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SOCIAL BEHAVIOUR AND THE SUPERORGANISM: IMPLICATIONS FOR DISEASE AND STABILITY IN COMPLEX ANIMAL SOCIETIES AND COLONY COLLAPSE DISORDER IN HONEYBEES

Niccolo Caldararo*

Department of Anthropology – San Francisco State University
San Francisco, U.S.A.

Department of Biology – City College of San Francisco
San Francisco, U.S.A.

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ABSTRACT

Sociability, mass response to threat, food production and food sharing and an adaptable communication system are a suite of traits involved in the evolution of complex society in animals. Cycles of interaction characterize members of such societies and those of species in association that can affect disease structure in time and virulence. Colony Collapse Disorder (in North America, Honey Bee Depopulation Syndrome, or HBDS elsewhere) shows similarity to a number of mass behavioural responses in other social animals, especially in ants. A number of questions regarding the cause of CCD continues to make progress in fighting the disease difficult. Here information is provided that may result in an isolation of factors to identify the syndrome of effects that lead to the disease, based on studies of disease avoidance and illness behaviour in other animal species. Most of the work to date to discover a cause has focused on a direct relationship between a pathogen or parasite or environmental condition and the Disorder. Dysfunctional mass behaviour is even seen in humans, as during the Black Plague. Disease avoidance is an important survival tactic for many animals and if the mechanism is modified by a pathogen or toxin unusual outcomes may result. In complex animal societies the opportunity for other forms of disruption of social life are numerous.

KEY WORDS

colony collapse disorder, complex animal societies, disease avoidance, illness and behaviour

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*Corresponding author, η: cald@sfsu.edu; +1 415 405 2536;
Anthropology Department – College of Liberal & Creative Arts, San Francisco State University
1600 Holloway Ave SCI 377, San Francisco CA 94132, U.S.A.

INTRODUCTION

Avoiding disease certainly has value to the individual in escaping pain, suffering and death. It would seem obvious that mechanisms would evolve to enhance the ability of an individual to recognize and avoid contact leading to infection or exposure to infection. Social animals especially display evidence of behaviour that avoid or limit disease and death, as in the grouped behaviour of the water flea Daphnia where grouped animals give off more carbon dioxide than single ones and this extra CO_2 can neutralize some toxic substances in the water [1].

It is clear from animal research in the wild and captivity that behaviour can play a significant role in infection and the spread of disease and the production of mortality [2]. Such behaviour would then have a selective role to play in evolution, as Allee argues [1] concerning Cryptocerus, the wood-eating cockroach. These insects can only feed on wood with the aid of wood-digesting protozoans in their alimentary tract. Transmission of these protozoans can only take place in a social context and Allee proposed that as termites evolved from a common ancestor of cockroach and rely on a flagellate protozoan for wood digestion, the foundations of the social situation can be seen as essential for survival. The balance of pathogens or parasites or the lack of a factor they produce for daily life and mean the end of the social context. The same problem may be involved in CCD, and the abnormal behaviour of the bees not a matter of a new pathogen, but a change in the host-parasite relationship, for example, a lack of a factor a pathogen once produced or a change in its chemical make up.

Hart [3, 4] has documented a variety of behaviours that can be described as sanitary, preventing the spread of infection among animals. Bees engage in a number of behaviours that clean the hive, these can be affected by disease. Sanitary behaviours in humans are often integrated in rites, but new disease avoidance behaviour can become ritualized or codified as threats of serious disease consequences are demonstrated, as in the Black Death and the development of quarantine [5]. Douglas [6] found that in studying the varieties of human religious practice, pollution and danger were often associated with a positive effort to organize the environment.

