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ORIGINAL ARTICLE

Task Allocation and the Logic of Research Questions: How Ants Challenge Human Sociobiology

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Abstract
After biologist Deborah Gordon made a series of experimental discoveries in the 1980s, she argued that a change in terminology regarding the division of labor among castes of specialists was needed. Gordon's investigations of the interactive effects of ants in colonies led her to believe that the established approach Edward O. Wilson had pioneered was biased in a way that made some alternative candidate adaptive explanations invisible. Gordon argued that this was because the term "division of labor" implied a division among specialists that was unwarranted, and proposed "task allocation" as a better description that did not bias research against the alternative causes she had discovered. Gordon's empirical findings and theoretical proposals also vindicate the initial critics of Wilson's human sociobiology who have been dismissed as political radicals, but her proposals have been widely misunderstood by many contemporary behavioral ecologists. The terminological and methodological confusions rampant in contemporary discourse can be clarified by applying a framework developed by Elisabeth Lloyd involving an analysis of the constraints imposed by different research questions. Applying this framework will show how the methodological problems involving description raised by the initial critics of Wilson's human sociobiology extended to his analysis of ants, indicating that they were not challenging Wilson's naturalistic approach to the study of human evolution, but rather his methods. It will also show how confusion over how Gordon's proposed research questions have been conflated with the possible answers she has argued ought to be investigated. This in turn will clarify contemporary disputes over her proposal to abandon the term "division of labor."

Keywords Adaptationism · Caste · Division of labor · Logic of research questions · Proximate · Response threshold · Sociobiology · Task allocation · Ultimate

Introduction

There is a logic underlying many of the methodological controversies surrounding the initial objections to Edward O. Wilson's human sociobiology. That same logic is involved in contemporary disagreements over whether the term "division of labor" is adequate to describe and investigate the adaptive behavior of insect colonies. This logic has been obscured in both cases by terminological confusions and accusations of the biased neglect of particular potential causes for collective behaviors (Lewontin 1976; Wilson 1976; Gordon 2016; Jeanne 2016). The aggressive tone and explicit social concerns expressed by Richard Lewontin in his criticism of Wilson's human sociobiology have distracted from the substance of these objections, and fostered a misleading historical account of the controversy implying that these objections were merely political and without scientific merit (Lumsden and Wilson 1983, pp. 36–42; Segerstrale 2000, pp. 18, 101; Alcock 2001, p. 4). These objections hinged on the importance of avoiding descriptions of traits that would bias their evolutionary analysis. Just such a problem is at the heart of a contemporary dispute involving Wilson's work on the adaptive behavior of eusocial insect colonies, which he has described as a division of labor among castes of specialists (Oster and Wilson 1978). Wilson's efforts to defend the methods he employed in human sociobiology led him to present his work on ant colonies as a demonstration of their quality, but Deborah Gordon's work has called that quality into question (Oster and Wilson 1978; Gordon 1988). By analyzing key historical exchanges in the sociobiology controversy, and subsequent developments in

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the study of eusocial colony behavior, I will show how Gordon applied the same logic underlying Lewontin's objections to Wilson to consider a broader range of possible explanations for patterns of group behaviors, and why her efforts to reform the study of eusocial colony behavior remain so widely misunderstood.

Clarifying some specific aspects of Lewontin's methodological objections to Wilson requires differentiating them from broader concerns with adaptationism, as well as the political arguments against Wilson's human sociobiology that Lewontin developed with his colleague and coauthor, Stephen Jay Gould. Adaptationism, as it was articulated by Gould and Lewontin in "The Spandrels of San Marco and the Panglossian Paradigm" in 1979, amounted to a willingness to accept poorly supported adaptive explanations for traits, while tending to ignore competing nonadaptive alternatives (Gould and Lewontin 1979). They argued that adaptationism was fostered by a broad array of distinct methodological problems that, if neglected, tended to make weak adaptive explanations appear more plausible. Significantly, those methodological problems relate to more than just a failure to consider nonadaptive candidate explanations. One of the problems involves how to accurately describe atomized traits when organisms are actually integrated entities (Gould and Lewontin 1979, p. 585).[1] The same problem applies to describing the traits of eusocial colonies. This problem is only briefly mentioned in Gould and Lewontin's joint article, which was primarily drafted by Gould based on their extensive collaboration and Lewontin's ideas about adaptation (Gould 1993, pp. 315–316; Lewontin 2015). However, it was the main focus of Lewontin's early criticism of Wilson's sociobiology.

Lewontin repeatedly emphasized the methodological importance of difficulties related to describing traits that might be subject to natural selection. This problem of description was the main focus of Lewontin's address to the Philosophy of Science Association in 1976, which he titled "Sociobiology—A Caricature of Darwinism," and provided the basis for "Sociobiology as an Adaptationist Program" in 1979. While Wilson conceded that this last paper contained some good scientific criticism, he explicitly and repeatedly dismissed the specific problems Lewontin raised regarding the descriptions, and insisted that both Lewontin and Gould were too politically biased against adaptive accounts of human nature to give sociobiology a fair scientific hearing (Wilson 1975a, c, 1976, 1994; Lumsden and Wilson 1983, pp. 40–44; Segerstrale 2000, p. 101). This dismissal was unfortunate, because methodological problems involving description would undermine Wilson's attempts to utilize his study of ants to refute his critics (Oster and Wilson 1978, p. 23; Segerstrale 2000, pp. 18, 101–102), as Gordon would demonstrate empirically in the 1980s (Gordon 1988, pp. 246–252). Yet the threat Gordon's work poses to Wilson's project has often been misunderstood, in large part due to confusion over the problem of description and the logic of the research questions being pursued (see Lloyd 2015).

Wilson dismissed his critics in part because he thought he had good evidence that his approach was an unbiased means of describing and investigating nonhuman behavioral adaptations. His first book on sociobiology, *The Insect Societies*, was well received by the scientific community in 1971. It was only when he extended his analysis to human beings, and other vertebrates, in 1975 that he attracted his critics' attention and was accused of weak methods and biased conclusions, he claimed (Wilson 2004, pp. xi–xvii; Allen et al. 1975). In 1978 Wilson wrote two books defending sociobiology. One was titled *On Human Nature*, which was an expansion and defense of his treatment of human beings in *Sociobiology: The New Synthesis* that had raised the ire of critics. In *On Human Nature*, Wilson recapitulated and expanded his arguments that (1) sociobiology was a good means of studying animals, (2) human beings were animals, so (3) sociobiology was a good means of studying human beings (Wilson 1978a, pp. 2–10). However, Wilson emphasized that this was a speculative defense of the prospect of a human sociobiology, on naturalist grounds: "*On Human Nature* is not a work of science; it is a work about science, and about how far the natural sciences can penetrate into human behavior before they will be transformed into something new" (Wilson 1978a, p. xxi). While Wilson's critics challenged the methodological credibility of human sociobiology, Wilson emphasized tangentially that human beings ought to be seen and studied as a part of nature (Allen et al. 1975; Lewontin 1976; Wilson 1978a, b). His book won a Pulitzer Prize in 1979.

The second book defending sociobiology that Wilson published that year was about ants. Wilson coauthored *Caste and Ecology of the Social Insects* with George Oster, who specialized in mathematical modeling, and presented it as a defense of his scientific methods. This book presented an argument that, contrary to the assessment of his critics, Wilson's approach to sociobiology was a good means of understanding the adaptive significance of animal behavior (Oster and Wilson 1978, p. 23). He developed the view that colony behavior was best understood in terms of the adaptive division of labor among castes of specialists, and together with Oster he built models of these castes' optimal distribution under a variety of ecological conditions.

[1] Although the related problem of "reification" in descriptions, or confusing some representation such as a mathematical construct with a trait subject to selection, occupied both Gould's and Lewontin's attention as a descriptive problem that played a central role in their critiques of the controversy involving human IQ testing (Lewontin 1970, 1976; Gould 1981).

