain. He first developed a passion for fossil insects when he was in the ninth grade and happened across a picture of a fossil butterfly in a library book he'd borrowed. "When I saw it, my eyes bulged," Carpenter later recalled. "I told my father when he came home from work that what I wanted to do was work on fossil insects" (qtd. in Brosius, 1994, p. 120). Toward that end, he enrolled at Harvard in 1922, and selected Wheeler, the world's leading entomologist, as his doctoral advisor. Although Wheeler was at the height of his organicist theorizing during this time, this evidently had little effect on Carpenter, who pursued his love of fossil insects with single-minded devotion. Over the next seventy (!) years, Carpenter earned a reputation among his colleagues as perhaps the greatest paleo-entomologist of all time. Even so, he was never particularly interested in the nature of insect sociality.

Although Wheeler passed away in 1937, the superorganism metaphor that he had championed throughout his life did not die with him. Throughout the 1930s and 1940s, the Biology Department at the University of Chicago (where Whitman and Wheeler had both once worked) carried the torch on his behalf (Mitman, 1992). Alfred Emerson, the world's foremost authority on termites, was also the group's most passionate advocate for the superorganism concept. He owed this interest in organicism to a chance encounter with William Morton Wheeler, whom he first met at the Kartabo Research Station in British Guyana in 1919. At the time, Wheeler was already the world's most famous entomologist and Emerson was just a fresh-faced grad student with a nascent interest in termites. They both returned to Guyana in the summer of 1920, spending a considerable amount of time together in the field, and one year later, Wheeler recommended Emerson for a position teaching entomology at the University of Pittsburgh (Mitman, 1992, pp. 112–113). This early association with Wheeler transformed Emerson's understanding of the biological sciences for the rest of his life. A half-century later, Emerson continued to gush that "there is hardly a living biologist who has not, knowingly or unknowingly, been influenced by William Morton Wheeler" (Emerson, 1971, p. 769).

Interestingly, though Emerson endorsed the superorganism metaphor, his understanding of the concept differed from Wheeler's in one very important way. While he continued to cite division of labor, ontogenetic growth, and individuality as evidence for the colony's organismic nature, Emerson added that natural selection also demarcates the boundaries of the colonial organism. What's more, he continued, the same force shaped every other level of biological organization as well. It should come as little surprise, therefore, that

Emerson also adopted Wheeler's conviction that "ascending hierarchies of integrated units… form the basis of the concept of emergent evolution" (1939, p. 182). Alas, Emerson's description of multilevel natural selection failed to generate much notice. The world was changing in profound ways, and organicist theories that had once carried the day now stood little chance in the reductionist, atomist, and isolationist wake of World War II.

The Long, Strange Career of Edward O. Wilson

Edward Osborn Wilson was born in 1929, and lived his early years along the Gulf coast of the Florida panhandle and south Alabama. The region boasts an incredibly rich assemblage of flora and fauna, and Wilson began exploring its diversity at a very early age. He always knew that he wanted to be a naturalist, but he didn't know what kind. The decision was all but made for him in 1937, when an unfortunate run-in with a spiny pinfish left him blind in one eye. Thereafter, he trained his focus on the animals that could be held in one's fingers and brought close to the eye for inspection. "I was destined to become an entomologist, committed to minute crawling and flying insects, not by any touch of idiosyncratic genius, not by foresight, but by a fortuitous constriction of physiological ability" (Wilson, 1994, p. 15).

In 1945, at the tender age of sixteen, Wilson decided that it was time to get serious. "The time had come to select a group of insects on which I could become a world authority," he later recalled (Wilson, 1994, p. 58). He chose ants for pragmatic reasons (they could be kept in prescription bottles), and set about learning everything known on the subject. The first book he bought was William Morton Wheeler's *Ants* (1910), which featured the author's colony-as-organism hypothesis. He also designed glass observation nests based on Wheeler's specifications (Wilson, 1994, p. 94). It is difficult to overstate the effect that Wheeler's research had on the aspiring naturalist. "Although Wheeler died in 1937, when I was still a little boy, I have studied his research so closely and heard so much about his life since that I feel as though I also personally knew him," Wilson recently remarked (Wilson, 2012, p. 139). He was thus well versed in the organicist tradition by the time he began his professional training. This fact is significant, because Wilson began his early tutelage just as science was entering one of the most stridently reductionist periods in its history. Mastery of the atom had just secured victory for the Allied forces, and the wholesale faith in neo-reductionism permeated biology no less than physics. Uniting genetics and natural selection, the recently congealed evolutionary synthesis foretold a new era in biology. Holistic theorizing was replaced by rigorous, empirical analyses.

