CHAPTER TWENTY-FIVE

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Social Insects and the Individuality Thesis: Cohesion and the Colony as a Selectable Individual

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Social Insects, Cohesion, and the Units-of-Selection Problem

EVOLUTIONARY THEORY IS GENERAL in a way that is often not appreciated (Okasha 2006), partly because of the long-standing focus at the organism and gene levels. In the abstract, however, there is nothing special from an evolutionary perspective about any particular level of biological organization. One concrete problem for researchers is determining which levels are special because of the causal or historical circumstances of evolutionary change. John Maynard Smith captured the issue with characteristic pith in 1988: "Any population of entities with the properties of multiplication (one entity can give rise to many), variation (entities are not all alike, and some kinds are more likely to survive and multiply than others), and heredity (like begets like) will evolve: A major problem for current evolutionary theory is to identify the relevant entities."

Our task in this chapter is to point to a new way to frame this problem as it pertains to social insect colonies and to colony-level selection. We argue below that there are two general superorganism approaches: one focused on similarities between organisms and colonies that has its roots in the developmental and organicist traditions followed by William Morton Wheeler (Wheeler 1911, 1928; Seeley 1995; Moritz and Southwick 1992; Moritz and Fuchs 1998), and one that emphasizes the colony as a unit of selection and has its roots in kin and group selection theory (Wilson and Hölldobler 2005; Reeve and Hölldobler, 2007). The similarity approach is very widely used, but we think it obscures important issues about

evolution. The selection approach does attend to evolutionary subtleties, but it largely ignores development.

Here we offer an alternative conceptualization of colonies in terms of the individuality thesis of Ghiselin (1969, 1974) and Hull (1976, 1978) that brings together the best features of both superorganism approaches while avoiding the shortcomings of each. The individuality thesis says that complex or higher-level biological objects *are* individuals, rather than that they are *like* organisms. While the individuality thesis was originally articulated to address a set of issues around the reality and nature of species, we argue that it applies well to colonies and that it frames an important set of questions about colony-level multiplication, variation, and heredity, thus throwing light on the colony as a unit of selection. Most importantly, it helps reopen a discussion about development at the colony level.

Understanding what colonies are and how they function from an evolutionary perspective turns out to be very similar to understanding species and how they function. We draw out this parallel below to illustrate the individuality thesis in detail, and argue that all real biological taxa are concrete, spatio-temporally located individuals rather than abstract classes or sets, and that the individual, rather than the organism, is the paradigm unit. We also begin to apply the individuality thesis to colonies. In particular, we situate our arguments within an evolutionary framework by sketching a picture of reproduction at the colony level—a *sine qua non* of colony-level selection. In the final section we point to some work that remains in applying the individuality thesis to colonies.

Individuals, Not Superorganisms

The central idea in this chapter is that colonies are individuals. This thesis is worth arguing for two reasons. The first is that it frames the discussion of colony-level selection in a way that can be obscured by thinking of colonies as superorganisms. We think the similarity approach to superorganisms is metaphorical in a manner that leads away from the most interesting questions about social insects because it relies on the brittle notion that colonies and organisms are similar.

The second reason that attention to the individuality thesis is worthwhile is that it frames a more general set of questions about what it means to be an evolutionary unit and reframes disagreements over what it means to be a superorganism within a selectionist approach. As we shall see, the

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selection approach to superorganisms that is being developed by Höll-dobler and colleagues is a shift away from, and an improvement on, the similarity approach and toward an account given in terms of the evolutionary consequences of sociality, but it still has some shortcomings that can be addressed by thinking about colonies as individuals. One important reason the individuality approach is superior is that it connects the selection approach to a developmental account of social insect colonies.

