Scientific Natural History: Telling the Epics of Nature

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Scientific natural history, which addresses all biological aspects of individual species, one species at a time, then compares many together, is as important to science as any of the umbrella biological disciplines. With most species yet undiscovered and the vast majority of those known yet unstudied, most biological phenomena are probably also unknown and unimagined. Closing this gap calls for a renewed emphasis on the disciplines of the taxonomic -ologies, treating each species as an evolutionary epic, summoning information from all of the umbrella disciplines. We argue from the example of the once-obscure red fire ant, Solenopsis invicta, *whose economic importance made it a model species for research on the superorganism, offering excellent opportunities for addressing many profound questions about superorganism organization, function, development, and ecology. Had scientific natural history been properly emphasized in recent research, theory testing in areas such as competition and kin-based selection would not have led to decades of distraction.*

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By habit and convention, most biologists devote their careers to a single species out of the 2 million known and then only to its contemporary populations. Their choice is influenced by one or the other of two principal rules of biological research: For every problem in biology there exists an organism ideally suited to solve it, and, conversely, for every organism there exists a problem that the organism is ideally suited to solve. Furthermore, only one aspect of the species' biology is typically chosen. Research is conducted in the laboratory or at the blackboard rather than in the natural environment. The knowledge produced is assigned to one or another of the umbrella biological disciplines somewhere along the span from molecular biology to ecology. Such is the essence of biological reductionism, often derided by nonscientists but consistently successful and immensely creative; *Drosophila*, the white mouse, *Escherichia coli*, and flour beetles have, each in its own way, presented us with biological epiphanies.

Outside this conventional framework, there is scientific natural history. This oldest paradigm of research is organized as the taxonomic *logos*—for example, herpetology for reptiles and amphibians, entomology for insects, nematology for roundworms, and so on, studied species by species across the entire landscape of biodiversity. The motivating force is a passionate interest in species and higher taxa studied for their intrinsic importance through observation, pattern detection, and experimentation. The naturalist does not ask what problem in biology his subject might solve. He asks simply what the species can tell him.

The strength of scientific natural history is in its feel for the organism, the fingertip familiarity with not just one aspect but all aspects of its biology. It is strongly empirical, serving no prejudging theoretical master. It asks simply, what does it do? How does it do it? What are the consequences? The product is an abundance of serendipity: The best discoveries are those neither anticipated by any prior knowledge nor prescribed by any theory. This delightful property has been experienced by countless biologists in many disciplines, including our own—sociobiology (e.g., Lindauer 1961, Wilson 1985, Tschinkel 1991, 2011, von Frisch 1994, Seeley 1995). The guiding philosophy of scientific natural history is that every living species is the shining culmination of an evolutionary epic. It is a survivor, whose story unfolded across perhaps thousands of millennia through continuous testing and whose story needs to be told.

From the stories of dozens or hundreds of individual species emerge patterns of nature not predicted by theory. When Charles Darwin began his epic voyage on the HMS *Beagle* in 1831, he did not set out to test the theory of evolution. Although he expected to make collections of animals and plants, his aim was to study geology, using the geographical distribution of organisms to work out the past from the present. Only gradually, as he recognized the patterns established by barnacles and, later, by the birds and reptiles of the Galápagos Islands, did he begin the journey to evolution. Not until early 1837, after he learned that the endemic Galápagos finches had been classified as different species, did he become an evolutionist, and, in 1838, after

18 months of hard work, he devised the theory of natural selection.

The structure of biological and social theory

A deep and time-tested principle of both the biological and the social sciences is that fact and theory should alternate closely. Furthermore, proven fact is paramount. Nature, in the offhand expression, defeats theory. There has, nonetheless, been a tendency to give theory a great deal of license and status in evolutionary biology, ecology, and the social sciences, because these disciplines are the ones that address the most complex of all systems. Scientists working on them are understandably impatient to discover principles that organize at least a part of the chaos of observable phenomena.