Even the entomological sciences had grown increasingly reductionist. Theodor Schneirla's report about the army-ant death vortex spurred new research into the chemical signals that induced such behavior, analyses that had little use for talk of "superorganisms" (Schneirla, 1944). The metaphor, which had sustained entomology during the first half of the century, was quickly abandoned at the start of the second half. "Although the term superorganism has a venerable pedigree," Peter Corning recently remarked, "it became a pariah among biologists during the middle years of the twentieth century and was widely criticized as an inappropriate, even mystical metaphor" (2005, p. 187). During this reductionist revolution, Wheeler's grand organicist theory of emergent evolution was grouped with other discredited ideas and cast out of the biological sciences. "Directed evolution (aristogenesis, nomogenesis, orthogenesis, etc.), Lamarckian inheritance, and emergent evolution, among others, were ejected from mainstream evolutionary studies, as what appeared to be a narrowing or streamlining of evolutionary theory took place," observes historian Smocovitis (1992, p. 26).

It was during this increasingly reductionist Cold-War era that Wilson began his career as a professional entomologist in earnest. In 1949, the Alabama Department of Conservation asked Wilson (who was just 19 years old at the time) to conduct a study of the fire ant and evaluate its impact on the region (Buhs, 2004). When he enrolled at Harvard in 1951, he selected the renowned paleoentomologist Frank Carpenter as his advisor. Wilson described Carpenter as a hands-off advisor, one who encouraged students to pursue their own interests (Wilson, 1992). In the early 1950s, those interests included, among other things, the anatomy and taxonomy of the ant genus *Lasius*, chemical communication through pheromones, and collecting expeditions in the South Pacific. It should be noted, however, that Wilson also revealed an early inclination toward organicism. In one essay on the origin and evolution of polymorphism in ants, he observed that "the ant colony behaves as a superorganism, the basic unit upon which natural selection operates" (Wilson, 1953, pp. 153–154). His appeal to the superorganism received a generally tepid response, however, and he avoided the metaphor for many years thereafter. "The pendulum had begun to swing away from holistic conceptualization and toward piecemeal, experimental analysis of individual physiological mechanisms and patterns of behavior," he later recalled (Wilson and Michener, 1982, p. 164).

Wilson had hoped his work on polymorphism would attract more notice, but he could hardly compete with the discovery of the double helix, which James Watson and Francis Crick had reported that very same year (Watson and Crick, 1953). Their discovery dramatically accelerated the wholesale shift to reductionism, and its implications bled throughout every branch of biology. As a discipline, molecular biology began to monopolize funding and institutional appointments. Wilson, who returned to Harvard to serve as an assistant professor in 1956, had a front row seat for the revolution. James Watson arrived at Harvard with the same rank and at the same time, but with a wildly different conception of biology. ''He arrived with a conviction that biology must be transformed into a science directed at molecules and cells and rewritten in the language of physics and chemistry,'' Wilson later explained. Ever the naturalist, Wilson dared suggest that other levels of biological organization might also warrant one's attention. Doing so put him at odds with molecular biologists, the most strident of whom believed that *all* biological phenomena were reducible to physics. Wilson watched as ultra-reductionism swept through biology like a ''flash flood,'' laying claim to more and more of his department's resources. Helping matters but little, Wilson considered Watson ''the most unpleasant human being I had ever met'' (Wilson, 1994, p. 219).

Labeling these frosty relations the ''molecular wars,'' Wilson learned two valuable lessons from them. First, the experience left him radicalized concerning the future of biology, and it sowed within him an appreciation for scientific adversaries. This inclination toward provocation has revealed itself many times during his long career, often to great effect. Second, though Wilson assumed the organicist position in this debate, inasmuch as he recognized higher levels of organization, he also saw the writing on the wall. Biology was growing increasingly reductionist, and he better get on board if he didn't want to get left behind.