As an entomologist, Wilson's perspective on the description of adaptive variation differed significantly from population geneticists like Lewontin. Wilson depended on identifying polymorphisms to inform his taxonomy, which he explained had a specific technical meaning in entomology: "Polymorphism is defined in a special sense in the social insects as the coexistence of two or more functionally different castes within the same sex" (Wilson 1971, p. 136). It was important to Wilson that the differences between these castes were functional. Slight variations in color or morphology without some functionally adaptive significance did not qualify, and neither did pathological forms. Wilson acknowledged that this use of the term "polymorphism" more commonly referred to genetic variation within a population, especially among geneticists, but Wilson argued that "caste variation has been labeled as polymorphism at least as far back as Emery (1896), with little overlap into or confusion with the genetic usage, and a change hardly seems necessary now" (Wilson 1971, p. 136). Wilson was confident he could identify adaptively significant traits among individual ants to distinguish their caste membership. This was a crucial step in his efforts to reconstruct the optimal behavior of a colony from the behavior of its individual members (Wilson 1971, p. 227; Oster and Wilson 1978).

Some of Wilson's most significant contributions to entomology and animal behavior involved delineating castes according to proposed adaptive functions. In 1953, Wilson argued that polymorphism resulting from differences in the allometry of adult workers not only formed the basis of distinct morphological castes among some colonies of eusocial insects, but that the proportion of those castes in a colony was adaptive. Wilson was cautious to note that species with conspicuously specialized morphological forms were not necessarily more adaptive than species with more uniform, general-purpose forms, but emphasized that even the slightest morphological differences might be subject to selection in favor of specialization (Wilson 1953, p. 153). Wilson differentiated his approach to castes from that of Wheeler (1937), who referred to castes as synonymous with phases or anomalies without reference to some adaptive function. Wilson aimed to simplify and clarify Wheeler's categories of castes by delineating and defining them in terms of functional morphological differences (Wilson 1953, pp. 136, 144). Wilson focused his investigation on species with extreme morphological variation among workers, and found evidence supporting his view that extremely different morphological worker groups in a colony could perform specific tasks more efficiently (Wilson 1953, 1963, 1968, 1980, 1983).[2]

While Wilson took castes to be delineated by their adaptive functions, he did not consider all adaptive functions to be identifiable by recognizing conspicuous morphological variations. In 1963, he expressed some frustration over the ambiguity of the term caste, since "job preference" or "division of labor" could be distributed among castes based on age, reproductive roles, or physiological predispositions (Wilson 1963, p. 357). These different ways that a caste delineated different specialists were captured by the definition Oster and Wilson proposed in *Caste and Ecology in the Social Insects* in 1978: "A caste can be roughly defined as any set of individuals that performs specialized labor in a colony for sustained periods of time" (Oster and Wilson 1978, p. 19). Having identified this broad array of possible castes, Oster and Wilson wrote that: "Ideally, the full description of all roles together, in so far as they can be meaningfully separated, will fully define the society" (Oster and Wilson, p. 20). While they did not argue that all mass colony behavior could be fully decomposed into optimal proportions of specifically morphological castes, they did argue that it could be decomposed into optimal proportions of castes of individuals engaged in some sustained specialized labor.

It is the assumption that mass behavior can be decomposed into optimal proportions of specialists, which is implied by describing mass behavior as a division of labor among castes, that has proved to be problematic. In the 1980s, Gordon's manipulation of groups of workers in colonies of red harvester ants (*Pogonomyrmex barbatus*) demonstrated that their overall patterns of colony behavior could not be accounted for by identifying the proportions of different types of worker castes in the colony (Gordon 1986, 1987, 1988). She then argued that a change in terminology regarding the division of labor among castes of specialists was necessary to avoid biased research into colony behavior, because presuming that colony behavior was always reducible to proportions of caste members tended to make alternative candidate explanations invisible to research (Gordon 1996). Gordon argued that problems with Wilson's descriptions and research questions led to the neglect of the aspects of the colony behavior she had discovered, and proposed a change in descriptive terminology in 1996. This change in terminology had serious implications for the research questions

[2] The implications of these differences remain a point of some controversy. In cases of extreme morphological variation among workers, many entomologists have taken Wilson's work as decisively supporting the view that the variation is the result of a colony adaptation

Footnote 2 (continued)

(Wheeler 1986; Jeanne 2016; Lillico-Ouachour and Abouheif 2017). Gordon has questioned this as a default assumption and suggested that while it is a possibility, more empirical evidence tracking the differential fitness of colonies is necessary for the specific cases in question (Gordon 2016, p. 1103), and that the presence of a specific fitness contribution among those species with extremely diverse morphological castes is inadequate to explain the broader question of why tasks are allocated in colonies more generally (Gordon 1988, p. 251).

Adaptationist Research Question:

"What is the function of this trait?"

Possible and responsive answers:

A: The function of this trait is F.

A: The function of this trait is G.

A: The function of this trait is ... etc.

Fig. 1 Lloyd identified this question as representing Ernst Mayr's methodological approach to investigating adaptations. The potential answers, labeled A, are those that are both considered possible in light of contemporary evolutionary theory, and also responsive to the question. Note that this question need not be posed by the scientist explicitly, and can be extracted based on an analysis of those answers the researcher is willing to consider relevant possibilities as research is ongoing (Lloyd 2015, p. 346)

that could logically be pursued, but these implications were obscured by confusion over how to construct research questions according to distinctions between causal explanations that had been popularized among animal behaviorists in the 1960s by Nikko Tinbergen and Ernst Mayr (Jeanne 2016).

The logic underlying these proposals can be made clear by applying what Elisabeth Lloyd has called the "Logic of Research Questions." Lloyd developed this framework in her analysis of adaptationism in 2015 by exploring the different consequences of asking *if* a trait has an adaptive function as opposed to asking: what is the function of this trait? (Lloyd 2015). Each of these questions has different implications for the development of ongoing research and potential discoveries. The choice of research question is not harmless, even if the trait under investigation is held to be adaptive only for the sake of inquiry (cf. Mayr 1983). Possible explanations may easily become invisible under the investigation of a narrow question. Consider, for example, a scientist asking the following question: what is the function of this trait? Evidence might be gathered supporting the hypothesis that the function is F, or G, or some other function (Fig. 1).

If F is disconfirmed, consider G. If G is disconfirmed, recall that there are many different ways a trait might be adaptive, and consider H, and so on. If evidence supports more than one possibility, the weight of evidence may be appealed to. But note that the question implies that the answer must involve some sort of adaptive function. Compare this question to an alternative that is more compatible with the broad range of possible explanations under contemporary evolutionary theory (Fig. 2): "What evolutionary factors account for the form and distribution of this trait?" or "Does this trait have a function?" (Lloyd 2015, p. 346).

Under this research question, adaptive functions are perfectly acceptable possible explanations. A researcher may ask what might be expected if the trait happens to have a function F, or G, or so on. Various methods such as optimality modeling may be employed to gather evidence for these functions, and in cases of ambiguity, the weight of evidence supporting different possibilities may be considered. However, under this research question, nonfunctional explanations may also be considered as logically possible responses to the question.

Lloyd developed this framework to illustrate how methodological adaptationism, as a heuristic approach to investigation, was far from a harmless heuristic in practice, because it amounted to a commitment to asking the question, "What is the function of this trait?" with its concomitant strictly functional answers, and nothing else. The logical pursuit of an answer to this question involves the systematic neglect of the investigation and evaluation of nonfunctional explanations, resulting in biased research (Lloyd 2015). Such research might still be quite fruitful in cases where a trait does in fact have the function being sought, which has made the underlying problem with methodological adaptationism difficult to diagnose.[3]

Poorly constructed research questions can also lead to the neglect of more than just nonadaptive possibilities, especially when there are problems with describing the trait in the first place. By applying Lloyd's framework to the types of answers that Wilson and Gordon have been willing to consider, I will show how their different choices in descriptive terminology operated in the questions that guided their research and evaluation of observed colony behavior. The technique of analyzing research questions and their possible and responsive answers will clarify Lewontin's

[3] Since Gould and Lewontin introduced the problem of "adaptationism" in "The Spandrels of San Marco and the Panglossian Paradigm" in 1979, a philosophical industry has grown up around distinguishing different types of adaptationism and evaluating their respective merits. In 2009, Tim Lewens identified seven different types of adaptationism (Lewens 2009).