The Similarity Approach to Superorganisms

One problem with the similarity approach to superorganisms is that similarity is a notoriously difficult relation to capture meaningfully (Goodman 1974), for the reason that, as Sterelny and Griffiths (1999) have put it, "similarity without theory is empty." There are any number of similarities (and dissimilarities) between any two biological entities, and the similarity approach to superorganisms gives very little guidance about what the *relevant* similarities are or how to capture them. Put another way, the superorganism metaphor has had the effect of hiding rather than emphasizing the theory that is needed to put flesh on the bones of similarity claims.

This objection can be put more concretely. In their defense of the superorganism metaphor, Wilson and Sober (1989) argue that a superorganism is "a collection of single creatures that together possess the functional organization implicit in the formal definition of an organism." There are two strains to Wilson and Sober's argument. On the one hand, they sometimes speak of superorganisms as being real entities. On the other hand, they sometimes argue that colonies are relevantly *like* organisms because both are functionally organized. We are sympathetic to the former notion but wish to raise some concerns about their reliance on metaphor in the latter. Colonies are not individuals because they are functionally organized, but are functionally organized because they are individuals. Wilson and Sober argue in favor of the superorganism concept partly, at least, to advance their thesis that natural selection operates at multiple levels of biological organization. We are quite sympathetic to this thesis for reasons that will be clear in the next section, but superorganism talk of this sort is not illuminating precisely because it provokes commentators to ask after the closeness of the similarity, rather than directly about the quality of the causal claims being made. Moreover, what counts as similar *enough* varies

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with one's theoretical perspective in a way that renders the matter virtually impossible to settle.

Take, for instance, the objections to Wilson and Sober raised by Mitchell and Page (1992). Mitchell and Page are also proponents of multi-level selection, but argue that Wilson and Sober's defense of the superorganism metaphor "obscures our vision" because there are important respects in which functional organization at the colony level varies across species of social insects and, thus, that colonies are unlike organisms. Again, colonies and organisms are both similar and dissimilar in different respects and to different degrees, and refining the superorganism metaphor has not led researchers to a better understanding of or agreement about selection at the colony level.

We hope to do better. Approaching colonies in terms of individuality allows one to ask what it means for them to participate in relevant evolutionary and ecological processes, rather than what similarities there are (or are not) between colonies and organisms. From our perspective, it is because colonies are individuals that participate in various biological processes that they are relevantly similar to individual organisms and are functionally organized (as opposed to Wilson and Sober, who argue that it is *because* colonies are functionally organized that they are superorganisms). Despite this talk of similarity, however, the individuality approach shifts the discussion substantially. The new emphasis is on the particular causal relations that hold between parts of a whole such that they form a cohesive individual, as well as on what it means for that individual to participate in evolutionary processes.

The Selection Approach to Superorganisms

The selection approach to superorganisms, exemplified in the strain of Wilson and Sober's (1989) argument that takes superorganisms to be real things, and in the work of Hölldobler and collaborators, places participation in evolutionary processes at the fore of defining what a superorganism is. From this approach, to be a superorganism is to be a colony in which within-group competition is nearly nonexistent, while between-group competition is high (Reeve and Hölldobler 2007). This approach is explicitly about natural selection (and implicitly about the causal relations that hold between the organisms in a colony such that they form a "selectable" unit) because in a scenario in which cooperation within groups and

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competition between groups are both pronounced, the case is made that selection is operating at the level of the group.

This approach has the advantage that it puts evolutionary processes in the foreground and is clearly in line with the individuality thesis, but it has the disadvantage that it does not obviously have the resources to address colony-level multiplication, variation, and heredity directly. It also leads to some disagreement about how social a colony must be before it is properly called a superorganism. Should a colony only be called a superorganism when within-group competition is nearly nonexistent as Hölldobler argues, or whenever within-group competition is a less powerful evolutionary force than between-group competition, as E. O. Wilson (1975) apparently argues (Keim 2007)? This disagreement is not necessarily over ontology, but may be usefully recast (and redirected) by placing it in the context of the individuality thesis. As will be seen, this amounts to prioritizing the question of what it means to be a colony, the result of which is to resurrect talk of development and shift the important foci of the debate away from superorganism talk. The advantages of understanding colonies this way can be made clearer by analyzing what it means to say that colonies and other kinds of biological entities are individuals.