Thus, despite his organicist inclinations, Wilson was in an especially reductionist mood in the spring of 1965, when he embarked on a now-fabled train ride from Boston to Miami. As the train rambled south away from New England, Wilson picked up an article that he had been meaning to read. Written by an unknown British grad student named William Hamilton, the paper described the principle of ''inclusive fitness,'' according to which an organism can improve its chances of genetic success by cooperating with close family members (Hamilton, 1964a, b). As evidence, Hamilton seized upon the peculiar method of reproduction in *Hymenoptera*, a group that encompasses most (but not all) eusocial insects. In haplodiploid species, he explained, fertilized eggs (with two sets of chromosomes) produce females, while unfertilized eggs (with only one set of chromosomes) produce males. As a result, sisters are more closely related to their sisters than anyone else in the family, and their apparently altruistic behavior is in fact a selfish strategy to propagate each individual's own genes.

When he finished reading the article, Wilson felt confident that Hamilton's thesis couldn't possibly be true. There were several reasons for his misgivings. First, Wilson considered himself the world's foremost authority on social insects, and scoffed at the possibility that anyone else would uncover the secret to insect sociality before him. What's more, the explanation seemed so obvious. Wilson read the paper again, and then he read it a third time. For the entire eighteen-hour train ride, he pored over Hamilton's claims, wrestling with their implications. "By the time we reached Miami, in the early afternoon, I gave up. I was a convert, and put myself in Hamilton's hands. I had undergone what historians of science call a paradigm shift," Wilson later recalled (Wilson, 1994, p. 320). He was particularly enchanted with what would eventually become known as the haplodiploidy hypothesis, and was thus convinced that kin selection explained insect eusociality with mathematical precision and Newtonian elegance. Individual ants are not altruistic for any beneficent reasons, he concluded. Instead, they assist the colony because doing so ensures that part of their genotype will survive. In other words, sociality is an individualistic strategy, and altruism is nothing more than the accumulation of certain kinds of genes that find expression when in sufficient genealogical proximity to similarly inclined genes.

Subsequent events helped sustain the gene-centered momentum that Hamilton had initiated in 1964. That very same year, for example, John Maynard Smith published an equally influential article in *Nature*, in which he described a process very similar to inclusive fitness, but provided it with a new name. Maynard Smith invented a new phrase, *kin selection*, to define "the evolution of characteristics which favour the survival of close relatives of the affected individual" (Maynard Smith, 1964). The article proved popular and kin selection quickly became synonymous with inclusive fitness. Hamilton was apparently perturbed that Maynard Smith (who refereed his articles and actively slowed their publication) had co-opted his ideas and relabeled them (Dugatkin, 2006, p. 99), and one could hardly blame him. Whether it was because of *Nature*'s wider readership (Hamilton's papers had appeared in the *Journal of the Theoretical Biology*) or because Maynard Smith's label was simply more intuitive, kin selection has proven the more popular moniker.[5] As time would soon tell, however, the two theories (inclusive fitness and kin selection) were perhaps not as similar as they had appeared at first blush.

Hamilton and Maynard Smith were not the only ones promoting gene-selectionist theories at this time. In 1966, George C. Williams published *Adaptation and Natural Selection*, among the most influential books in twentieth-century biology. Williams allowed for the possibility that multilevel selection could, in theory, exist, but he also insisted that it almost never did. He wrote that selection acts on the individual, and thus ultimately on the genes which comprise it. His explanation proved very persuasive, and helped nudge biology toward an ever more reductionist state. "The trend toward molecularizing biology had been under way for more than a decade," Borrello writes, "and Williams's sweeping critique of group selection theory marked the beginning of a new age of genic selection" (Borrello, 2010, p. 130).

Wilson felt confident that the gene-centered explanations provided by Hamilton, Maynard Smith, and Williams heralded the dawning of a new age, one that found little use for his forebears' reckless organicism. Surveying the professional landscape in 1967, Wilson deemed the superorganism metaphor all but dead. "Its decline exemplifies the way holistic, inspirational ideas in biology often give rise to experimental, reductionist approaches that supplant them," he remarked. And yet, tellingly, Wilson retained a certain sentimental appreciation for the abandoned idea, which, he acknowledged, might still prove useful in the future. "To the present generation which is so devoted to the reductionist philosophy, the superorganism concept nevertheless served as a very appealing mirage," he explained. "It drew us to a point on the horizon. But as we worked closer, the mirage dissolved – for the moment at least – leaving us in the midst of unfamiliar terrain whose exploration came to demand our undivided attention" (Wilson, 1967, pp. 28–29).