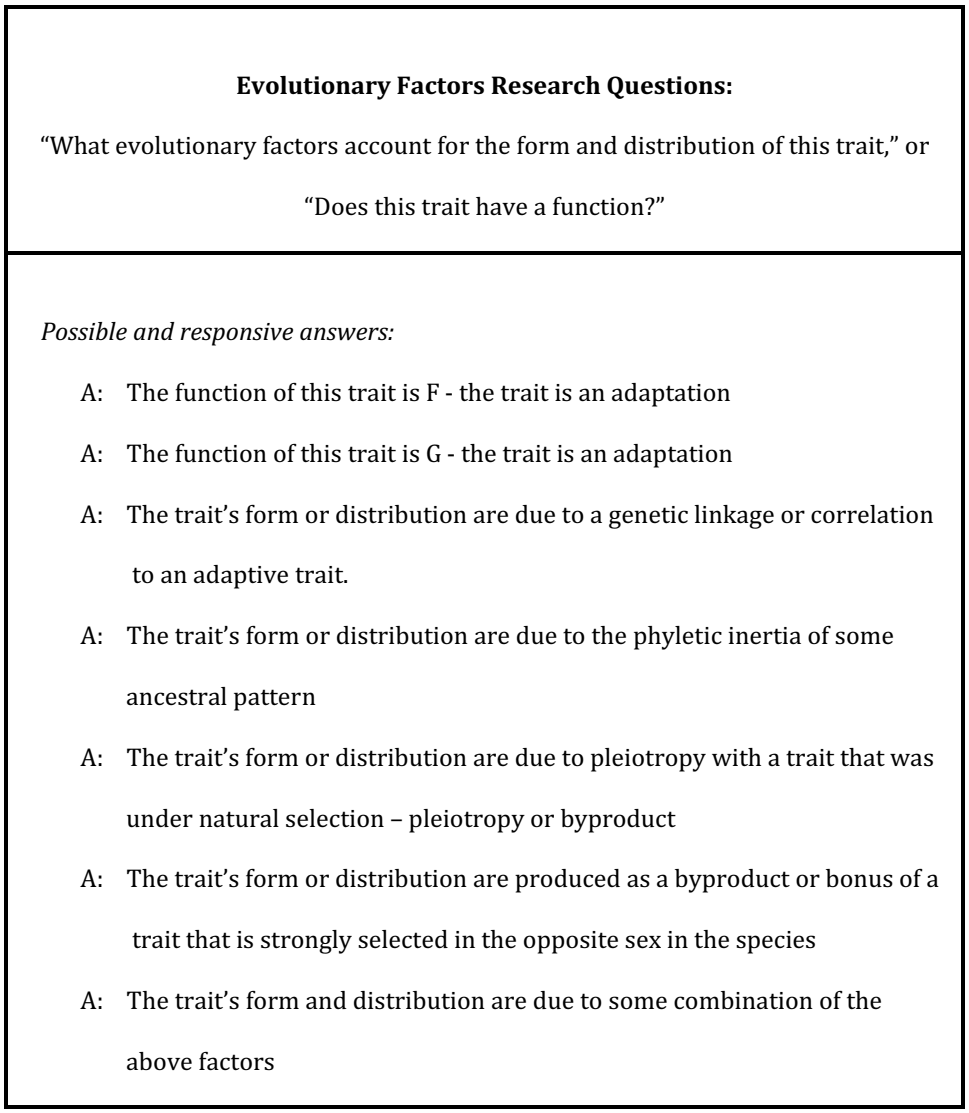

Fig. 2 This figure paraphrases Lloyd's presentation of her research question in 2015. She shows that the responsive answers to this research question include the full range of possibilities in contemporary evolutionary theory (Lloyd 2015, p. 346)

methodological challenge to Wilson, and show how that challenge bears on contemporary research.

The Critics and Wilson's Defense

The political dimension of Lewontin's criticism of Wilson's human sociobiology has not only distracted from important details of his methodological critique, it also served as a powerful motivation for Wilson to present his study of ants as a defense of both his methods and his scientific credibility. Lewontin's initial criticism appeared in a book review of Wilson's *Sociobiology: The New Synthesis* in 1975, which Lewontin coauthored with a group of activists in Boston concerned with the abuse of scientific authority. One of the most significant methodological concerns they raised was the problem of describing a trait without bias. In particular, they were concerned that (1) the choice of arbitrary or anthropomorphic terms could not only skew the investigation of the social behavior of nonhuman animals, but also (2) serve as a means of justifying similar human behaviors as natural (Allen et al. 1975). This second part of the argument was one Wilson was eager to refute, as he insisted that "is" does not imply "ought," and that he had no intention of justifying human behaviors by identifying their evolutionary origin. However, he was also eager to find constraints that an evolved human nature placed on social policies, and so the question of whether he was overconfident in his assessment of what "is" a constraint had a strong bearing on what policy makers "ought" to do in light of his human sociobiology (Wilson 1976). Thus, methodological worries that reduced confidence in Wilson's account of human nature had a direct bearing on how that information ought to be used. This concern added a moral dimension to the discussion of appropriate methods, and has fostered the false impression that the initial objections raised by Lewontin and the Sociobiology

Study Group did not contain a scientific critique of those methods (cf. Segerstrale 2000, pp. 18, 101).

In 1976, Lewontin elaborated on the methodological concern that the initial description of a trait could bias its investigation in both humans and other animals. His objection was not just that nonadaptive explanations might be neglected by Wilson's ardent efforts to assign adaptive significance to behaviors, but that a failure to take care in initially describing behavioral traits would amount to an ad hoc "Darwinizing" that was vulnerable to biased research. Lewontin was especially worried in light of Wilson's ambitions to use sociobiology to reform anthropology, when "anthropologists have long been acutely conscious of the difficulties of describing human behavior in such a way as not to dictate the analysis by the categories of description" (Lewontin 1976, p. 24). This sort of difficulty was not unique to anthropology, but Lewontin described the social threat of disregarding it when studying human beings as particularly acute.

For example, Lewontin objected to the use of the term "aggression" to refer both to warfare and to individual antagonistic behavior. Lewontin saw war as "a calculated political phenomenon undertaken for economic and political gain by a collectivity" that was poorly explained by hostility between the specific individuals participating in it. "People kill each other in wars for all sorts of reasons, not the least of which is that they are forced to do so against their own wishes by the political power of the state" (Lewontin 1976, p. 26). Lewontin presented war as a collective behavior that was not reducible to the identification of types of aggressive individual members of that collective. War was not the sum of soldier aggression. Consequently, the conflation of collective and individual behaviors could lead sociobiologists astray and care needed to be taken when initially describing a social trait, so as not to "dictate the analysis" (Lewontin 1976, p. 24).