Two opposing modes of entry have emerged from attempts to advance the understanding of ultracomplex systems. One is predominantly top down and evidence tested. An attractive and reasonable principle is formulated, then data from the real world are sought to confirm or disconfirm it. The advent of computers, along with the appeal of simplicity, has created a cottage industry of theory and modeling. Because biological and social systems are intricately connected in so many ways, there is a good chance that some amount of covariance exists in any two variables chosen. The weakness of this approach is that, without a thorough empirical background, major factors and alternate explanations may be undetected, a point that Seeley (2010), for example, made eloquently. Pure theory and modeling, however, may not be the major problem. Rather, it is that many practitioners construct poorly conceived or biased hypotheses and poor experimental tests, because they do not have sufficient, detailed empirical knowledge of the natural history of the organism or ecosystem under study. There is therefore a tendency to use theory to pose weakly supported hypotheses (referred to as *chasing theory*), to believe compelling stories, and to ignore or be unaware of alternate hypotheses and explanations. For example, the abundance of one species of ant over others at food baits is commonly and compellingly regarded as competition, but Tschinkel (2006) showed that a detailed knowledge of ant natural history would have suggested several more interesting and nuanced hypotheses having little to do with direct physical conflict. These include microhabitat preferences, thermal preferences, differences in foraging area size, differences in speed and style of food retrieval, circadian activity differences, and preference for different sizes and types of food. Indeed, even individual fire ant colonies have highly idiosyncratic food preferences (Glunn et al. 1981). A similar lack of natural history knowledge also led to the attribution of fire ant ecological dominance to superior competitiveness, whereas closer scrutiny eventually showed that habitat disturbance was the culprit, as we discuss in more detail below. The decades of attention to kinship selection (Abbot et al. 2011) distracted from testing stronger hypotheses based on empirical natural history. Some compelling but incorrect stories are even known to the general public, including sexual cannibalism by female mantids (Berenbaum 2000) and the honey badger–honeyguide story (Dean et al. 1990).

We believe that far the better approach to any complex system is the stepwise buildup of knowledge by natural history, scientific in nature but only tentatively guided by preexisting broad theoretical concepts. The most enduring knowledge, of both fact and theory, is thereby bottom up and evidence based, with models built piece by piece from well-documented phenomena and cause-and-effect explanations, tested and linked together to generate increasingly broad principles and, eventually, overarching theories. The result will often be radically different from that obtained by top-down, empirically tested theory. History provides examples that range from the cell theory to the chromosome theory and the theory of evolution, itself. Life history theory, experimental ecology, and comparative studies are examples of opportunities for building from the bottom up. In our view, empirical evidence is the horse that pulls the cart of theory through testing, and the three move along the road to understanding. When theory is the force that pushes testing, it is likely that the whole assembly will go off the road. The human imagination is always far less fertile than biological innovation.

An opportunity exploited: The red fire ant, *Solenopsis invicta*

Such was the vision, perhaps born in naiveté, by which the present two authors separately began to discover everything we could about the red fire ant, *Solenopsis invicta*. In 1942, EOW, as a 13-year-old working on a Boy Scout project in the city of Mobile, Alabama, found the first colony of this soon-to-be-famous pest in the United States. Six years later, while he was a senior at the University of Alabama, he was hired by the state to study the spread of the species as it moved out from its disembarkation at the Mobile docks. And later, at Harvard University, EOW used the species in studies of chemical communication, revealing the chemical signals that regulate several functions.

WRT, arriving as a newly appointed assistant professor at Florida State University, in 1970, began the first comprehensive studies with students and collaborators on many aspects of fire ant biology, including pheromones, food traffic, colony founding, territoriality, foraging, colony development, life cycles, longevity, and more, culminating in his overall synthesis *The Fire Ants* (Tschinkel 2006). In the meantime, *S. invicta* had become a favored species for studying ant biology by many biologists in North America and Europe.

Prior to its notoriety as a global insect pest, *S. invicta*, like over 95% of the more than 14,000 known ant species, existed in almost complete obscurity, a minor species even in its South American homeland. It turned out that *S. invicta* is a member of an adaptively radiated group of at least nine species (the *saevissima complex*) of South American fire ants with native ranges mostly in the subtropical and warm temperate regions of the continent (Pitts et al. 2005). *Solenopsis*

invicta, itself, is native to the very heart of South America, a broad area from southern Amazonia to northern Argentina. It is believed to have been carried inadvertently to Mobile in the 1930s, hidden in some unknown cargo. Its precise point of origin was probably northern Argentina (Ross and Trager 1990, Trager 1991, Pitts et al. 2005, Ascunce et al. 2011). Aided by human commerce and the ability of the newly mated winged queen to fly distances up to 8 kilometers, the ant spread rapidly throughout most of the southeastern United States, skipping across the West Indies to Trinidad (Davis et al. 2001, Wetterer and Snelling 2006); across the United States to California; and on to Taiwan, China, and Australia (Ascunce et al. 2011). Its continuing journey is that of a classic synanthropous species, its well-being aided by the humans who hate it.

