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Social Processes and Disease in Nonhuman Primates: Introduction to the Special Section

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Abstract

Most nonhuman primate species are remarkably social, but their social nature presents many challenges, including increased opportunities for pathogen transmission and development of disease (both physical and psychological). An interdisciplinary symposium was convened at the 2010 annual meeting of the American Society of Primatologists on the topic of social processes and disease in nonhuman primates, and four articles from that session, as well as a fifth that was separately solicited, appear in this special section. The articles reflect a variety of disciplines and perspectives that highlight the many ways that social processes can impact disease processes (and vice versa) in this highly social taxon. This is an increasingly active area of research interest as a consequence of technological developments and the availability of long-term field data. The continuing loss of primate habitat in the wild, climate change, and the need to manage high densities of primates in captivity, however, all add urgency to our need to better understand the bidirectional relationship between social factors and disease processes.

Keywords

pathogen transmission; captive management; parasite ecology; depression; interspecies transmission; emerging infectious disease

Nonhuman primates are remarkably social—most species live and forage in social groups that contain multiple adults, that comprise animals of multiple ages and both sexes, and that persist year-round [Kappeler & van Schaik, 2002]. Contrast this pattern with the typical mammalian pattern of solitary living, with the most persisting social unit being a female with her immature offspring. Exactly why nonhuman primates are so social, and how they became so, is still the subject of debate [Shultz, et al., 2011; Thierry, 2008]. What role did the distribution of food resources play? How did diurnality, terrestriality, and predation pressure factor into the evolution of sociality? And how did the various patterns of sociality found in nonhuman primates today emerge through evolutionary time [e.g., Di Fiore and Rendall, 1994]?

Regardless of why primates evolved to be the social creatures that they are, the fact of their sociality is not without its problems. Many researchers have focused on potential costs of feeding and mate competition. Beyond this, however, is a (still) relatively unstudied cost of

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social life—increased opportunity for disease transmission. As Claud Bramblett wrote in his 1976 textbook (p. 249): “... diseases caused by parasitism or pathogenic microorganisms constitute one of the major problems confronting living primates. These predators undoubtedly have influenced both the behavior and social organization of primates.” Two years earlier, Richard Alexander [1974] noted more broadly that while increased disease transmission was a universal detriment to social living, once group living occurred, behavior would evolve to “reduce” the likelihood of disease and parasite transmission. Alexander’s idea was greatly elaborated in another article from 1976, entitled “Pathogens and the evolution of primate sociality,” written by W.J. Freeland.

Freeland’s article [1976] was filled with thought-provoking ideas and hypotheses. For example, he noted that one of the defining characteristics of primate groups is their stable membership and generally low rates of interaction with members of other groups. Because there must be transfer between groups to avoid inbreeding, however, some immigration is necessary. Freeland argued that animals should be selective about who they let into a group, because an outsider might possess a different set of pathogens than would the in-group members, and this could put the health of the residents at risk. One way that residents can identify which potential immigrants are not diseased is to make the process of immigration a gradual one; because for the immigrant this is likely to be a stressful process, any latent pathogens may be more likely to become obvious to the residents, who might then decide to reject the potential immigrant. Freeland did the best he could to muster evidence for his ideas, but of course, in the mid 1970s, there were simply too few data available that were pertinent—while disease had been noted at a number of field sites (and there was the intriguing suggestion that yellow fever may have been a contributor to a change from a multimale to a unimale social organization in howler monkeys [Collias & Southwick, 1952]), there was generally very little parasite analysis performed, and even the process of immigration was not well-described. Nevertheless, discovery of this article as a graduate student a couple of years after its publication was significant for me personally. Not only did it cause me to think about primate social evolution differently (despite the thin database of evidence), it was my very first introduction to the idea that social stress could have an impact on a disease process, a topic that has been a major focus of my own work [e.g., Capitanio & Lerche, 1991; Capitanio et al., 1998].

The social nature of primates has implications for disease processes in a variety of contexts. First, the year-round associations between individuals result in the establishment and maintenance of social relationships that possess particular qualities. One quality is that of social power, and this is often manifested in the establishment of dominance hierarchies, which can provide stability and predictability in relationships [Bernstein, 1981]. However, this aspect of social relationships carries with it some costs—attainment of rank can be stressful, and failure to attain high rank can potentially lead to chronic stress [Abbott et al., 2003]. Social relationships can also be disrupted by separations or death. And, for some individuals, there may be a mismatch between the kinds of relationships they have and the kinds of relationships they may prefer—some animals may experience something like loneliness [Hawkley & Cacioppo, 2010]. All of these situations derive from primates’ social nature, and can increase risk for disease, both physical and psychological [Capitanio, 2011].