Threats derived from the 9/11 attacks resulted in mass responses to avoidance of disease by taking medications [7]. The appearance of a new and deadly strain of coronavirus in China and Hong Kong resulted in a variety of mass behaviour including wearing masks, fleeing urban centers and contact with crowds [8] paralleling responses seen during the 1918-1919 flu. Images in the world press, for example, the Financial Times (January 12, 2006), show government workers spraying cars to prevent the spread of bird flu at frontier posts. A deluge of “precautionary 77 measures” are recommended in the early stages of perceived serious pandemics, as the refusal to shake hands with a chicken farmer (Christopher Caldwell, in the Financial Times 15 January 2006), the avoidance of perceived gay waiters during the 1990s all seem familiar from past experience. In 2004 MRSA or drug-resistant Staph (Staphylococcus aureus) was found to be infecting healthy people [9] and by early 2008 was recognized as a new public health problem no longer confined to hospitals [10]. Avoidance of touching others, wearing masks and washing hands has recently been stressed during the H1N1 flu.

A number of scientists have written on the potential transformations of society by war [11] and disease [12]. It is the change in the survivors that matters in death and illness whether their reflection on life produces any change in social institutions or behaviour. Influence of the social environment has significant effects on the individual in other species, for example, in bees. Amos Ives Root noted the fact that hives bees who become infected or ill will leave the hive to die alone, published in his studies of the bee in 1879 as The A B C of Bee Culture.

Whether instinctual or a socially reinforced altruism, this act of a highly social animal is remarkable, especially in the context of the new disease, Colony Collapse Disorder, where the immature nurses of the bee hive have been found to abandon the hive before they are prepared, perhaps in response to a disease agent [13].

Recent research has shown that human population diversity is distributed by the effects of climate, pathogens and habitat diversity [14]. Also, Guegan [15] found that human fertility increases with the diversity and structure of disease types. The human immune system as it shares features such as innate immunity with insects [16] and others with early vertebrates [17], is much older than our species, yet it shows a remarkable degree of diversity which predates our Neolithic population explosion and the transition of humans to large populations living in dense, sedentary groups [18]. Some biologists have proposed theories of the evolution of social systems based on patterns of selection [19-21].

The pattern of selection that would produce complex social animals capable of building structures (humans, bees, ants, perhaps termites), but also produce food (humans, bees and ants) is rare in evolution. The fact that both humans and ants have domesticated both plants and animals for food production is also rare [20]. That humans and bees have developed complex communication systems capable of considerable plasticity is not found in other complex social animals given our present sensitivity in analyzing ant communication [22]. However, communication by food (trophallaxis) is poorly understood and may provide an insight into communication and order in ant species [23]. An interesting parallel in the fossil record concerning the evolution of ant complex society and that of humans is the correlation of the appearance of both during climatic optimums, the ant's origin of fungus-growing coincides with the early Eocene climatic optimum of about 50-55 mya [24] and human food production and domestication appears during the Holocene Climatic Optimum [25, 26].

To avoid catching a disease, many human societies have evolved standardized behaviours [27]. These behaviours, which are, at times, neither prescribed nor sanctioned, may be ritualistic, stereotyped or taken to extremes by individuals [28]. Understanding human responses to disease has many important applications to public health, as well as to the individual. Such a study can help answer questions such as “How does individual behaviour affect the transmission of infectious disease?” While epidemiological study has resulted in techniques to control transmission and to identify patterns of disease transmission, the cross-cultural and historical study of the psychology of disease transmission has seldom been attempted.

Other questions than may be answered include: “How dependent is disease avoidance on culture?” and “What types of intervention can best be assumed to influence behaviour, affect transmission and increase aid to the infected?” The nature of human consciousness and its reactivity, is a major issue in social science research that can be addressed in this inquiry. For while it is logical to assume that avoiding disease might be destructive to social bonds and association, another aspect of this stress could be of a unifying nature – the origins of the structure of the kind of human social behaviour whose root some theorists like Fabrega [29] have argued lies in the mutual aid extended to the sick and injured. He points out [5] that the cultural definitions of the sick role also pattern withdrawal of the person identified as ill as well as avoidance by those defined as well.