Descriptions of ant societies also played an important role in these exchanges. In the book review of *Sociobiology: The New Synthesis* that Lewontin coauthored in 1975, he objected to Wilson's descriptions of "slavery" among ants that co-opted related species to serve the interests of their colony, as well as descriptions of "castes" of specialists acting in those colonies (Allen et al. 1975). As mentioned above, these terms were in use well before Wilson adopted them (for example, see Wheeler 1937), but Wilson's efforts to strictly define castes as groups of adaptive specialists appeared to Lewontin to be presuming adaptive explanations for human castes, and then applying that presumption to the study of social behavior in ants. Expanding on this objection in 1976, Lewontin argued that the term "caste" as it was applied to the social behavior of insects was the most famous case of false metaphor in Wilson's sociobiology. The reason he took the metaphor to be false was that, on his view, castes were a product of specifically human cultural and economic arrangements, rather than inherent differences between individual caste members:

> Caste is a human phenomenon, originally a race or lineage, but later a hereditary social group associated with particular trades and social position....Class structure is an economic and social phenomenon related to and coming out of human historical events and regulating the social and material power of individuals. Castes in India were the outcome of an invasion and conquest of Dravidians by Aryans. High caste Hindus had a monopoly on social, political and economic power while untouchables lived at the margin of existence. What has all that to do with ants? (Lewontin 1976, p. 26)

Lewontin insisted that ants did not have the same social dynamics that produced human caste structures. While some cultures might understand castes to be mapping the natural divisions dictated by the intrinsic characteristics of their members, Lewontin was eager to present this as a misunderstanding of human castes. Applying the term metaphorically to ants therefore ran the serious risk of smuggling meaning into the analysis of the social behavior of insects. That meaning might be smuggled in a variety of ways, including through the conflation of group behaviors as mere aggregates of the behavior of their members.

Wilson responded that Lewontin was being ridiculous. In his 1976 reply, "Academic Vigilantism," he insisted that his use of metaphorical language was perfectly appropriate to science and quite widespread outside of sociobiology. Wilson considered Lewontin and the other cosigners to the critical review of *Sociobiology: The New Synthesis* in 1975 to be political activists looking for something to object to, even if they had to invent a problem involving metaphors:

> The cosigners do not like to see terms such as slavery, division of labor, and ritual used in both zoology and the social sciences. Do they wish also to expunge communication, dominance, monogamy, and parental care from the vocabulary of zoology? (Wilson 1976, p. 187)

Wilson considered the attempt to police metaphorical language to be on a slippery slope. Scientists regularly adopted metaphorical terms to describe their objects of study with specific technical meanings related to their discipline and context. Wilson saw the objection to terms as "insubstantial" because the "definitions and limitations of the concepts of analogy and homology have been well worked out by evolutionary biologists" (Wilson 1978b, p. 10). Identifying an anthropomorphic meaning associated with a word used in ordinary language was not enough to criticize its adoption as a technical scientific term. It had to be shown that the

term affected the science. Attempts to police sociobiology on these grounds appeared to Wilson to be highly selective, and biased towards criticism of a new discipline that promised to expand human self-knowledge at the expense of threatening the Sociobiology Study Group's political agenda (Wilson 1978a, b, 1983, pp. 36–44).

While Wilson argued that his critics were politically biased, and completely dismissed their concerns regarding neutral and biologically relevant descriptions of traits, he did marshal a detailed response to their challenge to his general preference for adaptive explanations, and presented that defense with George Oster in *Caste and Ecology of the Social Insects*. In their book, Oster and Wilson (1978) aimed to show how optimality models could be built to represent and predict the most adaptive proportion of castes among workers in colonies of ants dividing labor.

Oster and Wilson were acutely aware of the criticisms raised by Lewontin regarding their dependence on plausibility arguments and optimality models to support their biological claims about behavior.[4] They took their project to be more than just an exploration of the sociobiology of ants. It was a proof of the concept of sociobiological methods, especially the use of optimality models to look for social adaptations:

> Because optimization plays such a central role in our model building, we foresee an additional, more general benefit from the study of caste: a test of the concept of evolutionary optimization itself. If detailed and falsifiable hypotheses can be fashioned in advance of experimental research, they will serve to test not only caste theory but also the fundamental assumption of evolutionary optimization routinely made by biologists. If this assumption should fail in the social insects, which can be characterized as the 'squid axon' of sociobiology, the debacle could have major repercussions for general evolutionary biology. A whiff of danger adds excitement to our subject and should help to attract more of the imaginative investigators that it clearly deserves. (Oster and Wilson 1978, p. 23)

In the 1930s, the nerve fibers found in giant squid were identified, and their enormous size and visibility facilitated ongoing investigations of how nerves functioned (Keynes 2005). Eusocial insects appeared to be an analogous case in their clear and observable displays of adaptive social behavior that might provide Wilson with an exemplar for sociobiology. Wilson was confident that his efforts to construct rigorous optimality models of the division of labor among castes of specialists would vindicate his claim that sociobiology was a good means of understanding the social behavior of animals. Oster and Wilson were right that optimality models could be powerful tools for gathering evidence for adaptations, and they have continued to be routinely used to evaluate whether some social trait might have a function, but they are poorly suited to detect errors when deployed to investigate questions such as, "What is the function of this caste?" (see Lloyd 2015).

Task Allocation and the Logic of Research Questions

Oster and Wilson approached the behavior of eusocial insects as an object of study in its own right, but also as the kind of adaptive social system that ought to be particularly suited to sociobiological analysis. Their study was not just about understanding eusocial insects in nature; it was a test of understanding sociobiology as an approach to understanding social adaptation. Oster and Wilson explicitly laid this out as a challenge, when they emphasized, "A whiff of danger adds excitement to our subject and should help to attract more of the imaginative investigators that it clearly deserves" (Oster and Wilson 1978, p. 23). Deborah Gordon was one of those investigators.

It was Wilson's work on pheromonal responses that attracted Gordon specifically to the red harvester ants (*Pogonomyrmex barbatus*) that she would come to specialize in (Gordon 2010, pp. 6–7). One of Wilson's major scientific contributions to understanding ant behavior had been the discovery of the pheromonal signals ants sent to each other that triggered many of their response patterns. Wilson had been inspired by Konrad Lorenz to look for triggers for fixed-action patterns, and discovered chemical cues that provoked ants to forage, gather in alarm, and dispose waste in the nest. In studying waste disposal, Wilson reported how red harvester ants he had treated with oleic acid, a pheromone present in refuse and dead ants, would be treated by their nest mates as though they had died (Wilson 1994, pp. 285–296). Gordon was particularly struck by Wilson's reports of this experiment, that treated ants would

[4] In his autobiography, Wilson described how he has been fortunate to collaborate with a series of gifted modelers, including Oster, Robert MacArthur (MacArthur and Wilson 1967), William Bossert (Wilson and Bossert 1971), and Charles Lumsden (Lumsden and Wilson 1981), all of whom he has strongly depended on for their mathematical ability. Wilson saw his contribution to these collaborations as involving his intuition, background knowledge, and the identification of problems to address (Wilson 1994, p. 122). Oster visited Harvard for a year to collaborate with Wilson to write *Caste and Ecology of the Social Insects*, working at the same time with Lewontin in an effort to develop a rigorous approach to optimality modeling (Nuzzo 2006). Many aspects of those models are strongly defended in Chap. 8 of *Caste and Ecology of the Social Insects*, but the problem of assuming that the division of labor among castes of specialists is an adequate description of colony behavior is not adequately addressed.

be carried "live and kicking" to the refuse pile by fellow workers compelled by the pheromonal cue (Gordon 2010, pp. 6–7). Gordon was unable to replicate the experiment (Gordon 1983), and through correspondence with Wilson she discovered that he had chilled the treated ants to make them more manageable to the pheromonal treatment. This led Gordon to consider: "An ant's response to a chemical cue was not fixed, but depended on what the ant was doing. Then what determined what the ant was doing?" By trying to find an answer to this question, Gordon challenged the prevailing efforts to reconstruct observed colony behavior by understanding individual ants (Gordon 2010, pp. 6–7).

In 1981, Gordon began what has become the longest-term tracking study of a population of eusocial insect colonies on record (Gordon 2016). Rather than examine the "division of labor" of these colonies, Gordon focused more generally on the tasks they engaged in on their daily rounds. The patterns of behavior these colonies exhibited seriously complicated efforts to reduce those patterns to optimal caste distributions, as will be explored below. By 1988, Gordon suggested that the problem involved research questions that aimed to explain dynamic colony behavior by appeal to static concepts, like castes (Gordon 1988, p. 250). By 1996, she proposed "task allocation" as a more neutral description of colony behavior (Gordon 1996, p. 121).