In 1975, Wilson published *Sociobiology*, a massive and wildly ambitious tome that not only sought to synthesize decades of research on sociality across all domains of life, but also promoted an explicitly gene-centric model. Adopting rhetoric that Richard Dawkins would make famous one year later (Dawkins, 1976), Wilson explained that all biological phenomena were reducible to genes. "The organism does not

[5] A quick search on the Web of Science database reveals that "inclusive fitness" has been mentioned in 916 scholarly papers since 1964, while "kin selection" has appeared in 1,802 scholarly papers over that same span. August 17, 2012.

live for itself," he wrote, "the organism is only DNA's way of making more DNA" (Wilson, 1975, p. 3). What's more, when discussing the origin of the social impulse, he leaned heavily on the explanatory power of kin selection. "How can altruism, which by definition reduces personal fitness, possibly evolve by natural selection?" he rhetorically asked in *Sociobiology*. "The answer is kinship; if the genes causing the altruism are shared by two organisms because of common descent, and if the altruistic act by one organism increases the joint contribution of these genes to the next generation, the propensity to altruism will spread throughout the gene pool" (Wilson, 1975, p. 3).

As historians and biologists are well aware, the sociobiology controversy of the mid-1970s was among the most tenacious of the twentieth century.[6] Critics worried that placing such emphasis on genes would serve to reify social inequalities, and they objected to the notion that certain power relationships are scripted into nature. In a letter to the *New York Review of Books*, one group of scholars compared Wilson to other "biological determinists whose work has served to buttress the institutions of their society by exonerating them from responsibility for social problems." They explicitly suggested that his science was designed to protect "existing privileges for certain groups according to class, race or sex" (Allen et al., 1975, pp. 43–44). The epicenter of protest famously emanated from within Wilson's own department. Richard Lewontin, Wilson's former collaborator, accused Wilson, the man whom molecular biologists once dismissed as hopelessly holistic, of "vulgar reductionism" and referred to his ideas as the "naïve reductionist program of sociobiology" (Lewontin, 1976, pp. 22, 30). Wilson was forced to defend not only his science but also his character. He denied that his scholarship construed support for the status quo, citing his published belief that environmental conditions influence human cultural evolution more than genetic expressions (Wilson, 1976). The controversy reached its fever pitch when a group of protesters dumped a pitcher of ice water over his head as he was giving a speech at the AAAS annual meeting (Wilson, 1994, p. 349).

But these were not the only challenges to Wilson's book. While many of his fellow biologists obviously objected to his purported neo-reductionism, others objected that he was too holistic. These complaints stemmed from his interpretation of the levels of selection. In addition to

[6] For more on the sociobiology controversy, see: John Alcock, *The Triumph of Sociobiology* (New York: Oxford University Press, 2003); Neil Jumonville, "The Cultural Politics of the Sociobiology Debate," *Journal of the History of Biology*, vol. 35, no. 2 (Autumn, 2002), pp. 569–593; Ullica Segerstråle, *Defenders of the Truth: the Battle for Science in the Sociobiology Debate and Beyond* (Oxford: Oxford University Press, 2000).

his aforementioned support for gene selection, Wilson also professed belief in group selection, which he conflated with kin selection. "If selection operates on any of the groups as a unit," he wrote, "the process is referred to as kin selection" (Wilson, 1975, p. 106). In Wilson's interpretation, the various levels in a colony were not at odds with one another, but intimately connected. Genic selection did not nullify group selection, it enabled it. This seemingly paradoxical belief set him apart from many of his contemporaries, who instead believed that natural selection acted solely on the gene and that apparent acts of altruism were, in fact, selfish.

Around the same time that Wilson was placing kin selection at the center of his grand interpretation of sociobiology, one of the concept's principle architects, William Hamilton, was starting to change his mind. His doubts had first surfaced in 1968, when an American geneticist named George R. Price contacted him out of the blue with probing questions about the purported origin of altruism. By the time the two men finally spoke on the telephone one year later, Price explained how he had reworked Hamilton's equations to show that genetic relatedness was not an essential prerequisite of sociality (Harman, 2010, p. 223). Applying covariance mathematics to evolutionary dynamics demonstrates that altruism can evolve anytime between-group selection overrides within-group selection. This insight reframed the entire evolutionary process as a nested hierarchy, each level governed by natural selection. During that initial phone conversation in 1969, Price confessed that his derivation was something of a "miracle," and that he was especially excited about the equation's implications for group selection (Harman, 2010, p. 221). Hamilton initially received this claim with skepticism, but within a few months he acknowledged conversion. "I am enchanted with your formula," Hamilton wrote to Price. "I really have a clearer picture of the selection process as a result. In its general form I can see how we might use your formula to investigate 'group selection'" (quoted in Harman, 2010, p. 227).[7]