Individuality and Cohesion: Two Parallel Cases

The thesis that species are biological individuals has been much discussed and, we think, widely misapplied. Misapplications result in part from thinking that the thesis gives particular advice about what sorts of individuals species are (e.g., Ghiselin 1997) or about what processes drive macroevolution (e.g., Eldredge 1985; Cracraft 1987). As we read it, all the thesis says is that (i) species are defined by ancestry, not by possession of any properties or characters, and (ii) that species are spatio-temporally located biological wholes constituted by parts (as opposed to having members).

What determines whether something is a part of a biological whole are the relations between it and other parts of that whole, as opposed to possession of any particular (set of) property(ies). That is, biological taxa are not sets, classes, or any other kind of abstract entity (at least not as these are traditionally understood). The thesis denies essentialism of the kind decried by Mayr (1959) and others (Cain 1958; Simpson 1961; Hull 1965; see also Winsor 2006), but taken alone, says nothing at all about what par-

ticular relations do or must obtain for parts to be unified into a given biological whole or how cohesive an individual must be in order to be a unit of selection. In other words, the individuality thesis makes a very general ontological cut, and leaves a fair bit of work to be done in specific cases.

Our contention, developed below, is that there are many causal relations by which parts cohere into biological wholes—many cohesion-generating relations (CGRs)—and that the most familiar one is not always the one at work in a given case (Haber and Hamilton 2005; Hamilton and Haber 2006). The individuality thesis says that physically scattered entities, like colonies and species, are no less individuals than are more familiar ones that are bounded by membranes or skin. The cohesion-generating glue that binds the parts into a unified whole is somewhat different with colonies than with species or organisms, but this difference is not ontologically relevant. More importantly, this difference is not visible to natural selection, provided that other conditions are met.

Given this reading of the individuality thesis, its usefulness lies in framing a discussion about multiplication, fitness, variation, and heredity at the colony level, rather than in giving information about how we should understand particular entities or the relationships between their constituent parts. To say that something is an individual is to say something incomplete. One wants more information: What unifies the parts such that they form a single entity? Among the various kinds of relations—gene flow (Mayr 1963; Ehrlich and Raven 1969), phylogeny (Mishler and Theriot 2000; Wheeler and Platnik 2000), shared evolutionary fates (Wiley 1978; Wiley and Mayden 2000), and so on—that generate cohesion, which are salient in particular cases? Under what conditions do particular CGRs break down? In particular cases of CGR disruption, what happens? When and why do new relationships obtain and how do they causally partition the world into parts and wholes? We attempt to orient the reader first by framing answers to these questions for species. We then move on to discuss CGRs for social insects, with a focus on sociality.

Species as Individuals

As biological individuals, species are both made up of biological parts and are themselves parts of larger biological entities (wholes). What these various parts and wholes are is, famously, controversial. Furthermore, it is not enough to simply be composed of biological parts and to be a part of a

larger biological entity. To be a species is to be made up of parts that stand in some appropriate CGR, and to stand in relevant relationships to other species (e.g., phylogenetic relationships). What these relations are is also famously controversial. These controversies are tightly linked to, and often simply map onto, debates over species concepts. So, for example, one theory of what it means for something to be a species is that it is composed of individual organisms that interbreed, and is itself a part of a lineage of populations. Species, unlike (most) individual organisms, are not bound by membranes; instead their parts cohere in other ways.