Gordon's proposal remains controversial among many behavioral ecologists. The issue is complex and easy to misrepresent. In his defense, Wilson had presented a serious argument that there are many other metaphorical terms with technical meanings that do not appear to impede investigating evolutionary theory. It was not enough for his critics merely to identify an everyday use of a term that is anthropomorphic. For there to be a scientific problem, there needed to be evidence that the use of the term was interfering with the science (Wilson 1976, p. 187). Such evidence does exist in this case. But recognizing it has been difficult in light of the entrenchment of the term "division of labor," and the various ways "castes" and "specialists" have been interpreted.

The situation can be made clear by applying the "Logic of Research Questions" framework, mentioned above (Lloyd 2015). This framework involves evaluating researchers' questions in light of the responses they are willing to consider informative and responsive, and comparing those responses to what possible answers may be implicated by contemporary theory. This technique is useful both as a philosophical and a historiographical tool, by making underlying commitments explicit and transparent, so they may be compared to the actor's categories and interpretations, along with the dominant theory at the time.

Applying this framework to Gordon's research on colonies of red harvester ants in the Arizona desert (*Pogonomyrmex barbatus*) will show how it undermined Wilson's sociobiology. Red harvester colony workers do not display pronounced morphological differences. They are typical in this regard; only about 50 of the 326 living ant genera do (Gordon 2016, p. 1103). Over the course of a day, a worker in one of these colonies may engage in one of various tasks, including patrolling, maintaining the nest or the midden (trash) area, or venturing into the surrounding desert to forage for seeds (Gordon 1988, p. 246). In the 1980s, Gordon conducted a series of experiments to evaluate whether the pattern of colony behavior these ants produced could be explained by the number of specialists present. She wanted to know how tasks were allocated among colony members without presuming that they were necessarily divided among specialized laborers, although she considered that as a possibility (Gordon 1987, 1988). Her research question can be framed this way (Fig. 3): what determines the allocation of tasks among individual ants in a colony, producing the colony's pattern of behavior? Gordon recognized that those patterns could be due to the properties of individual ants, such as morphological differences or behavioral preferences that could constitute caste differences. Or maybe the pattern was due to age-related castes, as ants developed new specialties as they moved out of the nest and grew older (Gordon 1996, p. 121). Or maybe it was due to some other means of determining task groups that led ants to specialize in their work for sustained periods of time (Gordon 1986, 1987, 1988, 1996; Oster and Wilson 1978, p. 19).

To find out, Gordon marked groups of individual ants, each engaged in one of various tasks, and perturbed their work to determine how they would respond. Three results were particularly significant (Gordon 1986, 1988, pp. 246–252). First, she found that if she perturbed the activities of one task group, the behavior of ants working on other projects would change. Second, she found that if she perturbed more than one group at a time, the total changes in behavior in those groups were greater than if their activities were disrupted one by one. Third, she found that the age of the colony made a difference in response, even though they had individual workers of the same age (Gordon 1986; 1987; 1988, pp. 246–252). In 1988, colonies were known to live for more than 15 years (although 25-year-old colonies have now been identified), while workers tend to live for only one year (Gordon 1988, 2016). Gordon found that younger colonies responded more erratically to perturbations, and that repeated perturbations prompted increased foraging more reliably in older colonies (Gordon 1987, 1988).

These patterns of behavior could not be determined simply by the proportions of specialized caste members in the colony. But what else could it be? Gordon argued that a better explanation involved the dynamic network of interactions between the internal properties of individual ants, as well as their physical and social environments (Gordon 1988). Advancements in computer science had produced models of dynamic systems that could correspond to observed worker

Gordon's Research Question:

"What determines the allocation of tasks among individual ants in a colony, producing the colony's pattern of behavior?"

Possible and responsive answers:

A: Morphological differences delineating task groups of workers

[Wilson delineated a type of morphological caste]

A: Worker age – temporal task group

[Wilson delineated a type of temporal caste]

A: Behavioral task groups

[Wilson delineated a type of behavioral caste]

A: Dynamic interaction between internal properties of workers and their physical and social environment

Fig. 3 Gordon's research can be framed in terms of the question shown here. By 1988, Gordon was considering the possible and responsive answers listed in the figure, which include those considered by Wilson as types of castes, which are set off in brackets. Gordon's research question also accommodated the novel possibility that adaptive patterns of colony behavior are caused by dynamic interaction networks that cannot be decomposed to proportions of worker types, or castes (see Gordon 1988)

behaviors, even if workers were functionally identical. Her research question could accommodate this possibility (Gordon 1996).

By 1988, Gordon's findings were well established, and she became quite explicit in her concern that research questions aiming to explain the division of labor among worker castes were problematic because they tended to look for static explanations of dynamic systems, as Lewontin had cautioned against (Gordon 1988, pp. 244–245). Setting out to explain colony behavior in terms of division of labor tended to narrow the possible causes that were seriously considered, because static worker types were not the only way dynamic colony behaviors could develop.

It was out of concern that the term "division of labor" could bias the direction of research, and make some possible explanations invisible, that Gordon proposed the term "task allocation" as an alternative in 1996. Under her new approach, Gordon surveyed possible explanations for task allocation being pursued in contemporary research. She presented it as better suited to finding out just "what determines, at any moment, which individuals are engaged in each task, and how does a colony adjust its efforts to the demands of a changing environment?" (Gordon 1996, p. 121). Any one of these answers, or some combination of them, was responsive to her question (Fig. 4).

Compare Gordon's research question and its possible answers to those posed by Wilson. In his 1971 book, *The Insect Societies*, Wilson wrote that, "the reconstruction of mass behavior from a knowledge of the behavior of single colony members is the central problem of insect sociology" (p. 227). Wilson aimed to solve this problem by identifying types of individual colony members, and grouping them in terms of castes. So in *Caste and Ecology of the Social Insects*, Oster and Wilson presented models representing the optimal number of castes in a colony. They wrote:

> The guiding proposition of our inquiry is that variations in caste structure and division of labor reflect differing adaptations on the part of individual species of social insects. Thus, caste is not just central to social organization; it should provide the key to the ecology of social insects, insofar as those insects differ from their solitary counterparts. We regard many of the principal processes of colony life, including communication, physiological caste determination, and trophallaxis, as subordinate to the evolution of caste.

Gordon's Research Question:

"What determines the task allocation among individual ants in a colony, producing the colony's pattern of behavior?"

Possible and responsive answers:

A: Morphological differences delineating task groups of workers

[Wilson delineated a type of morphological caste]

A: Worker age – temporal task group

[Wilson delineated a type of temporal caste]

A: Behavioral predisposition

[Wilson delineated a type of behavioral caste]

A: Immediate environmental conditions

A: The dynamic interaction network produced by the distribution and number of other workers engaged in tasks in the colony

A: Colony age

A: Some combination of the above factors interacting

Fig. 4 The introduction of the term "task allocation" allowed Gordon to consider a greater range of possible answers without neglecting the possibilities considered responsive to the investigation of "division of labor." In 1996, as her research developed, she explicitly considered the answers listed here as possible explanations for task allocation (Gordon 1996)

> We postulate them to be the enabling devices by which labor is allocated and by which the colony as a whole precisely adjusts its relationship to the nest environs. (Oster and Wilson 1978, p. 21)

Their research question can be put this way (Fig. 5): what determines the proportion of castes that cause the optimal division of labor in a colony? Oster and Wilson were willing to consider many different types of castes as possible causes for adaptive mass colony behavior. They were perfectly aware that there was task overlap and behavioral plasticity between castes. Yet they took caste proportions to be the explanation for division of labor between specialists, which ruled out consideration of several alternatives that Gordon would investigate.