Its status as a potential worldwide insect pest has drawn scrutiny from a great many researchers in multiple biological disciplines. By the time of the Tschinkel (2006) synthesis, *S. invicta* had joined the honeybee to become a model species for the study of advanced social behavior and the organization of the superorganism (Tschinkel 2006, Hölldobler and Wilson 2009). The approach taken by most of its investigators has been that of scientific natural history. The reward has been discoveries spanning fields as disparate as ecology, physiology, molecular genetics, and human history. We believe, nonetheless, that the attention given the red fire ant is deserved by all species, regardless of their economic, medical, or otherwise immediately human-related importance. Each one has the potential to be a model species across the increasingly divided and subdivided domain of umbrella biological disciplines. Each one has stories to tell, stories that we cannot necessarily imagine until study has revealed them.

The epic of the fire ant

Who is this once obscure South American ant that burst so suddenly and spectacularly onto our scene? *Solenopsis invicta* is an extreme superorganism in which workers lack ovaries, which results in their reproductive future being synonymous with that of the colony. Its colonies are large and can exist in both single-queen and multiple-queen social forms, which invites study of the genetic, developmental, ecological, and evolutionary aspects of queen number and social form. *Monogyne* (single-queen) fire ant populations exist as a dense mosaic of territories, neighbor competing relentlessly with neighbor through a mechanism only dimly understood at the present.

As the subject of scientific natural history, fire ants have been a magic well, as von Frisch (1994) said of his beloved honeybee: The more you draw from it, the more there is to draw. And much remains to be drawn. Fire ants seem especially well suited for answering seven larger (groups of) questions about superorganisms:

(1) How is the superorganism integrated, regulated, and self-organized? In the absence of central control, all functions of the superorganism emerge from the self-organization of dozens to millions of competent colony members. Food

is obtained and distributed appropriately to all colony members. Territory is gained and defended, a nest of appropriate size and architecture is excavated or constructed, brood are moved within the nest to track a favorable microclimate, workers move to the appropriate region of the nest or territory as their jobs change with age, investment in sexuals versus workers is seasonally adjusted, and mating flights are properly timed and organized. The outlines of many of these and other superorganismic processes are visible (Tschinkel 2006) and suggest a rich field for the student of self-organization, complexity, and collective outcomes.

(2) What reproductive options are open to the superorganism? Claustral colony founding is widespread among ants. After a nuptial flight, newly mated queens seal themselves into a chamber to produce the first workers from large metabolic reserves. Although this mode greatly predominates in *S. invicta*, colonies also produce low-reserve female sexuals designed to found new colonies by parasitizing the labor of unrelated orphaned fire ant colonies (Tschinkel 1998; also see question 6 below). In the North American–native fire ant *Solenopsis geminata*, this has resulted in two sizes of female sexuals, each specialized for a different mode of colony founding, one-third parasitic, two-thirds claustral, and each produced in a different season. Within-species social parasitism is understandably hard to detect, because the host and parasite queens look alike. It is possible—indeed, highly likely—that many ant species pursue this mode of colony founding. In stable, saturated habitat in which the success of independent founding is low, how could they not?

In the multiple-queen social form, newly mated queens are adopted back into their natal nests that subsequently fission, with a portion of the queens residing in each daughter nest (also see question 7 below). Much as vegetative reproduction in plants occurs through heavy investment in somatic tissue, *polygyne* (multiple-queen) reproduction by fission depends on heavy investment in workers. Are the costs of reproduction different in the polygyne and monogyne forms? For that matter, what should be included in the cost of reproduction in a superorganism? Sexuals of course, but how should the cost of workers be assigned between growth and reproduction? The existence of three different options for reproduction in a single species of superorganism—two pursued within a single colony—invites questions of why, where, when, and under what conditions each option occurs. What ecological conditions favor each mode? What internal mechanisms switch the superorganism among the options? What costs and benefits accrue from each, and how are they balanced against one another?