Were the boundaries of species easily discernable, then debates over the CGRs that are the glue of species may have been more easily resolvable (though membranes hardly settle the matter for organisms). Unfortunately, the beginning and end of a species (both spatially and temporally) rarely presents itself in any obvious manner. The matter is not simply an epistemic one; data alone will not be sufficient to determine the boundaries of a species. Which data are salient depends on the theoretical and conceptual framework in which they are implemented. Researchers working with different species concepts may agree on the data, but disagree over what constitutes a species boundary, or even over which data count as evidence for a that boundary. This situation may be resolved in many ways. One option is to advocate a pluralistic approach to species and species boundaries (Ereshefsky 2001). Another is to argue that a particular species concept is the only or best one. Species also may be more or less cohesive, and this complicates matters. The degree of cohesiveness necessary for a group of organisms to count as a species will be specified by particular species concepts. Again, this is an arena about which there is much controversy, and tracks very closely to the debates over how to delimit the boundaries of a species.

It is important to note the relevance of the individuality thesis in this case. Far from settling the question of which species concept is superior or even the question of whether one ought to be a pluralist or monist about species concepts, the individuality thesis helps to demarcate the contours of the debate. When two researchers advocate different concepts, it is often because of deeper commitments; namely, they disagree about which CGRs are most salient. Take, for instance, Mayr's (2000) criticism of the evolutionary species concept of Wiley and Mayden (2000). Mayr argued that "the capacity for evolving is not the crucial biological criterion of a species; that would be the protection of its gene pool." Mayr's objection,

essentially, is that he understands gene flow to be the most important causal process at the species level, whereas Wiley and Mayden take it that the suite of causal processes that render particular populations unique in their evolutionary trajectories are most important. Here we have a disagreement over species concepts that is driven by differing understandings of which CGRs are most important; that is, the dispute is over what kinds of biological individuals species are.

Colonies as Individuals

Now that we have seen how the individuality thesis applies to species, we can explore in detail what it means for colonies of social insects to be individuals. All by itself, the thesis carries no information about the features of units of selection that have interested Maynard Smith and other theoreticians. That is, the individuality thesis applied to social insects tells us little about colonies that reproduce differentially, vary, and have heritable traits. To fill in these details, it will be necessary to discover what *kind* of biological individuals colonies of social insects are by specifying which CGRs unify them. These details have to be worked out if the case is to be made that social insect colonies are both individuals and units of selection.

Colonies of social insects are individuals in the sense that they, like all other biological individuals, are defined by ancestry and are concrete rather than abstract (i.e., are spatio-temporally located). This line of thought can be fleshed out by anticipating an objection about dissimilarities between colonies and organisms. We take it that the latter are paradigm individuals for most people, and that some will not want to countenance colonies as individuals for the reason that colonies (and species for that matter) are not physically integrated in the same way that organisms are (Barker and Wilson, submitted). Organisms seem to have relatively clear boundaries set by physical membranes that enclose the parts of the organisms. Colonies are not like this. A social insect colony is composed of many discrete parts—the individual insects—which can be spread over space in a way that the parts of organisms generally are not.

This objection confuses what it means to be an individual with what it means to be an organism, and argues against the superorganism metaphor once again on the grounds that colonies are not relevantly like organisms. Not all individuals, however, are organisms (Wilson and Sober 1989). As

Ghiselin (1974) and Hull (1976, 1978) pointed out in their original articulation of the individuality thesis about species, being spatially spread out in a way that most organisms are not is no reason to discount individuality. All sorts of scattered objects are rightly regarded as individuals (e.g., universities, corporations, and solar systems).

Physical integration is just one kind of cohesion that unifies parts into wholes, and it comes in degrees. Sociality is another kind of cohesion (Queller 2000), and it also comes in degrees. Relatedness (Hamilton 1964; Gadau and Laubichler 2006) and functional integration (Wilson and Sober 1989) are other, relevant CGRs for colonies of social insects. Whether or not colonies are rightly countenanced as units of selection depends on whether they participate in causal processes *qua* unified whole rather than only by means of the interactions between their parts. The relevant colony-level causal processes for natural selection at the colony level are multiplication, variation, and the passing on of heritable, fitness-relevant traits. What these processes look like at the colony level is the topic of the next section.