It is clear from reports in several cultures, European in the 14th Century [30], the Near East in the 14th [12] and China in the 20th [31, 32] that the plague has had the ability to disrupt society and affect both commerce and religious practices significantly. Mass behaviour is reported with thousands of individuals travelling together over the countryside while in other cases people often fled from disease singly, while cases of aid and organized care are also typical during the Black Plague [30]. The power of this disease parallels some others in history as in the Plague of Athens in the 5th Century B.C.E. [33]. In Egypt Dols' [12] sources for the 14th Century report a substantial disruption in religious practice, but as the data here show a marked distinction with Europe in mass behaviour, there was little fleeing and no mass psychogenic events (MPEs). MPEs are also termed by psychologists epidemic hysteria (EH) and mass psychogenic illness/mass sociogenic illness [34]. This avoids the ends and means determination, for example is participation in a lynch mob an illness, in a charge in the army or a culturally defined chaotic behaviour (Dionysian rite) illness?

It seems that there must be a balance in behavioural response to disease by infection, between immediacy of action to avoid contact versus plasticity to assess danger. Instinct might provide various stimuli as signals or thresholds to response. Certainly cultural patterns can provide some foundation for these polar alternatives, based on embedded coding of ancient experience with disease as Mead has argued [35], and as we have seen with disaster events as in the case of the Andaman Islanders and the recent tsunami [36]. With regard to instinct, hygienic bees versus non-hygienic [37] do not seem to have fared any better in the challenge of Colony Collapse Disorder [38, 39]. Thus a behavioural system to avoid diseased or potentially diseased nest mates does not provide the level of hygiene or isolation necessary in every case of infection. Since pandemic disease is a characteristic of the late period of human adaptation to sedentary behaviour associated with populations dependent on massive food production, distribution and storage as well as increased population density, we might expect we are in the process of adaption to these conditions. Pandemic diseases have evolved in waves as Zinsser argued [40], mainly Black Plague, small pox, cholera, typhoid, flu, polio, AIDS. The last four have become endemic, perhaps with cancer if it can be separated from general ageing disease.

What is curious about CCD in bees is that bees have long been adapted as sedentary, densely populated food producers, why now do we see them susceptible to such a virulent pandemic? Most bees are not social, or live in socially constructed structures [41]. One argument might be that they have become domesticated human subjects and that recently they have been forced into mass production concentration of mobilized pollinators for agribusiness. Although there is no direct evidence linking this last innovation with CCD changes in lifestyle can produce stress and biological responses as disease. On the other hand, there is an analogy in an ant species that may provide a link and since ants are not domesticated animals we might find a clue to CCD and to modern human pandemic diseases not in only pathogens, but in stress patterns.

Even the course of this complexity and domestication is uncertain. Our knowledge of the evolution of complex societies among other animals, for example the insects, shows us that complexity is reversible. Research with various solitary insects has found that reversals from complexity back to solitary behaviour have occurred at least twelve times [42]. The ants, termites and corbiculate bees that are highly social with complex behaviour are from the Cretaceous period and their closely related solitary taxa have long been extinct. Varying degrees of complex social behaviour are found in wasps and Halictid bees and allow for comparative study.

Various philosophers and scientists have put forth proposals where the basis of human solidarity lies in similar scenarios, for example, where social displays are "epidiectic" serving as feedback to adjust or restore the balance between population density and consumable resources [43] through processes of group selection [19] and cooperation [44], others have produced more comprehensive, but elusive explanations, such as forms of social effervescence [45] and mass bonding which is thought to be the foundation of complex society [46]. Nevertheless, even these seem to have parallels in animal societies, as when

Wilson gives examples [20] of behavioural scaling in animal societies where the social organization specific to one species can change dramatically given changes in climate, season, daylight, or other factors. We see this same process in humans as in the case of the Prophet Cults and millenarian movements of Melanesia [47]. What is important to reflect on here is that a typical social organization based on ritual warfare between adjacent groups that was long established was transformed into mass organization based on cooperation to oppose European pressure. Gaius Julius Caesar noted the same phenomenon when he opposed the tribes of Gaul in the first century B.C.E [48].

Speculation on the cause of Colony Collapse Disorder (CCD) in bees has grown considerably in the past few years as the disease has spread in the bee populations and across continents [49, 50]. Characteristics of this disease include the abandonment of colonies and the apparent disorientation and death of individual members. There is some variation in the expression of this disorder and the conditions of its appearance [39]. While it has long been known that members of eusocial bee species cannot survive long without contact with their hive social environment [51], certain definite pathological conditions have been associated with the individual deaths of CCD that differ from separation deaths found under other situations [49, 50].