Hamilton expounded on the Price equation and its implications for multilevel selection in a very interesting chapter of an edited volume titled *Biosocial Anthropology* (Hamilton, 1975). He remarked that he'd always resented how Maynard Smith's label, kin selection, had become synonymous with his own label, inclusive fitness. Hamilton insisted that

[7] Price introduced his ideas in "Selection and Covariance," *Nature*, vol. 227 (August 1, 1970), pp. 520–521; for an excellent review of Price's life and his contributions to evolutionary biology, see: Oren Harman, *The Price of Altruism: George Price and the Search for the Origins of Kindness* (New York: Norton and Company, 2010).

his theory was broader than mere kinship. Citing Price's work on the nature of evolutionary dynamics, he showed that *un*related groups could also conceivably achieve sociality. "It obviously makes no difference if altruists settle together because they are related (perhaps never having parted from them) or because they recognize fellow altruists as such," he wrote (1975, p. 141). So long as all the relevant actors possess the requisite genes for socialization, it doesn't really matter whether or not they were obtained via recent shared ancestry. Hamilton insisted that this revelation did not obliterate his notion of inclusive fitness, but rather broadened it, emboldened it, and, most importantly, distinguished it from kin selection. Reaction to this reversal was mixed. Dawkins agreed that genes will target like genes, irrespective of ancestry. "They do not have to be close kin," he insisted (Dawkins, 1979, p. 5). For reasons that remain unclear, however, most biologists ignored Hamilton's clarification altogether (Harman, 2010, p. 322, Sober and Wilson, 1999, pp. 77–78). Even today, it is not uncommon to read publications that cite his kin-specific papers from 1964, but not his elaboration in 1975.[8]

Despite his infamy in some quarters, Wilson remained one of the most famous and highly regarded biologists in the world, as evinced by a litany of awards and citations. What's more, it was around this time that he slowly but surely began to soften his stance toward the superorganism metaphor. Eulogizing Alfred Emerson in 1982, Wilson remarked that Emerson's promotion of the superorganism "has had relatively little impact," but he did not overtly reject the idea (Wilson and Michener, 1982, p. 164). Two years later, he explicitly referred to the leafcutter-ant colony as a superorganism, but felt compelled to assure his readers that "I never see the colony as anything more than an organic machine" (Wilson, 1984, p. 36). Wilson did not expound on these ideas at the time, but others soon did. In 1989, philosopher Eliot Sober and biologist David Sloan Wilson famously championed the revival of the superorganism, while entomologist Thomas Seeley published "The Honey Bee Colony as a Superorganism" during the same year (Wilson and Sober, 1989; Seeley, 1989).

By 1990, E. O. Wilson had likewise thrown his full support behind the superorganism concept. "Old ideas in science never really die," he and Bert Hölldobler wrote in the Pulitzer-Prize-winning *Ants*. "They only sink to mother Earth, like the mythical giant Antaeus, to rise again with renewed vigor." Wilson based his analogy between the colony and

[8] To cite but one recent example: Raghavendra Gadagkar, "Sociobiology in Turmoil Again," *Current Science*, vol. 99, no. 8 (October 25, 2010), pp. 1036–1031.

the organism on similar functional and developmental division of labor. "The definitive process at the level of the organism is morphogenesis," he explained, while "the definitive process at the level of the colony is sociogenesis." Comparing these two processes promised to shed light on both. "This new effort will prove additionally useful in calling attention to poorly understood organizational processes and the techniques by which they are more precisely analyzed" (Hölldobler and Wilson, 1990, p. 359). As Sandra Mitchell astutely observes, E. O. Wilson's criteria for the superorganism differed from the ones championed by Sober and D. S. Wilson. She distinguished those (like EO Wilson) who invoked the superorganism on functional grounds, and those (like Sober and DS Wilson) who did so on more holistic grounds. "While the first approach emphasizes the developmental processes affecting the organism," she explains, "the latter is concerned exclusively with how natural selection operates on organism-like entities" (1995, pp. 234–235). Tellingly, neither Hölldobler nor E. O. Wilson viewed the revival of the superorganism as a threat to kin selection. "Kin selection in ants can now be considered fundamental to sociobiology," they wrote in *Ants* (1990, p. 180).