So despite Wilson's insistence that the technical meanings of division of labor and caste were harmless, a comparison with Gordon's research shows how they were actually a way of describing behavior that biased evolutionary analysis, fixated as they were upon giving answers in terms of castes. This was exactly the sort of methodological problem Lewontin had initially warned against, as it involved describing the pattern of colony behavior in a way that directed or dictated its analysis (Allen et al. 1975; Lewontin 1976, pp. 24–26). The scientific objection was a serious one, and it was not just relevant to the study of human beings. It was causing problems with the analysis of ants, which was the organism that Wilson knew best.

Confusing "Task Allocation" with Immediate Interaction

The logic underlying Wilson's commitment to reconstruct observed colony behavior by identifying types of individual ants in a colony has been made even more difficult to recognize due to efforts to differentiate between research questions that target different types of explanations popularized among animal behaviorists by Ernst Mayr and Nikko Tinbergen in the 1960s (Beshers and Fewell 2001; Jeanne 2016). Mayr

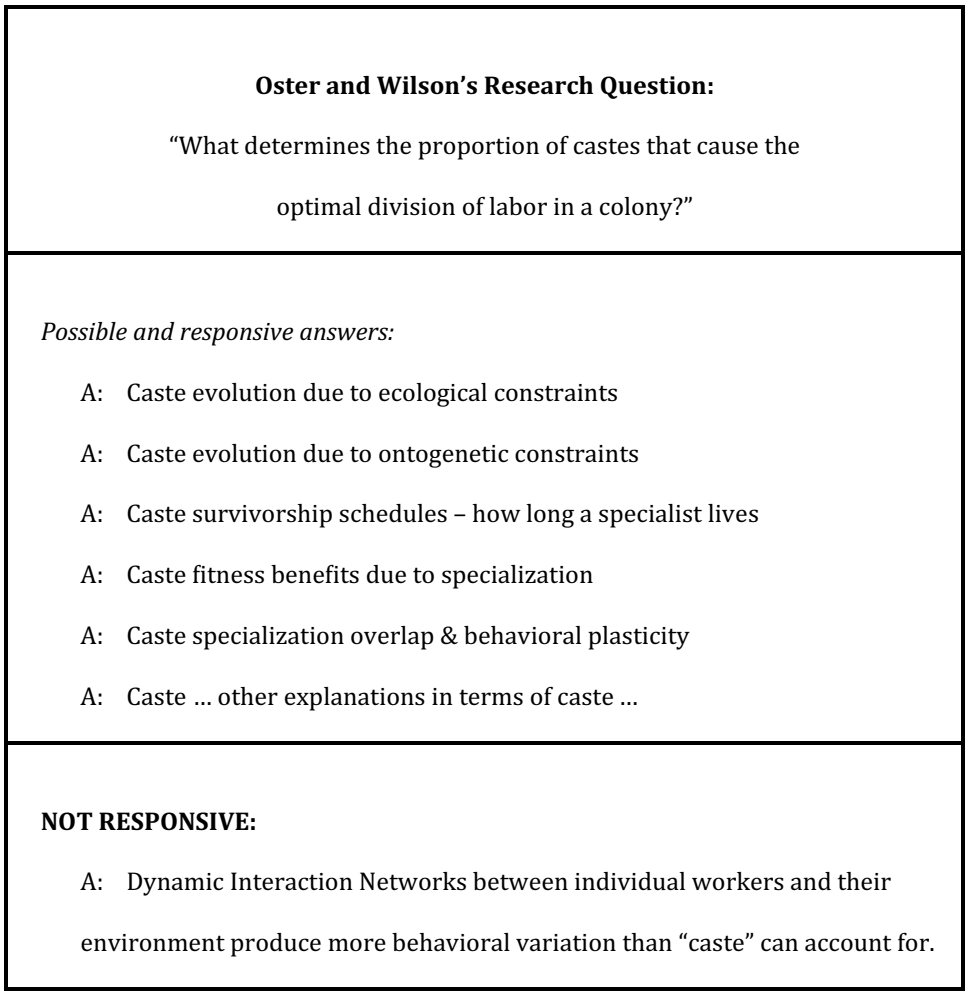

Fig. 5 By assuming that colony behavior is due to the optimal division of labor among some type of castes, only answers referring to castes are responsive to the research question, and these are just the type of answers that Oster and Wilson considered to be relevant (Oster and Wilson 1978, pp. 21, 180–181, 316–320). The penultimate possible answer listed indicates that other explanations could be responsive, so long as they involve castes. Note that the last possible answer is not responsive to Oster and Wilson's question, and they did not investigate it as a possibility. Also note that this last possible answer is not excluded by Gordon's research question, which was posed in terms of task allocation, as opposed to division of labor (Gordon 1988, 1996)

distinguished proximate explanations as involving an organism's response to events in its lifetime, while ultimate explanations involve evolutionary causes that precede it (Mayr 1961; Dewsbury 1999, p. 190; for a causal analysis of the interrelationships between proximate and ultimate causation see Otsuka 2015). Tinbergen went further in distinguishing questions investigating physiological mechanisms from those targeting ontogeny, survival value, and evolutionary history, although he acknowledged that these topics were interrelated, so that his classification of topics was "pragmatic rather than logical" (Tinbergen 1963, p. 426).

This interrelation has not always been well observed. Some theorists, like the behavioral ecologist Robert Jeanne, have relied heavily on these distinctions to interpret Gordon's efforts to investigate interactive processes as opposed to castes as strictly restricted to targeting mechanistic proximate causes as opposed to ultimate ones. Gordon had argued that processes like the interactive effects of individual worker communication networks were being overlooked due to misguided efforts to explain colony behavior in terms of the types of castes in the colony. In 2016 she described her efforts to replace the study of the division of labor among castes with task allocation as an attempt to shift the focus of research towards asking, "How does an ant come to be foraging right now rather than what makes an ant a forager" (Gordon 2016, p. 1102)? She wanted to know what causes led to a particular behavior rather than to a type of ant. Jeanne took her to be hostile towards the possibility that ontogeny could influence behavior:

> The two levels of proximate causation—ontogeny and physiology—are logically as discrete as past and present. … Gordon at best blurs this distinction, and at worst seems not to recognize or accept that ontogenetic causation plays any role at all in determining which individuals perform what tasks. (Jeanne 2016, p. 1112)

Jeanne saw Gordon's research involving task allocation as properly directed towards a mechanism by which interaction between individual workers led to a distinctly immediate proximate cause of behavior. By presenting Gordon's work as directed towards merely proximate explanations, Jeanne could ostensibly insulate Wilson's

evolutionary project from her findings, as they appeared tangential. If Gordon was asking how an ant had come to be acting in the present moment, it was not clear to Jeanne that she was addressing why that behavior might have evolved.

To further support this analysis of Gordon, Jeanne appealed to a 2001 survey of models being developed to explore possible mechanisms governing the division of labor, written by Samuel Beshers and Jennifer Fewell (Jeanne 2016, p. 1110). Beshers and Fewell took Oster and Wilson's approach to be "invaluable for studies of the ecology of division of labor," which addressed adaptive questions, but they argued that, in light of Gordon's research, it was inadequate to explain the physiological mechanisms determining the behavior of individual ants (Beshers and Fewell 2001, p. 415). So rather than see Gordon's findings as applying to colony adaptation, they took them to apply to proximate mechanisms determining individual decisions, screened off from evolutionary questions.

This was a significant reversal of Oster and Wilson's ambitions to develop adaptive accounts for the division of labor in eusocial insect colonies. In 1978, Oster and Wilson had described the mechanisms that led to caste development as being well understood, and presented their own work as opening up a new field of research aimed at finding adaptive explanations. They wrote that:

> By focusing attention on the ecological and evolutionary aspects of caste, as distinct from developmental and physiological processes, we hope to provide the beginnings of a unifying theoretical framework. (Oster and Wilson 1978, p. vii)

They considered the diverse descriptions of physiological and developmental details that had accumulated in the literature on eusocial insects to be subordinate to an overarching explanation of the evolution of castes (Oster and Wilson 1978, p. 21).