The broad nature of the process of abandonment and the pattern of individual disorientation and death of the bees in CCD seems quite similar to a disease described as Lomechusamania [51]. This syndrome was unique in the scientific literature of the late 20th century and was found in ant colonies. Chavin described a feature of ant behaviour in a certain context regarding the mutualist beetle from contemporary research including that of Pierre-Paul Grasse and Wassman (see [52]). While Grasse's full report was never made available in English it provides another example of mass behaviour induced in a highly social species, while it parallels the work of Wassman and Forel [53] with Lomechusa strumosa. Like L. strumosa, Dinarda a commensal that also inhabits nests of ants, is a beneficial scavenger of mites that attack the ants. It also eats the dead bodies of ants and nymphs preventing the growth of mold. Lomechusa, unlike Dinarda, has no beneficial effect but by its presence "drugs" the ants with a substance and survives off the food of the ants. Another commenual, Atemeles also feeds off the ants and is tolerated but has no beneficial effect. In fact, there is evidence they and Lomechusa affect the nest production resulting in a type of adult called a pseudogyne, a form of ant that works less in Forel's experiments [52], has a smaller brain and is sterile. The substance Atemeles gives off to placate or stupefy the ants can result in destructive behaviour in some cases, as one reported by Forel [52] where F. fusca nest members licked its body for the exuded substance so furiously they eventually caused wounds and then at times this led to its being eaten. While many act species have structured behaviour that acts to quarantine foreign species, these commensuals have adapted means to overcome this protective behaviour.

Here we can see a process of acceptance derived from defense. In one case Forel [52] describes how an L. strumosa entered the nest of F. rufibarbis and was immediately quarantined in a violent attack by F. rufibarbis who drench it with poison which caused the L. strumosa to respond with gaseous exudations. This exchange seemed to create a context for acceptance as the F. rufibarbis came to eventually start licking the L. strumosa and it became integrated socially. Humans have been using quarantine since it was invented in Venice in the 14th century during the Black Plague. It is often effective, but can cause social disorder and resistance as seen recently during the most recent Ebola epidemic.

A main difference in nest behaviour between ants, termites and bees is that ants and termites often share their nests with commensals [51]. One source describes the relation between the

Lomechusa beetle and ants as “commensal” [51] but it seems to be more parasitic, although another authority does not use this term [54]. The Lomechusa beetle lays its eggs among the ant brood. The Lomechusa grub is fed and can eat the ant brood as well. It utilizes a number of chemical signals to communicate or influence the behaviour of Formica sanquinea [51-53]. If attacked, the beetle displays its trichome hairs which the ant licks with relish. This is a way there is a transfer of substance from the beetle to the ant. Affected ants lose their usual behaviour, neglect the brood and abandon the nest.

Heinze and Walter have reported [55] experimental results that seem to confirm Grasse’s work. Ants exposed to the fungus Metarhizium anisopliae left their colony hours or days before death and away from nestmates. They also observed worker ants dying from other causes than disease leaving the nest. To test for the effects of the fungus on ant behaviour they used CO_2 and the vast majority exposed who survived left the nest before death.

Recently a pathogen, Nosema ceranae, was found to be the causative agent in some European apiaries and treatment of these apiaries to destroy this pathogen arrested the disease [56-58]. While it seems unlikely that this pathogen is responsible for all forms of CCD in all locations as it has been found in many non-CCD colonies [49], it is a welcome development and now study of the etiology of disease and the CCD behavioural consequences can be investigated. Nosema was also found in many CCD colonies in association with invertebrate iridescent virus strains (IIV) [56-58], but there is no explanation of how these pathogens could cause the features of the disease. It is assumed that all bees that do not return to the hive have expired due to the physiological degradation caused by Nosema ceranae, IIV or a combination of them . Investigations of bees found in CCD hives show distinct variation from Nosema ceranae infection or lack of it [50]. However, the spores of Nosema ceranae may have an effect on bees in addition to the pathological degradation, producing also an allergenic effect or behavioural modification. Bailey theorized [59, 60] that fungal infection might increase due to faecal contamination within colonies as it becomes “… greatest by the end of winter when bees have been confined for the longest period and is cleared away in summer in undisturbed colonies by the several generations of nest-cleaning bees that ingest any contamination and void their faeces in flight away from the colony.” Therefore a behavioural change that limited cleaning could increase fungal exposure and lead to levels of infection that would overcome a colony. Leaf-cutting ants have specialized workers who remove waste and corpse from the nest. Heinze and Walter propose [55] that species with smaller colonies can leave a nest easily without contaminating other nest mates, while in larger colonies specialized waste collecting workers function to effectively remove moribund ants from the more complex situations.