This conviction did not last long, however. By his own recollection, Wilson first began to doubt kin selection during the early 1990s (Wilson, 2012, pp. 171–172). These doubts were fueled, in part, by the failure of the haplodiploidy hypothesis. Termites had never fit the model, but other eusocial species, including platypoid ambrosia beetles and bathyergid mole rates, had also been discovered that reproduced via diplodiploidy. As a result of these discoveries, Wilson felt that the connection between haplodiploidy and eusociality fell "below statistical significance" (Wilson, 2012, p. 170). What's more, developments from outside entomology also influenced his outlook. For example, it was around this time that he became enchanted by Lynn Margulis's theory of endosymbiosis, which states that eukaryotic cells first emerged more than a billion years ago when various prokaryotic cells joined up with one another. The classic evidence are the mitochondria, which were once free living organisms and still retain their own DNA, but do not exist on their own outside their eukaryotic associations (Wilson, 1993, p. 245). The theory demonstrates that dissimilar units can become affixed in evolutionarily stable relationships, and its implications were not lost on Wilson. Inferring no exact correlation between kinship and eusociality, Wilson decided that a still more fundamental agent must be at work. In his opinion, that agent is natural selection.

Wilson and Multilevel Selection

The past seven years have been busy ones for E. O. Wilson. In 2005, he marked the fortieth anniversary of the publication of *Sociobiology* in a curious way: he officially abandoned one of the book's central tenets. That year he published two articles on the "fall" of kin selection, insisting that natural selection was sufficient to explain the origin of sociality. He coauthored one of these papers with longtime friend and collaborator Bert Hölldobler (Wilson, 2005; Wilson and Hölldobler, 2005). Hölldobler later reneged, insisting that while the colony is shaped by between-colony pressures, selection nevertheless remains focused on the individual (Reeve and Hölldobler, 2007). Wilson stuck to his guns, however, and has since upped the ante. He insists that so many diplodiploid species have been discovered that contain colonies with altruistic workers that both Hamilton's haplodiploid hypothesis and the predictive power of kin selection have failed (Wilson, 2005). He has collaborated with David Sloan Wilson (no relation) on several papers that advocate multilevel selection theory in place of kin selection (Wilson and Wilson, 2007, 2008), and recently published *The Superorganism* with Hölldobler, a follow-up to their wildly successful *Ants* two decades earlier. Despite their long friendship and many years of fruitful collaboration, however, Wilson and Hölldobler delayed publication of the book while they quibbled over the efficacy of kin selection (Pennisi, 2009).

The tipping point occurred two years ago, when Wilson teamed up with Martin Nowak, head of the Department of Evolutionary Dynamics at Harvard, whose research likewise hinges upon multilevel selection (Nowak and Highfield, 2011). Nowak applauded Wilson's recent change of heart, and suggested ways in which mathematics might buttress the argument. Together with Corina Tarnita, also from the Department of Evolutionary Dynamics, they published their incendiary data in *Nature* in August, 2010. Offering reams of mathematical equations as evidence, the trio insists that kin selection is not the cause of insect eusociality but rather the effect. They hypothesize that insect sociality probably first arose when individuals coordinated around a defensible nest, usually containing either food or brood. "Natural selection targets the emergent traits created by the interactions of colony members," the trio explained (Nowak et al., 2010, p. 1061). Natural selection, not kinship, provided the initial social impulse. "Relatedness does not drive the evolution of eusociality," they baldly asserted (Nowak et al., 2010, p. 1059).

As detailed in the introduction, the response to this paper has been swift and largely (though not exclusively) negative. Wilson's renunciation has obviously touched a nerve in the scientific community. One biologist compared the controversy to a "scientific gang fight," while others appear at a loss for words.[9] "They are wrong both empirically and theoretically," Edward Allen Herre of the Smithsonian Tropical Research Institute insists. "It's so wrong I don't think it will have any effect on what people in the field are doing," adds Oxford biologist Stuart West. As might be expected, E. O. Wilson has attracted the lion's share of attention. After all, he is one of the most famous scientists in the world, and his reputation was built, in large part, on his early advocacy for kin selection. Why jump ship now, his critics ask, right when the theory appears poised for paradigmatic status? "I don't know what's gotten into E. O. Wilson," Chicago ecologist Jerry Coyne recently remarked, adding that Wilson's decision to abandon kin selection "just sort of tarnishes him in people's eyes."[10]