(3) How does the superorganism develop (or self-construct) from a single individual? The mature fire ant colony is no more a magnified newly founded colony than an adult human is a magnified baby (Tschinkel 1993, 2006). From a solitary founding queen (or a group of queens) sealed in a subterranean chamber, the colony grows to a teeming mass of 250,000 workers. The average worker size increases fourfold, whereas the birth rate declines greatly. As seasonal

colony size variation more than doubles, spring alate production increases sharply, the specific metabolic rate drops greatly, and the labor mix shifts away from brood tending to foraging (Tschinkel 2006). Outside the nest, territory size balloons. The ease with which it rears and grows through five orders of magnitude makes *S. invicta* an excellent choice for untangling the ontogenetic mechanisms driving these changes. The data obtained will extend the principles of development beyond the unitary organism, and they will help identify the presocial origins from which these mechanisms evolved. Current research suggests that superorganisms are constructed through rather modest modification of preexisting rules and processes (Hunt and Amdam 2005, Amdam et al. 2006, Hunt 2007).

(4) How do superorganisms interact in an ecological context? In optimal habitat, fire ant territories blanket the ground like a tile mosaic. This array provides an opportunity to address the mechanisms of territory formation and competition and habitat use, uncomplicated by high levels of interspecific interactions. Intraspecific interaction among social insects remains mysterious and has received much less attention than has interspecific competition, despite evidence that intraspecific competition is the more powerful force shaping populations (King and Tschinkel 2006, Tschinkel 2006). Moreover, colonies can be transplanted in controlled experiments to tease apart community formation and ecological interactions (King and Tschinkel 2008). Such experiments need not be limited to ants but can include all co-occurring organisms.

(5) For each superorganism, there exists an optimal environment in which it prospers best. For fire ants, this is ecologically disturbed habitat, such as roadsides, pastures, and lawns (King and Tschinkel 2006, 2008). What are the critical life history and physiological characteristics that match the fire ant to this environment, and what are the habitat characteristics to which they are matched? These questions have not been clearly answered for any ant species to date. Because of the obvious and strong habitat preferences of *S. invicta*, the ant seems especially well suited to answer such questions—questions that are linked to its status as a recent addition to the company of cosmopolitan tramp ant species, transported around the globe by humans.

During the 1940s, as *S. invicta* first spread out from Mobile, it reached high densities in pastures and on grassy road strips, perhaps fueled by homopteran honeydew (Wilson and Eads 1949, Wilder et al. 2011). In a world in which every year brings news of a newly established tramp ant in some part of the world, *S. invicta* offers a ready opportunity to ask, *What makes a tramp, and what habitats do they exploit?*

(6) Yang (2007) argued that superorganisms offer an opportunity to study how natural selection produces local adaptation, and *S. invicta* could allow us to see this process in progress. *Solenopsis invicta* is a creature of early succession habitat. Newly mated queens start new colonies in such habitat without the aid of workers (independent founding). Their success is greatly reduced when mature fire ant colonies are present. However, *S. invicta* is also capable of starting new colonies through parasitizing the labor of a mature colony whose queen has died (*dependent or socially parasitic founding*, a process very different from independent founding; McInnes and Tschinkel 1995, Tschinkel 1996). Orphaned colonies arise mostly in aging or stable populations and disappear as normal ecological succession proceeds and the habitat becomes unfavorable for fire ants. *Solenopsis invicta* evolved in a situation in which founding opportunity depended mostly on newly disturbed, ephemeral habitat free of fire ants, which led to the strong emphasis on independent founding (more than 97% of female alates are designed to found independently). However, it now finds itself in a land where humans maintain its habitat in an early stage of succession and where fire ants exist as stable populations over long periods. This circumstance greatly reduces the success of independent founding and vastly increases the opportunities for socially parasitic (dependent) founding resulting from the deaths of aging colony queens. The question follows, is the naturalized population of *S. invicta* shifting emphasis from independent founding to parasitic founding? And if so, how? Here is an opportunity to see the evolution of a superorganism in progress.

(7) Several species of *Solenopsis* fire ants occur in two social forms: monogyne or polygyne. This apparently simple difference has profound functional and ecological consequences. More remarkable is that the social form results from differences in a single gene: Homozygotes for one allele are monogyne, whereas heterozygotes and homozygotes for the other allele are polygyne, accepting many queens (Ross et al. 2003). The genes appear, among other things, to code for an odor-binding protein, which suggests that the tolerance of multiple queens may operate through an olfactory route. Interestingly, social form determination by this gene seems not to be common to all fire ants, although other species (e.g., *S. geminata*) may also be polygyne.