Another context in which primates' social nature is important is the captive one. Animals are often kept in relatively high densities in primate facilities, and this higher density could facilitate the spread of diseases. Primates are also housed in social configurations as much as possible and understanding how these configurations influence disease dynamics is important, inasmuch as movement of animals and human caretakers could lead to a colony-wide spread of harmful pathogens. In addition, some primates that are kept in captivity possess pathogens that either pose serious health risks to human caretakers, or could potentially compromise research [Desrosiers, 1997; d'Offay et al., 2007]. During the late 1980s, this led to the development of specific pathogen-free (SPF) colonies of rhesus monkeys in the United States [Desrosiers, 1997]. And here was the conundrum: Because these pathogens are typically transmitted among the animals themselves via exchange of body fluids during social interaction (sex, aggression, etc.), the "obvious" solution of keeping animals isolated from each other presented serious welfare concerns. How does one raise monkeys that are well socialized, but at the same time are free of endemic pathogens that get transmitted during certain kinds of normal social behavior?

Another human-associated, disease-related context applies to animals in the wild. While members of most primate species live their day-to-day lives within a social context with conspecifics and may pass pathogens between them, they also live within a broader, interspecific social context that can also involve pathogen transmission. This includes animals that are pets, bushmeat, crop raiders, or brought into close contact with humans as a result of habitat destruction. Domesticated animals, such as dogs or cattle, can also serve as bridge species between humans and wild primates. The devastation that can result from interspecific transmission of pathogens is evidenced in the AIDS pandemic. The World Health Organization estimates that, as of the end of 2009, nearly 30 million people have died of AIDS, and that 33 million people are currently living with HIV infection. The AIDS pandemic has resulted in more than 16 million orphans worldwide, and there are countries in Africa where more than one out of every five adults is HIV positive [UNAIDS, 2010]. By now, there is little doubt that the virus that causes AIDS originated in nonhuman primates [Hahn et al., 2000; Marx et al., 2004] who, themselves, are largely unaffected by it [but see Rudicell et al., 2010].

AN INTERDISCIPLINARY SYMPOSIUM

In 2008, the American Society of Primatologists began a tradition of holding an interdisciplinary symposium at its annual meeting, and in 2010, I organized the symposium around the theme of "Social Processes and Disease in Nonhuman Primates." My goal was to bring together prominent scientists from a variety of disciplines and perspectives to highlight the many ways that social processes can impact disease processes (and vice versa) in this highly social taxon. As with previous interdisciplinary symposia, the session began with a major address by a featured speaker after which four scientists presented research from their own perspectives. Also in keeping with tradition, the participants were asked to write articles (which would be peer-reviewed) for inclusion in a special issue of the Society's journal, the *American Journal of Primatology*. Five articles (one of which was not based on a symposium presentation, but was separately solicited) follow, each of which bears on the issue of Social Processes and Disease.

Charles Nunn was our featured speaker and leads off our special issue. Nunn was the senior author of a major integrative book entitled “Infectious diseases in primates: Behavior, ecology and evolution” [Nunn & Altizer, 2006]. This book provided a state-of-the art review in this area (including discussion of issues originally raised by Freeland) and pointed out a variety of significant gaps in our knowledge. Nunn’s [2012] contribution brings us up to date on the research program he began in 1999 in primate disease ecology. His work is strongly comparative, and most recently has been a mix of modeling and empirical work. Importantly, he has developed a truly unique resource, the Global Mammal Parasite Database [Nunn & Altizer, 2005], which is an ongoing project that includes information on host-parasite relationships for nonhuman primates as well as for other mammalian taxa. The database, which is available at <http://www.mammalparasites.org>, permits others to test relevant hypotheses as well. In the present article, Nunn [2012] illustrates the power of his integrative approach by reviewing two examples and synthesizing these findings with previous comparative research on primate parasites. Building upon his previous empirical work demonstrating that parasite richness covaries with ranging intensity, he develops an agent-based model to answer some new questions about which mechanisms might explain that relationship. Based on this model, behavioral traits, such as ranging intensity, were found to have effects that are similar in magnitude to many standard epidemiological parameters. Nunn’s second example looks at why the relationship that one might expect between group size and disease risk (for example, larger groups should create more opportunities for parasite transmission) often is not found. Again, using an agent-based model, he shows that group sub-structure can have strong effects on outbreak size, and his empirical findings show that larger groups tend to have a sub-group structure that reduces parasite transmission. Nunn’s [2012] article makes a strong case for combining theoretical modeling with solid empirical research to address questions in primate disease ecology.