Colonies are certainly *logical* individuals, in that they are constituted by parts; the relevant question is whether they are rightly counted as *biological* individuals. To do this, it is necessary to resolve whether these parts stand in some biologically interesting CGR, whether colonies stand in relevant relations to other colonies, and whether colonies are themselves parts of larger biological wholes. Answering these questions will address whether colonies cohere enough to be "seen" as a selectable object from the "point of view" of natural selection, and whether they cohere enough and in the right way to be selectable. At a minimum, this will mean that colonies multiply, vary, and have heritable traits. Notice that the selection approach focuses on the cohesion that arises from within-group cooperation, allowing the confrontation of problems about how colonies participate in evolutionary processes from a particular theoretical perspective. What happens when we prioritize the ontology of development over any particular CGR is explored below.

Colonies as Selectable Individuals: Multiplication, Reproduction, and Development

Now that we have a clearer understanding of the individuality thesis as it applies to colonies, we can ask what it means for colonies to be the kind of

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individual on which natural selection operates. In other words, if colonies
are to be selectable, it must be the case that colonies reproduce differen-
tially in a way that leads to a fitness-relevant modification of a population of
colonies. Notice that, despite our focus on evolution, this is a substantially
different way of thinking about colonies than what is found in the selection
approach to superorganisms. Our approach prioritizes discussion about
what it means for colonies to reproduce other colonies rather than point-
ing at a particular CGR as *the* relation that marks superorganisms off from
other kinds of biological individuals. Instead, relevant CGR relations fall
out of empirical research and conceptual framing of colony reproduction.

Space considerations do not allow for elaboration of all aspects of
colony-level processes here, so we focus on multiplication/reproduction,
which we take to be the hardest case. In order for colonies to be selectable
individuals, they must reproduce other colonies. Though loose talk of
colony reproduction may be common, here we consider the details of
colony behavior against the background of individuality and a general the-
ory of biological reproduction, and it becomes clear that it is the
colonies—not just their constituent organisms—that reproduce.

In order to make the case that colonies, rather than only organisms, re-
produce, it will be necessary first to have a look at a general account of re-
production. The most highly articulated account that we know of is by
Griesemer (2000), who argued that biological reproduction has two com-
ponents: progeneration and development. Progeneration is a special kind
of multiplication on which material progenerants overlap across genera-
tions. The material overlap requirement is meant to distinguish reproduc-
tion from mere multiplication or copying, and thus to mark off the
biological processes that result in an increase in the number of entities
from other processes that have the same result; that is, there is no repro-
duction at a distance in biology.

With this definition, photocopying is multiplication because it increases
the number of entities of the same kind, but it isn't reproduction, partly
because there is no material overlap. Because reproducers come in various
shapes and sizes, the relevant generation-spanning material will vary by
taxon and level of organization. In our own species, the relevant material is
gametes and the subsequent fertilized egg with its complete diploid com-
plement of genes. In prokaryotic cells that reproduce by binary fission,
various cellular materials are shared between generations. With honey
bees, a new colony is born when a mated foundress and a contingent of

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workers leave their former hive and establish a new colony. In this case, the overlapping material is the individual organisms themselves.

A foundress and a contingent of workers (i.e., a colony propagule) does not, of course, make a colony any more than a gamete by itself constitutes a human being. This brings us to development, the second component of Griesemer's (2000) account of reproduction. Griesemer understood development to be the acquisition of the capacity to reproduce. Reproduction, then, is the progeneration by material overlap of entities or material that have the capacity to develop in such a way that the process is repeated. This way of thinking about reproduction is iterative, since developing into a reproducer is built in, but the account avoids circularity by bottoming out at null development. Not all reproducers need to acquire the capacity to reproduce; it is at least possible that some have this capacity at progeneration.