Many ant species occur in both monogyne and polygyne social form. *Solenopsis invicta* invites us to ask the following questions: Why are there two social forms, and why does one not completely displace the other? What advantage does each form bring, and under what conditions do these advantages appear? How do the two forms relate to each other, for relate they must, because they typically occur in mixed populations?

In summary, these are a few of some of the most obviously important questions in sociobiology that can be answered through continuing detailed study of the single model species *S. invicta*. Similarly detailed studies of multiple social species can begin to reveal unifying principles of their construction, variation, evolution, and operation.

Nature trumps *just* so stories

Nature provides countless breathtaking and amazing stories, but so many more are waiting to be told and, perhaps more importantly, recast in a different light because of new information. In cases such as the *S. invicta* invasion, new

insights are needed from natural history research, during which comparisons are made between native and alien species. A case in point is the widespread belief, held for decades, that the fire ants have superior competitive ability and, as a result, displace and even threaten with extinction native species of ants. The high local densities of *S. invicta* appeared to exemplify a widely accepted principle that invasive organisms succeed and dominate ecologically similar native ones because of their competitiveness. They are empowered, in part, because of the absence of their own natural enemies. However, these beliefs were based solely on negative correlations between fire ants and native ants. When fire ant colonies were extirpated from among other native and exotic species in plots of northern Florida, no changes occurred among the other ant species with which they had shared the habitat (King and Tschinkel 2006, 2008). The decline of native ants was the result of habitat disturbance, not fire ants. The fire ants were merely capitalizing on what they do best: exploiting disturbed habitat.

The result is therefore contrary to traditional assumptions, drawn largely from an as yet unproven fact for ant communities: that food (e.g., insect prey, homopteran-derived honeydew) or space is limiting and the species compete exploitatively for these resources. To date, only competition for nesting sites among acorn- and twig-nesting species and ant–plant mutualist species has been proven to be a limiting resource (Herbers 1986, Powell et al. 2011), and the competition occurs primarily among founding queens. The red fire ant is evidently not a superior competitor that suppresses native ants but an invader that flourishes in degraded habitats. Other factors, such as prior disturbance and limited recruitment; settlement-habitat choices made by dispersing, newly mated queens; and the success of colony founding in the chosen habitats, should be searched for the primary limiting factors of both the fire ants and the native ant species.

The case of the fire ant illustrates the principle that poorly applied or constructed theory inclines us to the *availability heuristic* fallacy—the tendency to accept an explanation simply because one can easily think of examples that fit the theory. For example, if theory offers only two possible explanations, under the availability heuristic, if one of these is in concordance with observations, it would be applied, in spite of the possible existence of any number of other explanations not included in the theory. Compelling stories, in which an outcome "just has to be so because it fits so well," also lead to widespread acceptance of explanations that may not actually be true or that, at least, may not be the primary explanation. Emphasis should be on those phenotypes prescribing, creating, or affecting social interactions, because they are empirically discovered to be the basis of social evolution. To understand the evolutionary dynamics of eusociality requires tracking the history of selection occurring at both the level of individual colony members and the level of competing groups. Such tracking would reveal how selection acts on the interplay of colony-level and individual-level phenotypes to maintain and facilitate eusociality. How should we assign controlling or subsidiary roles to phenotypes or combinations of phenotypes in a unifying theory of eusociality? A review of a few selected phenotypes will reveal that we know almost nothing for the great majority of social insect species (Tschinkel 1991, 2011), phenotypes that include colony size, worker sterility or fertility, worker size and size variation, queen number, queen size, queen longevity, queen fertility, division of labor patterns, fat and protein storage, founding-queen habitat choices, colony-founding patterns, habitat range, alate investments, seasonality, physical tolerances, and many more. How are we to construct meaningful theories of insect sociality when we know so little about its manifestations? How will we ever discover these manifestations if we get so easily distracted by trendy theories?

To put the matter as succinctly as possible, the best scientific natural history is an objective history of a species tracked over the long term through evolutionary time by biologists who never tire of prying into the secrets of their chosen taxon. The story of any species chosen at random is an epic, filled with mysteries and surprises that will engage biologists for generations to come. Each story will almost certainly surpass the mundane hypotheses and theories proposed by the humans who study them. Only when enough such stories are pieced together will we understand with certainty how superorganisms and other ultracomplex systems have evolved.

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