The first author on the second article, Colin Chapman, was a co-editor (with Michael Huffman) of the second major book in primate parasite ecology, titled “Primate parasite ecology: The dynamics and study of host–parasite relationships” [Huffman & Chapman, 2009]. The present contribution [Chapman et al., 2012] is an unusual empirical article, in that it reports on a study of parasite prevalence in the same species and in the same location that was studied by Freeland in the 1970s. Freeland [1979] studied multiple groups of several species of nonhuman primates in Kibale National Park, and found that, for each group, members were either all uninfected or all infected with specific protozoan parasite species. This led him to suggest that, because social interaction within groups was high but interaction between groups was low, individual groups could be considered “biological islands.” Using the same location, studying the same species, and employing the same methods, Chapman and colleagues found that their data did not support Freeland’s [1979] results. Does this mean that the biological island hypothesis is incorrect? Fortunately, both Freeland and Chapman worked in an area, Kibale, that had been managed since 1932, and there is good long-term environmental and census data demonstrating differences between the Kibale forest of the early 1970s when Freeland did his work, and the forest 35 years later. While it’s unclear whether these changes could explain all of the differences between the two studies, the article does show the importance of having long-term data from field

sites, and the value of continuing to test hypotheses in world whose climate and habitats are changing in major ways.

The third article moves the study of social processes and disease into a decidedly applied direction. Steven Schapiro is the Section Chief for Behavioral Care and Enrichment at the University of Texas M.D. Anderson Cancer Center primate colony in Bastrop, Texas. Schapiro's more than two decades of experience at this colony encompasses the period during which there has been a desire to derive SPF colonies of rhesus macaques. Schapiro & Bernacky [2012] are explicit that captive management of nonhuman primate colonies typically involves goals that are somewhat in opposition to each other: to minimize disease transmission and to maximize social opportunities. Moreover, they acknowledge that the determining factor in a captive management plan is more likely to be prevention of disease transmission, inasmuch as there are fewer options to successfully achieve this goal than there are options available for meeting the social needs of the animals. They describe the SPF derivation strategy that was employed at their institution, which was an attempt to balance these two needs, as well as the procedures used to minimize pathogen transmission—use of personal protective equipment, and standardizing human “traffic” patterns within the colony, for example. Finally, Schapiro & Bernacky [2012] present the interesting idea that captive colonies may be useful for testing some ideas about disease ecology. For example, population densities are extremely high (for rhesus monkeys, they report densities of 9.3 animals/km² in the wild versus approximately 17,241 animals/km² in their colony), and the goal of maintaining pathogen prevalence at zero is never actually achieved. How do pathogens spread within groups? Are some group sizes/compositions more effective than others at controlling pathogen transmission? And what might be the unintended consequences of the sometimes heroic veterinary efforts made to save animals that get sick from a pathogen like *Campylobacter*? Any predisposing characteristics [whether genetic, immune, social, etc.] may not be selected out of the population, such as might occur in the wild. Schapiro & Bernacky [2012] remind us that primates in captivity still exist within an ecological setting and within a selection environment that has implications for disease processes.

Yet another approach to the issue of social processes and disease is represented by Willard and Shively's [2012] contribution. Senior author Carol Shively has been studying the behavioral and physiological consequences of social stress and social subordination on psychological, physiological, and physical health outcomes for two decades, with a particular interest in females. This research program highlights another potential cost of the social nature of nonhuman primates and focuses not on an infectious disease, but on a psychological one: depression. Their approach is an animal modeling one, and data are reviewed reinforcing the idea that depression involves dysregulation in a number of physiological systems. Their article also contains an important discussion of the existing (primarily rodent) models of depression, and some of the advantages and disadvantages of them. For example, rodent models commonly utilize males; Willard and Shively [2012] note, however, that depression is twice as prevalent in women compared to men, and the true menstrual cycle that female macaques possess (unlike rodents) provides an ideal model for studying the role of ovarian steroids in depression in women. Furthermore, while virtually all rodent models of depression involve experimental induction of stress to produce

the desired outcomes, social subordination is not the same thing as stress. Their data speak not only to the importance of the social environment, but also to the characteristics (personality, qualities of resilience, etc.) of the individuals in determining a disease outcome. The research described by Willard & Shively [2012] shows the value of using challenges that are more naturalistic in inducing the disease condition, and the power of the animal-model approach in identifying mechanisms by which the social environment can affect a disease process.