With this brief sketch in mind, we can proceed to discuss colonies in more detail. The most familiar case of what Michener (1974) calls "colony multiplication" is, perhaps, the swarm behavior of eusocial bees. In swarming, the colony splits fairly abruptly, and a new colony site is located and communicated by forager bees turned scouts. A colony propagule then departs for the new location and establishes a colony. Swarm behavior is interesting in the context of our argument for two reasons. First, it is fairly easy to see that we have a case of material overlap, even if the material is not at the level of organization that we are used to thinking about with respect to reproduction: here the colony is the individual and the overlapping material is the colony propagule that make up the nascent daughter colony. Second, it is also clear that we do not have a case of organism-level reproduction by another name. The foundress will, of course, rear new workers quickly, but this, we suggest, is best understood as part of the development of the new colony. After all, it is not the reproduction of any particular individual that counts as the production of a new colony, but only the coordinated reproduction and development of individual workers that will tell the whole story of the establishment of a new colony. This is a function of what it means to be an individual colony.

Highly eusocial colonies like those in the apid subfamily Apiane are characterized by a high degree of task specialization. The gyne lacks the physical structure for pollen foraging, and thus cannot survive apart from the colony. Similarly, the workers generally do not reproduce (Visscher 1996). The set of tight functional relationships that obtain at the colony

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level are intrinsic features of the individual colony, though notice that these supervene on the extrinsic relational properties (CGRs) that obtain between the parts of that colony (i.e., the foundress and workers). To track individual colony reproduction is to mark the relevant CGRs of the parts of a colony, and to identify and discover the relevant patterns of CGR disruption and formation. The shape and nature of *these* patterns will determine whether colonies are units of evolution or selection.

A new colony cannot, of course, be the source of a second immediate swarm: in *Apis,* about two hundred bees are necessary (Michener 1974). Even if the relevant (non-density dependent) stimuli were present, the incipient colony would have to forage for pollen and nectar stores, scout a new location, and rear a new gyne. Two of these three tasks will usually require the building of comb, and this task also requires a minimum number of bees (Darchen 1957). This is just to say that the incipient colony has the capacity to acquire the capacity to reproduce: incipient colonies have the capacity to build a hive (development) that confers the capacity to be the parent colony for a swarm. This is development at the colony level. In becoming fully functional, the colony acquires the capacity to be the source of a swarm.

It should now be easy to see how to proceed along these lines by way of taking up the problem framed by Maynard Smith (1988): with a plausible account of reproduction at the colony level in place for highly eusocial Hymenopterans, accounts of variation and fitness of colony-level traits will follow without much difficulty given existing work on the evolution of eusocial colonies (e.g., the selection approach account). There will surely be competition for resources among proximate colonies, and the colonies are often more or less isolated reproductively from sister colonies. Indeed, there is already a large body of literature on these topics (Wade 1978; Owen and Harder 1995; Page and Fondrk 1995; Moore, Brodie, and Wolf 1997; Wilson and Dugatkin 1997; Sober and Wilson 1998; Fewell 2003; Tarpy, Gilley, and Seeley 2004). There is another, prior step to understanding selection and heritability, as they may or may not apply to colonies. The need for more conceptual work is illustrated by paying attention to variation in the kinds of sociality—the kinds and degrees of CGRs—among social insects. With eusocial colonies, the reproducer case is relatively easy to make because of the tight functional integration among the various task specialists. But what of colonies that are less social? Does it make sense to think that they are reproducers as well?

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Take, for instance, the extreme opposite case of sleeping clusters, in which a relatively small number of mostly male bees (or wasps) gather overnight. Michener (1974) reported that bees of all families except the Apidae form such clusters, and he further argued that sleeping clusters are not colonies because "the bees . . . in a cluster are not inhabiting a nest, rearing young, and the like." According to Michener, allodapine species—whose organization ranges from solitary to primitively eusocial—do form colonies, but these colonies are often or always founded by a lone female. Because all the young are reared together with care only from the mother, the colony is not social at this stage. Some allodapine species go on to behave cooperatively. For instance, in some species, some of the adult daughters will become workers while the mother becomes (temporarily, at least) a queen.