OBSERVATIONS AND AVOIDANCE BEHAVIOUR

Recent studies of the bee genome [61] have shown that they have few genes that regulate their immune system and this may be why they are subject to other devastating hive infections. The behaviour where individuals avoid the hive if ill or damaged would also go far to prevent general epidemics. One might argue then that in bees, avoidance behaviour is an important adjunct to immune system response and has acted in tandem with immune system gene selection in the evolution of complex social evolution. This hypothesis would fit with what proposed Loehle [2]. Avoidance surveillance would be particularly important in light of the fact that bees use pheromones to differentiate kin and outsiders. Mass induced behaviour by disease has been considered for over 100 years in humans, especially regarding remarkable examples from the Black Plague of the 14th century C.E. and other forms of stereotyped disease avoidance customs have been noted by several researchers (1951-1961). This is particularly interesting in the context of Cremer & Sixt review [62] of the analogies in the evolution of individual and social immunity. A successful response to infection requires identification of pathogen and an appropriate response at both the level of the individual in a biological immune response and a socially defensive behavioural response. These are both intertwined with the evolution of pathogen genomic variation to elude both responses.

Stimulation of distinct behaviour patterns has been long studied by ethologists. The work of Tinbergen [63] among others established the general principles of the field. The survival of individuals in threatening conditions by stereotyped responses to particular chemical stimuli has become a rigorous field of investigation with improved instrumentation to detect trace residues in the past few decades. For example, the presence of trimethylthiazonline (TMT) a component of fox feces was found to elicit freezing in rats, a prominent behavioural sign of fear [64]. A new discipline has grown up in the past thirty years that has focused its attention on social behaviours influenced by selection for pathogen avoidance [2]. Many animals, especially Hymenoptera expend considerable energy removing foreign objects from their nests, such behaviour could have infection reducing results, and similar sanitary actions have been documented in other animals [2-4, 65, 66]. However, viral interaction of interference with gene expression for hive behaviour could also be a causative factor in CCD, as it has been found that a single gene is centrally involved in hive sociability [61].

However, the fact that infection in CCD can be transmitted by the reuse of equipment from CCD colonies and that irradiation of such equipment can eliminate transmission [49] suggests a specific causation that is similar to Lomechusamania. Seminal studies in the denaturing of proteins by ionizing radiation began with work by Fricke [67] in the 1950s, since it was assumed that a substance is transmitted from the beetle to the ant in Lomechusamania, a similar substance that could induce CCD might be denatured by irradiation.

The production of social barriers to the spread of disease has been noted as a peculiar, but not infrequent aspect of eusocial animals [68, 69]. It has also been noted that behaviour and chemical signals of sick animals can produce stereotyped responses from healthy ones [2]. Three general trends can be identified that are of interest in eusocial animals and CCD: 1. location avoidance due to sensing of chemical signals of pathogens or danger, 2. avoidance of individuals or herds due to signals indicating illness and 3. sensing illness in other conspecifics and in self. Interruption of any of these response bases could explain the etiology of CCD in bees. It would also explain the lack of a uniform set of symptoms and pathological expression of disease state from colony to colony. A stimulus that induced a malfunction in surveillance could produce a general colony avoidance. Recent research in honey bees and discovered a negative feedback signal that can reduce recruitment [70]. Panic in humans is often induced through language such as honeybees communicate with a language that is not only versatile in modifying detail [71] and allows for individual adaptation in learning different languages [72] but is similarly distorted by drugs [73] as in human language we might consider the role of a specific negative feedback pathology.