The final article in this special issue focuses on still another domain within the general topic of social processes and disease, and reflects the idea that nonhuman primate species exist within a broader world that includes other species with which they interact, a principal one being *Homo sapiens*. The authors, Gregory Engel and Lisa Jones-Engel, have been conducting research on cross-species transmission of infectious agents between humans and nonhuman primates for more than a decade. Their contribution to the symposium and to this special issue targets an interesting human population—attendees at the 2009 annual meeting of the American Society of Primatologists. Using questionnaire data, the authors sought to characterize the contexts and mechanisms that lead to exposure in this unique group. Their results indicate that, over a career, primatologists often work with multiple species of nonhuman primates in numerous contexts and diverse geographical locations. Many of the subjects (e.g., 49.0% who worked with rhesus monkeys) reported exposures, such as having been bitten or scratched, thought to have the greatest potential to transmit pathogens. Engel & Jones-Engel [2012] caution that, as they move between captive and field settings and work with multiple species, primatologists may link reservoirs of infectious agents, producing recombinant pathogens with enhanced pathogenicity. They also point out the potential for primatologists to act as conduits by which nonhuman primate pathogens could enter the human population. The growing interest in emerging infectious diseases, and the importance of protecting the health of both humans and nonhumans, has resulted in recent attention among field workers to adopting practices to actively reduce the chance of transmission events in either direction (see the many contributions in the special issue of the American Journal of Primatology (August, 2008, Volume 70[8]) on Disease Transmission, Ecosystem Health, and Great Ape Research). In this regard, the American Society of Primatologists made an early statement about the need to protect the health of wild primates (https://www.asp.org/society/resolutions/primate_health.cfm)

CONCLUSION

This is a very exciting time to be interested in the topic of social processes and disease for a number of reasons. First, there is now a substantial number of field sites that have been in operation for decades, and for which long-term data are available to test hypotheses in this area. Second, technological advances now provide investigators with tools, such as PCR (polymerase chain reaction), to identify and quantify pathogens quickly, cheaply, and accurately. Third, an explosion of information technology now puts investigators in touch with each other immediately, and permits development of databases and query tools that facilitate data sharing and collaboration on an unprecedented scale. Fourth, there has been a growing sophistication in our understanding of how different biobehavioral systems interact to affect the organism's functioning in the face of an attack by pathogens. The infected

individual's immune system will lead the charge, but we now know that that system is influenced significantly by the individual's psychological state, neuroendocrine milieu, and degree of social connectedness with others. Indeed, there is a growing interest in the molecular mechanisms by which the social environment "gets under the skin" of individuals to affect health [Miller, et al., 2011], both physical and mental. Fifth, and related to the previous point, there has been growing recognition that "one size does not fit all;" that is, the relationship between precipitating factors on the one hand (e.g., adverse early experiences, encounter with a pathogen) and physical or psychological disease outcomes on the other hand is often moderated by host factors, such as sex, genotype, and personality. In human medicine, this has been referred to as "personalized medicine," and parallel studies in nonhuman primates of moderated relationships involving, for example, personality and genotype, [e.g., Capitanio et al., 2008] fit easily within, and contribute to, this development in medicine. Sixth, there has been a greater awareness that the management of captive populations of nonhuman primates must focus not only on preventing disease, but must also attend to the social needs of these highly social animals. There are now many examples of how these two management goals can both be achieved. Finally, a common purpose seems to be developing between the seemingly disparate fields of conservation biology, emerging infectious disease, and public health—protecting the habitat of a nonhuman species often involves managing the encroaching human populations, and doing so effectively should reduce the risk of cross-species pathogen transmission.

Nonhuman primates are, for the most part, social, as are human primates. The study of social processes and disease within primatology, from the various perspectives described in this special issue, has something important to contribute to the study of similar phenomena within our own species. The reverse is true, as well, of course. It is important that individuals that are interested in similar phenomena, but from different perspectives, communicate with each other, because the resulting dialog can potentially further the goals of all.

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