But in 2001, Beshers and Fewell described the investigation of mechanistic explanations as a distinct *new* field of inquiry recently being rescued from neglect. While they accepted Oster and Wilson's challenge that "the reconstruction of mass behavior from a knowledge of the behavior of single colony members is the central problem of insect sociology," and Oster and Wilson's authority in regard to adaptive accounts of caste distribution in different ecological conditions, they argued that Oster and Wilson's neglect of the proximate causes of those adaptations had left open a new area for research (Beshers and Fewell 2001, p. 414). This area was being explored by the construction of a variety of simple exploratory models, which they argued all had to simulate effects that fit Gordon's findings. But they insisted that these models were of proximate causes, as opposed to the adaptive optimality models of ecological conditions and caste distribution that had been proposed by Oster and Wilson (Beshers and Fewell 2001, pp. 414–415).

The mechanism for generating behavioral castes that they favored most was the response threshold, which explained overlapping behavioral dispositions between individuals by positing differences in tolerance to provoking stimuli. Response thresholds were proposed as a primary mechanism for colony behavior in the late 1980s, and were considered to be genetically determined at that time (Robinson and Page 1989; Beshers and Fewell 2001, p. 418). But subsequent work in the 1990s has opened up the possibility of considering response thresholds as being set by a variety of genetic, social, and environmental sources, as opposed to being strictly attributed to relatively invariant genetic causes (Beshers and Fewell 2001). These response thresholds provide a means of representing "behavioral" or "physiological" castes that Wilson identified as potentially differentiating behavior systematically even among monomorphic workers (Wilson 1963, p. 357).

In his defense of "division of labor" in 2016, Jeanne relied on Beshers and Fewell's discussion of response thresholds to support his objection to Gordon's proposal. Jeanne took response thresholds to be the best-supported mechanistic account available for individual worker behaviors. Response thresholds could vary even within morphological or age-related castes, so behavioral castes could be acting independently of other types of caste affiliation (Jeanne 2016, p. 1109). Again, Gordon's research question does not preclude the possibility that there was a variety of response thresholds among workers, or that this variety might even be significant enough to delineate types of workers under specific conditions, but Jeanne mistook Gordon to be claiming that all colony members *must* be equally likely to respond to a demand for a particular task (Jeanne 2016, p. 1109).

To come to this erroneous conclusion, Jeanne misread Gordon's term "task allocation" to just mean the interindividual interactions between workers involved in distributed processes. Jeanne relied on Beshers and Fewell's 2001 review of models (Jeanne 2016, p. 1110), which included consideration of Gordon's collaboration with Brian Goodwin and L.E. Trainor (Beshers and Fewell 2001, pp. 425–426, 432–433). In 1992, Gordon worked with them to build an exploratory model based on the assumption that all the workers were exactly the same (Fig. 6). This model simulated colony behavior, and provided more evidence that specialists may not be necessary. But this did not completely bar the possibility that some sort of specialist might contribute to the overall pattern of colony behavior (Gordon et al. 1992, p. 293).

Gordon's research question could accommodate any of these possibilities. The possible answer could also include dynamic networks of workers interacting with each other and their environments, and those workers could be either

Gordon's Research Question:

"What determines the allocation of tasks among individual ants in a colony, producing the colony's pattern of behavior?"

Possible and responsive answers:

A: Morphological differences delineating task groups of workers –

[Wilson would delineate a type of morphological caste]

A: Dynamic interaction networks with **identical** workers

A: Dynamic interaction networks with **specialized or predisposed** workers

A: Other factors….

A: Some combination of these factors interacting

Fig. 6 Gordon's research question does not exclude the possibility that workers are identical or that workers are specialized or predisposed towards tasks, as shown here in bold. The list of possible and responsive answers is abbreviated for space, with other factors referring to the range of castes and dynamic interactions discussed in the text

different or identical. Thus, her modeling assumption involved an exploration of one of the possible answers to her research question. Assuming identical workers was a temporary methodological commitment for this single study (Gordon et al. 1992, p. 293). This was quite different from Wilson's search for castes, which were required in every possible answer to fully explain colony behavior, in his research question logic. By pursuing her research question, Gordon could not assume she knew the answer ahead of time. But she could ask whether the answer might involve identical workers, and then build a model to see if that could be the case. This was an important step in identifying what sort of stimuli were involved in prompting individual behavior, and the order of those steps mattered. In 1999, Gordon explained that, "If we try to figure out how individuals differ before we know what they are responding to, it is all too easy to confound individual differences with changes in external cues" (Gordon 1999, p. 137). Hence, Jeanne mistook a temporary and heuristic model assumption as Gordon's ontological commitment.

With this misreading in hand, Jeanne argued that Gordon's proposal to replace division of labor with task allocation amounted to a call to abandon any research into how differences in response thresholds among workers might develop. Jeanne framed this argument by reviewing the two types of proximate research questions, presenting Gordon as strictly addressing mechanistic accounts of behavior that act in the present moment, such as immediate interindividual interactions (2016, pp. 1109–1111). He mistook her to be rejecting questions such as: "'What sets an individual's likelihood of performing a given role or task within the colony?' and 'How do behavioral differences among individuals arise?'" (2016, p. 1110). Jeanne took Beshers and Fewell to have established that response thresholds were the best answer to these questions, so research should be directed towards finding out how response thresholds are set by a variety of influences, first as the individual enters its adult stage, and then on throughout its life (Jeanne 2016, pp. 1110–1111).

The research question Jeanne was trying to save can be put this way: "Given the evidence for behavioral plasticity, how do colony members develop response thresholds that allow them to allocate tasks among behavioral castes in order to divide labor optimally in a colony?" With the controversial exception of "learning," all of the answers that Jeanne considers are also considered by Gordon, and every possible answer is logically responsive to Gordon's question (Jeanne 2016, pp. 1110–1111).

Replacing "division of labor" with "task allocation" is thus no threat to ontogenetic research. This is vividly evident in a paper published in 2016 that investigated the role of environmental effects on regulating the expression of a foraging gene influencing *task allocation* among red harvester ants (*P. barbatus*). Gordon was the second author on this paper, and no division of labor was discussed (Ingram et al. 2016). But it presents evidence for an interactive effect between a gene associated with foraging behavior, worker physiology, and responses to environmental light exposure. Differences were found over the course of two timescales, one of which involved alterations in gene expression over the course of hours, as a worker engaged in its daily round, and the other over the course of weeks or months, as the

Gordon's Research Question:

"What determines the allocation of tasks among individual ants in a colony, producing the colony's pattern of behavior?"

Possible and responsive answers:

A: Morphological differences delineating task groups of workers

[Wilson delineated a type of morphological caste]

A: Worker age - temporal task group

[Wilson delineated a type of temporal caste]

A: Ontogenetic predisposition

[such as a response threshold - Wilson delineated a physiological caste]

A: Immediate environmental conditions

A: The dynamic interaction network produced by the distribution and number of other workers engaged in tasks in the colony

A: Colony age

A: Combinations and interactions between these factors

Such as **gene x physiology x environment interaction**

Fig. 7 Gordon's research question can be identified as underlying her investigation with Ingram et al. (2016). The question does not exclude the possibility that ontogenetic predispositions or response thresholds are involved in either individual or colony behavior. The evidence they gathered supports the last possible and responsive answer listed here in bold (Ingram et al. 2016)

worker matured (Ingram et al. 2016, pp. 2–5). It was not assumed that workers had to be identical in every respect all the time, and it was found that as they interacted with the dynamic network, they could be in significantly different physiological states, biasing them towards one sort of behavior or another. This is thus an example of ontogenetic research undertaken in the context of a task allocation research question (Fig. 7).