Objections to Wilson's reversal generally fall into one of two categories. First, some biologists continue to insist that kinship plays an essential role in the origin of eusociality, and that Wilson is wrong to dismiss its significance. For example, Jacobus Broomsma and his coauthors assert that Wilson and his colleagues are wrong to downplay the role of kinship, writing that "high relatedness always preceded or coincided with eusociality" (Broomsma et al., 2011, p. e4). Joan Strassmann and several of her colleagues at Rice University contend that "kin selection is a strong, vibrant theory that is the basis for understanding how social behaviour has evolved" (Strassmann et al., 2011, p. e6). Meanwhile, Ferriere and Michod (2011) hold that the available evidence confirms inclusive fitness theory's "fundamental prediction that high relatedness is key for the evolution of eusociality" (Herre and Wcislo, 2011, p. e8). Finally, Richard Dawkins insists that "kin selection is logically entailed by standard Darwinian theory."[11] In response to this criticism, Wilson has readily acknowledged that kinship

[9] Christopher X. J. Jensen, "Robert Trivers and Colleagues on Nowak, Tarnita, and Wilson's 'The Evolution of Eusociality.'" Christopherxjjensen.com. URL: http://www.christopherxjjensen.com/2010/10/13/robert-trivers-and-colleagues-on-nowak-tarnita-and-wilsons-the-evolution-of-eusociality/ Accessed August 18, 2012.

[10] Herre and West were quoted in: Elizabeth Pennisi, "Researchers Challenge E. O. Wilson over Evolutionary Theory," *ScienceInsider*, March 23, 2011. URL: http://news.sciencemag.org/scienceinsider/2011/03/researchers-challenge-eo-wilson.html, accessed August 18, 2012; Jerry Coyne, "A Misguided Attack on Kin Selection," *WhyEvolutionIsTrue.com*, August 30, 2010. URL: http://whyevolutionistrue.wordpress.com/2010/08/30/a-misguided-attack-on-kin-selection, accessed August 18, 2012.

[11] Richard Dawkins, "The Descent of Edward Wilson," *Prospect Magazine* (May 24, 2012). URL: http://www.prospectmagazine.co.uk/magazine/edward-wilson-social-conquest-earth-evolutionary-errors-origin-species/, accessed August 18, 2012.

might play some role in the evolution of eusociality. He just no longer thinks that kinship explains the *initial* impetus for sociality, the *vera causa*, if you will (Wilson, 2012, p. 175).

Interestingly, the second type of objection complains about just the opposite. These biologists insist that Wilson is wrong to conflate inclusive fitness with kin selection, and that the former concept is much broader than the latter. According to this view, inclusive fitness accounts for evolutionary dynamics without recourse to genealogical relatedness (also known as pedigree kinship). As James A. Marshall writes, "Relatedness can be estimated from pedigree under certain assumptions, but what matters for inclusive fitness theory is genetic identity, not identity by descent" (Marshall, 2011, p. 326). Andy Gardner, Stuart West and Geoff Wild all agree, explaining that "genetical relatedness is distinct from genealogical relationship" (Gardner et al., 2011, p. 1026). In response, Wilson has questioned whether this approach, which stretches the concept of "relatedness" to the point that it loses meaning, is worth all the trouble (Wilson, 2012, p. 174). Without a special emphasis on "relatedness," he asks, what exactly distinguishes inclusive fitness from good old-fashioned natural selection? "If there is a general theory that works for everything (multilevel natural selection) and a theory that works only for some cases (kin selection), and in the few cases where the latter works it agrees with the general theory of multilevel selection, why not simply stay with the general theory everywhere?" he asks (Wilson, 2012, p. 175).

