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Forum Article

Does sanitation facilitate sociality?

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Living organisms produce waste products, the presence of which can handicap an individual's fitness, if they are not eliminated, either through attraction of predators or the promotion of disease. The simplest way of avoiding reduced fitness, effects of waste is by leaving it behind and moving on. However, for central place foragers and especially those living in social groups, the build-up of waste at a stable nest site presents a potential hazard. Problems associated with waste become especially acute when large group size makes waste accumulate in hazardous amounts. In human societies we know that certain diseases become commonplace when crowded populations exceed threshold amounts which facilitate the maintenance and transmission of pathogens (Wolfe et al. 2007). Living in a group is widely predicted to lead to increased parasitism and disease in animals (Poiani 1992; Schmid-Hempel 1998), but this prediction lacks firm empirical support partly because successful animal societies have solved the problem of waste control.

Most social animals have solved the problems of waste by depositing it directly in a dedicated place isolated away from the colony, or by removing waste from the colony as it is produced (Putman 1984). Intuitively we expect that such sanitary practices will enhance the health and success of colony members. Social living, despite its many benefits (Axelrod 1990), does not come without costs and maintenance of sanitation measures is expected to be time consuming. Health benefits of sanitation should exceed the time and energetic costs incurred for this practice to remain a viable component of a social lifestyle.

Before proceeding, we must draw the distinction between sanitation, which refers to practices conducted in the local environment that promote health by guarding against disease, and hygiene which concerns the promotion of health by personal care of the body. In our own societies sound sanitation practices and hygiene management strategies can reduce the risk of pathogen transmission, but when practices fail, the consequences can be serious. High and lethal occurrences of MRSA and other 'super bugs' in U.K. hospitals have been widely attributed to poor hospital sanitation and management practices (Rao 1998). To enhance sanitation we usually make use of disinfectants to eliminate viruses and bacteria and this practice is also found in animals, especially social insects. For example, the wood ant, *Formica paralugubris*, incorporates solidified coniferous resin into its nest to inhibit growth of both pathogenic bacteria and fungi effectively (Christe et al. 2003). Further hygienic or sanitary measures are used by insect societies to protect colonies from the spread of parasites and disease, for example grooming and avoidance.

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Hygienic behaviour and other highly sophisticated mechanisms that promote 'social immunity' have recently been reviewed by Boomsma et al. (2005) and Cremer et al. (2007). These practices are highly likely to have evolved after the transition to sociality and so cannot be considered as primary facilitators of social evolution. Instead, we contend that the bigger problem of waste management presented a major initial obstacle in the transition to social living. In this forum article we discuss the problems that waste causes for animals living in social groups and focus on the 'blind gut', a probable preadaptation found in the social hymenoptera that may have facilitated the transition to eusociality.

PROBLEMS OF WASTE AND WASTE MANAGEMENT

Digestive waste, unlike metabolic waste, typically has low toxicity but it can contain high levels of pathogenic viruses, bacteria, fungi and parasites, all of which are potentially hazardous to health (Weiss 2006). Animals must avoid continued contact with their waste after they have eliminated it into the external environment. In aqueous environments this is rarely a problem because of environmental dilution, but in confined or constrained aqueous environments disease can arise. For example, pathogens or parasites associated with waste are a major hazard for large-scale fish farming (Cusack & Cone 1986). For most terrestrial animals the obvious solution is to expel waste and move on. However, this may not be a simple option for groups, or even solitary individuals, if they feed on a fixed resource, such as leaf-mining caterpillars (Needham et al. 1928).

The problem of sanitation is much more serious for individuals living in social groups because high-density occupation of a central site means that waste can rapidly accumulate. Furthermore, waste takes up physical space that may be a limiting factor to increased success in enclosed nesting sites. In spider mites and aphids feeding on plant sap, the stickiness of their faeces creates mobility problems. To solve these problems, colony members of the social spider mite *Schizotetranychus miscanthi* always defecate at the same location within their nest (Sato et al. 2003). If the nest is manipulated so as to increase the likelihood of faecal contact then an increased mortality rate results.