This study was framed explicitly to research task allocation, and found evidence for a complex interaction of causes (Ingram et al. 2016, pp. 5–7). Gordon's term and research question is especially well suited to detect these sorts of interactions, because it is not committed to Wilson's ambition to reconstruct colony behavior from an understanding of individual workers. It is better suited to investigate processes, while Wilson's approach is restricted to focus on the investigation of some type of caste(s), as is evident in their research questions, just as in the "function" question and answers in adaptationism (Lloyd 2015). At the same time, task allocation does not bar the possibility of differences among workers that contribute to the overall pattern of behavior.

Conclusion

In a special issue of *Behavioral Ecology and Sociobiology* targeting contemporary studies of division of labor in 2016, Gordon expressed frustration that the *meaning* of task allocation, as she had introduced it, now appeared to sometimes be assigned to the *term* "division of labor" (Gordon 2016, p. 1102). For example, in his rebuttal of Gordon's proposal to change terms, appearing in that same issue, Jeanne had argued that the division of labor had always only implied "some degree of specialization," where specialization

merely referred to whatever activity an ant happens to be presently engaged in performing (Jeanne 2016, p. 111).

This claim is problematic. Not only does Jeanne co-opt the meaning of Gordon's task allocation, he distorts the history of research into division of labor since Wilson's work in the 1960s and 1970s (Jeanne 2016, pp. 1109–1110). Since then, specialization has alternatively been used to refer to either being predisposed to do a task, or to be better at doing it (Wilson 1953, p. 153; 1963, pp. 356–357; Oster and Wilson 1978, p. 19; Bourke and Franks 1995, p. 401; Beshers and Fewell 2001, p. 415; Dornhaus 2008, p. 2368; Duarte et al. 2012, p. 947; Naug 2016, p. 1113). But the notion that figures like Wilson did not consider specialists to be identifiable as specializing in distinct adaptive behaviors for "sustained periods of time" is simply inaccurate (Oster and Wilson 1978, p. 19). There have been many different ways that castes of individual specialists might be delineated, and those differences provided alternative possibilities for researchers like Wilson who have looked for the right sort needed to reconstruct mass colony behavior (Wilson 1963; Oster and Wilson 1978; Beshers and Fewell 2001). This variety of possible answers does not imply that specialists do not specialize, but it has served to obscure how the research has developed. Given the recent history of confusion over the theoretical implications of Gordon's experimental findings, the history of this debate is not just an issue about semantics or terminological priority. It is about how research questions are formulated, and theoretical possibilities explored. Mistaking the meanings these terms have had makes continued research vulnerable to the same sort of mistakes that task allocation was introduced to correct.

Gordon and Wilson might be easily mistaken as simply overgeneralizing from the extensive work they have done on specific species of ants with dramatically different characteristics (see Winther 2001, p. 269; Yang 2010, p. 535). Wilson's extensive studies of *Pheidole*, a species with extreme morphological variation among workers, may have made the causal influence of some kind of caste on overall colony behavior appear especially salient. *Pogonomyrmex* workers, by contrast, are morphologically uniform, and have been the focus of a great deal of Gordon's work. Wilson and Gordon might then be mistakenly seen as advocating extreme views on an identical spectrum involving the amount of causal influence interactive effects or types of castes might have on colony behavior.

It may be correct that there is a difference of opinion over just how much influence types of ants may have on overall colony behavior, but there is a more serious problem at hand. The spectrum just described presumes that both Wilson and Gordon are willing to consider the full range of possible influences on colony behavior, and that the difference between their views is based on their estimation of the power of the influences involved. What I have shown is that framing the dispute this way fails to capture the bias inherent in Wilson's approach, which does not consider that full spectrum. That failure is a logical consequence of theoretical commitments instantiated in Wilson's terminology. It is built into his research questions, which must first be rejected in order to consider a full range of possibilities.

Jeanne's mistaken interpretation of Gordon's proposal is not just a terminological confusion made in defense of Wilson's research. Jeanne interprets Gordon as claiming that all workers are of a single behavioral caste, that they are all identical, because he is looking for explanations of some sort of division of labor in terms of caste (Jeanne 2016, p. 1109). Because it is obvious that perfectly physiologically identical workers are not occurring in nature, he takes Gordon's proposal to be ridiculous. But Gordon's identical workers were a simplified modeling assumption—a heuristic abstraction (Gordon et al. 1992). She is happy to allow for variation among individuals in actual populations, but has argued that those variations are not the only candidate explanation for observed colony behavior that needs to be considered. Presuming that colony behavior must be explained in terms of the types of agents involved amounts to a research bias (Gordon 2016).

Gordon's research question does not neglect the possibility that there exist some morphological castes, in some species, that have some predisposition to engage in behaviors that are distinct from their morphologically distinct counterparts among workers in a colony. The problem is the assumption that the collective behavior of the colony can be decomposed into sets of those morphological castes. Wilson was happy to acknowledge behavioral plasticity, and he called attention to the idea that there were comparatively few species that had conspicuous morphological castes (Wilson 1971, p. 136; Oster and Wilson 1978, p. vii). But Wilson wanted to explain the overall colony behavior in terms of some kind of caste membership, as he argued clearly with George Oster in *Caste and Ecology in the Social Insects* (1978). There are many meanings of the word "caste" that delineate different types of ants, but the trouble is that overall colony behavior is not always explicable by identifying types. That does not mean that some ants cannot be grouped into types or that those that can do not thereby contribute to the adaptive behavior of the colony. But if all those types were known, the colony behavior might not be explained, because interactive effects can lead to nonadditive behavioral phenomena (Gordon 1988).

What does all this mean for understanding the nature of the methodological objection raised by Lewontin to Wilson's human sociobiology? Wilson had taken Lewontin's concern about biased terms and descriptions as unwarranted. After all, biologists were well acquainted with the theoretical differences between analogies and homologies, and the use of anthropomorphic terms was common, and it did not

appear to Wilson that they posed a real threat to the practice of biology, so long as biologists remembered the technical meanings of the terms in their biological context (Wilson 1978a, b, p. 10). Lewontin expressed concern that Wilson's approach to the study of human sociobiology was politically dangerous, in part due to the way he used descriptive terms, and Wilson took this objection to be merely political (Wilson 1978a, b, 1983; Mayr 1983; Segerstrale 2000, pp. 102–126). Wilson took the accusation of adapationism more seriously, and presented *Caste and Ecology in the Social Insects* as a defense of his approach to the study of optimal social adaptations (Oster and Wilson 1978, p. 23). There he aimed to reconstruct the mass behavior of colonies based on caste proportions, which he had long taken to be the "central problem of insect sociology" (Wilson 1971, p. 227). Gordon's work has changed this central problem. Colony behavior could not reliably be decomposed into caste activities any more than warfare could be decomposed into the hostility of individual soldiers (Lewontin 1976, p. 26). Lewontin's methodological concerns with descriptions and terms were therefore not merely a rhetorical or political attack.

Wilson had proposed an excellent idea when he suggested that ants were a good test case for some of his methods (Oster and Wilson 1978). Human sociobiology was polarizing and the political dimensions were profound distractions from the methodological arguments. The adaptationism that Lewontin and Gould objected to involved a cluster of methodological problems, and not just the neglect of nonadaptive explanations (Lewontin 1976, 1979; Gould and Lewontin 1979). This is evident in Gordon's research, which has identified adaptive social behavior independent of the division of labor among castes, contrary to Wilson's expectations and theorizing (Gordon 1996). The problem of finding an adequate description of a trait cannot be disarmed by appealing to methodological adaptationism, because presuming a trait is adaptive just for the sake of investigation does not address the problem of adequately describing the trait in the first place (cf. Segerstrale 2000, pp. 102–126; Mayr 1983). Wilson's study of the sociobiology of castes in ant colonies was a good test case for some of his methods, even if the test didn't turn out the way he expected.

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