Location avoidance is common in many insects where pheromones are deposited to mark territory and can elicit aversive or aggressive behaviour, for example in Oecophylla longinoda [74]. Some animals' behaviour is changed in specific ways to suit a parasite's fitness as in fungal infection of millipedes and ants [75, 76]. This is an example of disease diverted behaviour (DDB). Research into specific pathways of DDB has recently focused on a number of mechanisms in infection, for example, inflammation [77] and is referred to as "sickness behaviour" in humans. Heinze and Walter have already shown [55] that this is not the case with their ant behaviour. Many vertebrates are affected in quite similar fashion behaviourally by infection with prion disease. A degradation of normal behaviour takes place resulting in purposeless sequences and wasting [78-80]. Since there are behavioural aspects of bee hygiene, as in the case of nest cleaning differences between strains, such behaviour can have a substantial effect on colony survival [37].

Along this line of investigation, Core et al. have demonstrated [81] that the parasitic phorid fly Apocephalus borealis can induce hive abandonment behaviour in in honey bees. While this cannot explain every example of CCD nor or bee die-offs, it fits the pattern of behaviour modification by infection resulting in avoidance I have described.

I am not suggesting that Lomechusamania (or the Heinze & Walter effect) and CCD/HBDS are the same syndrome, rather that they may proceed from similar pathways of causation. A Lomechusamania/ CCD could be induced by either a parasite as in the case of Nosema or varroa infections or Israeli Acute Paralytic Virus (IAPV) together with some other stress or co-factor as in some human disease conditions [82]. The fact that IAPV seems the best candidate due to time association and presence of disease would argue for IAPV to be the productive agent [49]. Interestingly we find that fungal prions act to induce invader fungus to die in certain cases acting like stress induced apoptosis in cellular death. Usually cascading stimuli are the triggers with no one source as an identified initiator. CCD could therefore be seen as an environmentally induced mass behavioural dysfunction, like Lomechusamania in pattern but taking different temporal form and structure due to different conditions and genetic variation. It is evident that the effect of the environment and genotype interaction can produce significant variation in pathogenicity in host-parasite interaction [83]. One obvious character would be the rhabdomeres of the eye that allow for the bee to “see” polarized light. In experiments conducted by von Frisch [84] blocking of the transmission of polarized light resulted in confusion and random behaviour in the bees so exposed.

Similarities between Lomechusamania and CCD center on the abandonment of the hive or nest by adults, random behaviour of the afflicted individuals, excess brood present relative to adult bees. However, the Lomechusa beetle (Lomechusa strumosa) has developed a mimic behavioural regime that allows it to be fed by the nursery ants of Formica sanquinea (Europe) [54]. Published research on the Lomechusa beetle is quite limited and should be extended to better characterize the relationships between beetle and ant especially how each responds to specific situations, for example, inside the nest in familiar conditions of interaction and outside where potentially hostile contact can occur.

Fruitful research might be directed to specific genetic sequences that might identify similar triggers in ants and bees to substances involved in parasite presence or environmental triggers. Another likely source could be related to the considerable taste and smell abilities of the bee, known now for almost 100 years [84]. Or epigenetic interactions on aspects of sociability, as in the genetic interaction that produces nest cleaning [85, 86]. There are a number of pathways that have been found in other animals to affect epigenetic expression of complex gene interactions [85, 87, 88]. Silencing of expression of DNA methyltransferase Dnmt3 results in changes in developmental outcomes and behavioural status in bees [89].

CONCLUSIONS

Some chemicals have been found to affect the behaviour of vertebrates in uniform ways [90] while epigenetic effects have been implicated in disease differences in human twins [91], epigenetic changes are also associated with aging [92] and the onset of characteristics of senescence could be a pathway to explain CCD in bees along with the production of other disease mimicking states induced in different genomes of bee populations. It is known from experiments von Frisch [93] conducted over half a century ago that under stress bees can change their stage of development and re-develop organs necessary for colony survival, like salivary glands. These are probably influenced by epigenetic pathways and may be susceptible to pathogenic changes.