The point of this look at different organizational strategies is that the account of colony reproduction we gave in terms of highly eusocial species of the Apini is a special case, and that it is unclear where the line should be drawn between colony-level reproduction and organismal reproduction for lesser degrees of sociality. Seeking a threshold on the continuum of sociality that marks the relevant degree for this particular CGR is probably a fool's errand. Whether or not it is relevant that there is material overlap in the case of allodapine bees (the mated foundress leaves one nest to establish another), and that in some cases this new nest will come to house a group that has varying degrees of sociality, will depend in turn on one's concept of a colony. In like manner, whether or not allodapine nest establishment means that we have a new entity that should properly be called a daughter colony established by colony-level reproduction will also depend on one's colony concept. None of this is worrying in an individuality context, as it is expected that individuality comes in degrees (e.g., of physical proximity).

Colony Concepts and Superorganisms

In the last section we sketched an account of colony-level reproduction, and ended up addressing colony concepts. Even where the relevant CGR is clear, there is still the matter of *degree* of cohesion, thus taking us back to disagreements stemming from Hölldobler's concept of superorganism. How much cohesion will we require before we mark something as a unit? How much disruption of this cohesion will we accept before we want to

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mark a unit as having broken into its parts? These two questions require clarity about colony concepts. Notice, however, that they are precisely the questions that systematists ask of species. The cases are parallel because they are doing the same work: they are asking where we might locate the boundaries of scattered individuals and acknowledging that the task is a conceptual one that turns on giving principled reasons for some CGR and for the degree to which that CGR should hold.

The benefit of this approach to colony-level selection is that it makes it possible to understand the two remaining issues related to selection. Accounts of colony-level variation, and colony-level heredity of those variations against a fitness environment, will depend on having an appropriate colony concept. Because there are several relevant CGRs, however, there is no reason at the outset to think that there is a privileged colony concept given in terms of some CGR. Again, this is exactly the case with species.

Given the mishmash of debate about concepts surrounding species, what productive work is the individuality thesis doing? And why is it applicable to thinking about colonies? We have argued that thinking about colonies as individuals will generate the right kinds of questions about colonies, facilitate useful theoretical and conceptual debates about the nature of social insect colonies, and, perhaps most important, provide a powerful explanatory and research framework for how colonies may (or may not) participate in various evolutionary processes.

For example, thinking of colonies as individuals provides new traction for debates over levels of selection. Given that biological individuals are parts of other biological individuals, and are themselves (often) constituted by biological individuals, we should not be surprised to find advocates of individual-level selection arguing that selection may act on individuals simultaneously at multiple levels (Sober and Wilson 1999); or, alternatively, that distinctions between kinds of group selections must be drawn (Damuth and Heisler 1988; Michod 2005; Okasha 2006).

Like species, colonies may be more or less cohesive. This is just to say that social insects, like species and every other kind of biological individual, exhibit a range of kinds and degrees of CGRs. This is why the argument over whether only eusocial colonies are the only true superorganisms seems to us to be wide of the mark: the interesting concerns are not over what constitutes a superorganism, but what kinds of cohesions generate evolutionary individuals. What degree of cohesiveness is necessary for a colony to count as an evolutionary individual is a matter that will not be

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settled by empirical facts alone. Conceptual and theoretical frameworks of being-a-colony are needed to determine which facts are salient; that is, which data are evidence one way or another. Likewise, what will count as colony-level variation or heritability will, in large part, be determined by the colony concept being pressed into service. Sociality and the functional integration that comes with it, clearly is a CGR that will play a central role in any theory of being a colony, but there is a great more conceptual work to be done than most applications of the superorganism concept suggest.

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