Wilson's sharpest critic is none other than Richard Dawkins, famed advocate for the selfish-gene interpretation of evolution, who regards multilevel selection theory as little more than a delusion. With the same snarky edge that helped make him famous, Dawkins writes that "biologists with non-analytical minds warm to multi-level selection: a bland, unfocussed ecumenicalism of the sort promoted by (the association may not delight Wilson) the late Stephen Jay Gould." He insists that genes are unique among all the apparent levels of life, for they alone replicate exact copies of themselves. This not only renders them the sole unit of selection, but also the sole target. "Evolution, then, results from the differential survival of genes in gene pools," he explains. One of the celebrated consequences of this gene-centric view is that individual people are little more than the unique temporary confluence of their respective genes, meaning the bonds that unite a society (or colony) are more ethereal still. In the spring of 2012, Dawkins summarized his contempt for multilevel selection in a scathing review of Wilson's new book, *The Social Conquest of Earth*. The review has generated more letters and online comments than any other article in *Prospect* magazine's recent history.[12]

It should be pointed out, however, that even though Wilson has wagered his legacy on the organicist tradition, he has not necessarily abandoned his commitment to reductionism. This may sound counter-intuitive, but consider: He still believes that the social impulse is latent within genes, but he has reinterpreted the way it finds expression. Unlike Dawkins, he no longer believes that sociality stems from the right admixture of certain kinds of genes that ultimately support one another because of their joint ancestry. Instead, he believes that certain genes are coded to facilitate cooperation when doing so proves advantageous, regardless of whether or not the organisms involved are closely related. In a multilevel context, genes (or, even more specifically, alleles) remain the ultimate unit of evolution, though not the exclusive target (Nowak et al., 2010, p. 1061). That kind of context-dependency no doubt appeals to Wilson, who has recently started describing multilevel selection theory as "group and individual selection combined" (Wilson, 2012, p. 290). As Sober and Wilson (2000) elsewhere explain, "a gene can evolve by increasing its fitness relative to other genes within the same individual, by increasing the fitness of the individual relative to other individuals within a group, or by increasing the fitness of the group, relative to other groups in the total population" (Sober and Wilson, 2000, p. 259). What's more, multilevel selection's latent context-dependency cuts both ways, so that even the hallowed gene is itself viewed as little more than a group of biochemical compounds. As Okasha explains, "Replicating molecules combining themselves into compartments is strictly analogous to individual organisms combining themselves into colonies or groups," (Okasha, 2005, p. 2015).

Just as significantly, multilevel selection theory has allowed Wilson to unite previously distinct strands of his intellectual heritage. For example, Herbert Spencer intuited the multilevel nature of evolution, but always insisted on the inheritance of acquired characteristics as its primary mechanism. An additional century's worth of research has convinced

[12] Richard Dawkins, "The Descent of Edward Wilson," *Prospect Magazine* (May 24, 2012). URL: http://www.prospectmagazine.co.uk/magazine/edward-wilson-social-conquest-earth-evolutionary-errors-origin-species/, accessed August 18, 2012. The claim about letters and online comments was made in Vanessa Thorpe, "Richard Dawkins in Furious Row with E. O. Wilson over Theory of Evolution," *The Observer*, June 23, 2012. URL: http://www.guardian.co.uk/science/2012/jun/24/battle-of-the-professors.

Wilson and many other biologists that evolution indeed occurs at multiple levels, but that the prime mechanism is instead natural selection. William Morton Wheeler also viewed evolution as a multilevel process, though his philosophy was always dogged by a nagging paradox. He insisted that a social impulse suffused all living things, but he also insisted that trophallaxis explained the origin of insect sociality. This was incongruous. If material processes like trophallaxis explain the insect colony's organismic cohesion, what bonds unite organisms at other levels? Wheeler responded by offering an ever more ethereal definition of trophallaxis, but this hardly answered the question (Wheeler, 1928b). It should be pointed out that Wilson's new interpretation accords surprisingly well with the one proffered by Emerson (1939) just prior to the Second World War. After all, Emerson's central insight, that natural selection demarcates and maintains the individual organism at various levels of biological organization, sounds an awful lot like modern interpretations of multilevel selection (Wilson and Wilson, 2008). But whereas Emerson's vision could not withstand the reductionist onslaught, multilevel selection is sufficiently broad to encompass gene selection and group selection, molecular biology and evolutionary biology.

This realization has allowed Wilson to reconcile previously conflicting aspects of his intellectual heritage, but the price has not been cheap. Many of his professional colleagues have aligned against him while others have openly pitied him. The ruckus doesn't seem to bother Wilson, for whom controversy is old hat. He wears the easy countenance of a man who is confident in his beliefs, and has taken to repeating Schopenhauer's comforting aphorism describing the three stages of a theory's acceptance: first ridicule, then outrage, and finally the declaration that it's obvious. Drawing equally from both his Darwinian and Spencerian pedigrees, Wilson is more convinced than ever that natural selection is the primary force behind the evolution of life on earth, and that it permeates every level of the biological hierarchy.

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