The accumulation of melanin [59, 60] is associated with aging and has been found in many bees in hives subject to CCD [50]. Epigenetic variations may be spreading through bee populations by several environmental stresses (risk factors). Like AIDS in humans, there may be one underlying causative agent. Melanosis another distinct disease condition [59, 60] has been found in many bees, has have a number of pathogens in like manner to the spectrum of pathogens found in early AIDS patients. Also, as in AIDS in humans, the expression of CCD may be masked by genetic differences in populations, in differences in different behaviours (risk factors) that promote the spread of the agent, and a variety of factors that make bee populations susceptible to infection and disease progression [94]. This scenario seems most likely when we consider the report by Higes et al. [56] and others [57, 58] where a variety of pathogens are found in the two populations studied, but an absence of Israeli acute paralysis virus (IAPV) and low numbers of Varroa, no agricultural pesticides but the presence of acaricides but with infestation by N. ceranae. Treatment with fumagillin resulted in survival of the colonies, absence of CCD symptoms and elimination of N. ceranae. The fact that N ceranae is found in many colonies where CCD has not developed [49] supports the idea of multiple factors including genetics as does the fact that N. ceranae was present in the infected colonies with acaricides reported by Higes et al. [56]. The relation of pesticides in CCD may be indirect but at present is unproven. A Chinese case from Sichuan Province seems in implicate pesticides where bees have been eliminated due to over spraying. However, this may not be related to CCD [95].

Modeling the epidemiology of the cases of disease helped to identify AIDS as a disease complex, characterizing the different factors associated with its different disease states and expression (e.g., slow responders, susceptible gene variants, quasi-species of virus) [94]. CCD may be controlled in a similar effort. It should be kept in mind that this recent phenomenon has taken place in the context of a substantial decline in native wild bees in North America and Europe since the mid 1900s [96].

Whether it is Lomechusamania, CCD or AIDs, it is obvious that the sedentary conditions of complex life for animal societies makes them liable to infectious disease that can induce behavioural correlates. In the evolution of human societies a number of diseases have become severe challenges to complex sedentary life, some of these have abated by genetic change and selection, e.g. the Black Plague, others by human response, like small pox. Human response is paralleled in bees by nest-cleaning varieties. Since there have been some reversals in social complexity in a number of insect species, and temporary ones in human history (e.g. after the Black Plague), it seems likely that disease, and especially epidemic infectious disease would be a likely agency for reversals. Humans would be especially liable to reversals in the past given the reliance on learning and memory and the potential loss of knowledge should elder cohorts of populations be lost in pre-literate groups. It is obvious that bee evolution is continuous, but what is unclear are the possibilities for increased complexity and plasticity in social bees. The implications for human social evolution are obvious as well, what are the prospects of what has been considered “stable” societies in human history given that contemporary capitalism is characterized by continuous destructive evolution [97]. Are bee, ant and termite societies “closed” in the sense that they have reached a limit of complexity given their behavioural capacity or are they representations of stable complexity? Waddington argued [98] that “…types of instability have been built into the epigenetic mechanisms by selection for response to environmental stresses.” Humans seem capable, on the other hand, to respond in a rather Lamarkian fashion to environmental changes but some authors have concluded that corrective responses are unlikely given the recent human past [99]. Other students of world systems research like Chew [100] see a revitalizing role for periodic instability and collapse of human social complexity. Perhaps we are too close to the evolution of complexity to be able to have the proper perspective to assess possible mechanisms of corrective change [101], or as Mead argued [35], we have not produced the necessary social science tools to discern the elements of such change and how to manipulate them. One example is in memory or knowledge transmitted over time. In ants it has long been known that pheromone traits "lead" colony ants to goals, but recent studies have demonstrated that the information encoded in the trails is complex and the trails are now referred to as part of the ant's "external memory" system [102]. Humans also could be said to have such systems in urban road signs, advertisements, or in simple form in some traditional societies in "message sticks" that are set along trails telling later passersby how long ago the individual passed that point, where the moon was, whether there was food or game available, etc.