Faeces are also known to be exploited by predators in prey location, and by parasites in host detection. Predators can rely on chemical cues to aid their search for prey (Vet & Dicke 1992), but Steidle & van Loon (2003) found that only 18.2% of specialist arthropod predators relied primarily upon faeces to locate their prey, while 10.5% of generalist species exploited faeces when locating prey. Parasites and parasitoids are more likely than predators to exploit faecal cues (Eller et al. 1988; Steidle & Fischer 2000; Steidle et al. 2001). Parasitic hymenopterans and dipterans are well known to exploit faecal volatiles as long-distance cues facilitating host localization (Lewis & Tumlinson 1988), while contact with host faeces often initiates a host-seeking response (Nordlund & Lewis 1985; Rogers & Potter 2002). The sciomyzid fly *Pherbellia cinerella* more frequently lays its eggs on substrates containing fresh faeces of its host, a terrestrial helicid snail (Coupland 1996). Host-searching behaviour in some entomopathogenic nematodes occurs solely through localization of host faeces (Grewal et al. 1993). Even the honeydew excreted as faeces by sap-feeding aphids is exploited as a host indicator by its parasitoid, *Aphidius nigripes* (Bouchard & Cloutier 1984).

The simplest method of eliminating waste build-up from a nest site is to dispose of it away from the nest. However, leaving the safety of a nest to defecate or dispose of other waste makes an individual prone to attack by predators or parasites, thereby negating a major benefit of living in an aggregation, that is, risk dilution. Many lepidopteran caterpillars occupy protective silken tents in large groups for all or part of their larval development. Caterpillars of the peacock butterfly, *Inachis io*, construct temporary tents on their food plant, where they consume the local vegetation, fouling their own tents before moving on to construct a new tent on a fresh foraging site (Bryant et al. 2000). In contrast, caterpillars of the eastern tent moth, *Malacosoma americanum*, produce a large central tent at the junction of tree branches, and constrain all defecation to the lower part of the nest (Dethier 1980). When this silken web 'latrine' becomes overloaded with faeces it detaches under its own weight and falls to the forest floor.

Animal groups that make a long-term commitment to a single nest site take much greater care to ensure good sanitation. The continuing presence of brood and waste in nests provides a suitable medium for proliferation of pathogens, and hosts for parasites (Schmid-Hempel 1998). Clutches of eggs deposited in ground burrows by Lesnei's earwig, *Forficula lesnei*, must be tended by their mother or they are rapidly destroyed by mould (Timmins 1995). Some social species possess specialized individuals that manage waste disposal. In gall aphids, *Pemphigus dorocola*, a specialized caste of the population collects faecal waste and dumps it outside the gall (Aoki 1980). Similarly many ant species include individuals that work on midden (refuse) piles processing waste (Hart & Ratnieks 2001). Other social insects are known to dispose of their waste in a dedicated chamber, such as the brood-tending social cricket *Anurogryllus* spp. (West & Alexander 1963). Members of mammalian societies, particularly subterranean rodents such as blind mole-rats, *Spalax ehrenbergi*, also dispose of their faecal waste in dedicated latrine chambers (Zuri et al. 1997).

In many animal societies waste is removed from nest sites, but a high workload of waste management is likely to be costly. We now consider the strategies that the hugely successful eusocial insect societies, termites and social hymenoptera, have evolved for dealing with waste.

EUSOCIAL SOLUTIONS TO WASTE MANAGEMENT

The most sophisticated societies are formed by the eusocial insects, with colonies of up to many millions of individuals. Clearly, we should expect that such large groups containing numerous overlapping generations of individuals will generate a vast amount of waste, and that its removal to ensure good health must have a major impact on colony labour demands. We can assume that adult workers in these colonies will defecate 'responsibly' away from the nest and many ants retain their solid waste in the infrabuccal pocket at the entrance to their pharynx, for later disposal by vomiting (Quinlan & Cherrett 1978). However, the biggest food consumers of the colony are the developing young being raised within the nest, and we might assume that they are also the biggest producers of waste. Here we consider this problem more deeply, because the problems of waste production and management for termites and social hymenoptera (bees, wasps and ants) are not as simple as they might first appear.

The special case of the nutritional economy found in termites means that they have solved the problem of waste in a unique way. Termites consume wood and acquire additional nitrogenous nutrients via proctodeal trophallaxis, presumably because their hindgut symbionts liberate nitrogen and these faecal exudates can then be shared with nestmates (Machida et al. 2001; Nalepa et al. 2001). Many termite species, especially the mound-builders, make use of their faeces in construction, which might be expected to create an environment favouring pathogens. However, termite faeces are very low in bacterial pathogens, a consequence of their unusually high gut alkalinity (pH 11–12.5), while control of the nest environment makes conditions unsuitable for fungal growth (Brune & Kuhl 1996). Furthermore, fungus-farming termites use their faeces to fertilize fungus gardens and in *Macrotermes* the nest architecture controls carbon dioxide levels in the nest to suppress