Recent research in ant societies has perceived these colonies as "superorganisms" and that the nature of the society has significant effects on the longevity of the colony and its individual members. Shik et al., found [103] that small colonies have shorter duration than larger ones and that this is mirrored in the shorter life spans of smaller colonies. Can we view human societies in a similar fashion, does this hint to patterns of survival in village life that determine shorter lives than those in human settings? The concept of the superorganism is not new, Wheeler proposed it in 1911, but the effects of selection in molding the nature of a society's members [104] has significant implications for our understanding of the evolution of complex societies. Social insects, often referred to as "eusocial" and Hou et al. [105] have extended this examination of selection on individuals of colonies and the evolution of complex societies in animals. This idea then results in other possibilities, especially if the selection acts on individuals as it acts on colonies [106]. This creates a central contradiction as we find that in eusocial animals there is a tendency for reduced genetic diversity as single queens produce all colony members at one time in the most successful species. Yet, such a clonal reproduction strategy while it might maximize altruism necessary for eusocial life, reduces the genetic foundations of resistance to disease and pathogen challenge [107].

A number of scientists in the 20th century (e.g. [40]) saw a role for disease in the evolution of society. Perhaps we can learn something about how complex societies adapt to disease by studying the behavioural responses of complex animal societies. It does seem apparent, however, that the fragility of complex societies, whether human or other animal, is related to basic factors of reproduction, density and communication. As Wilson has noted [20] most insect complex societies are highly interrelated and they tend to have short lives in either specific social ordering (as in bees) or in location (as in ants). The solution in these examples is different, in bees the colony may survive a year or two but require a new queen and reconstruction of the hive, often also in a new location. With ants there is often a periodic relocation to a new setting. Still, complexity in social insects is often attributed to their ability to choose the sex of their offspring, the 'haplodiploidy hypothesis.' Thus complex societies are liable to both genetic exhaustion and environmental degradation. In termites, however, instead of having a predominance of one sex, we find equal numbers of both sexes and yet complex society, this 'sex-ratio adjustment' hypothesis' has largely replaced the 'haplodiploidy hypothesis' [108].

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DRUŠTVENO PONAŠANJE I SUPERORGANIZAM: POSLJEDICE NA ZARAZE I STABILNOST KOMPLEKSNIH ŽIVOTINJSKIH DRUŠTAVA I KOLAPS KOLONIJE PČELA

N. Caldararo

Odsjek za antropologiju – Državno sveučilište San Francisco
San Francisco, SAD
Odsjek za biologiju – Gradsko učilište San Francisco
San Francisco, SAD

SAŽETAK

Društvenost, masovni odgovor na prijetnje, proizvodnja i dijeljenje hrane te adaptivni komunikacijski sustav predstavljaju kolekciju svojstava uključenih u evoluciju kompleksnih životinjskih društava. Ciklusi međudjelovanja, koji mogu utjecati na strukturu i podložnost zarazi, karakteristika su članova takvih društava kao i pripadnih vrsta. Poremećaj kolapsa kolonije (naziv korišten u Sjevernoj Americi za pojavu koja se drugdje naziva sindrom depopulacije pčela) sličan je brojnim masovnim ponašanjima drugih društvenih životinja, posebno mrava. Niz pitanja o uzroku poremećaju kolapsa kolonije otežava napredak u borbi protiv zaraza. U ovom radu razmatraju se informacije, koje mogu dovesti do izdvajanja faktora za identifikaciju znakova učinaka koji dovode do zaraze, dobivene na temelju istraživanja ponašanja izbjegavanja zaraze i bolesti kod životinjskih vrsta. Većina dosadašnjih istraživanja uzroka fokusirala se na izravnu vezu između poremećaja s jedne strane i patogena, parazita ili uvjeta okoline s druge strane. Disfunkcionalno masovno ponašanje vidljivo je i kod ljudi, kao tijekom epidemija kuge. Izbjegavanje zaraze značajna je taktika za preživljavanje mnogih životinja. Ako se mehanizmi taktika modificiraju patogenom ili toksinom mogu se javiti neuobičajeni ishodi. U kompleksnim životinjskim društvima brojne su mogućnosti za druge oblike remećenja društvenog života.

KLJUČNE RIJEČI

kolaps kolonije, kompleksna životinjska društva, izbjegavanje zaraze, bolest i ponašanje