Available online at www.sciencedirect.com
SCIENCE DIRECT®

Behavioural Processes 68 (2005) 263–266

ELSEVIER

BEHAVIOURAL PROCESSES

www.elsevier.com/locate/behavproc

Commentary

Parasitic manipulation: a social context

David P. Hughes[a,b,*]

[a] *Department of Biology, University of Oulu, Oulu 90014, Finland*
[b] *Department of Zoology, University of Oxford, OX1 3PS, UK*

Received 15 September 2004; accepted 23 September 2004

Thomas et al. (2005) conclude their interesting review of parasitic manipulation in an optimistic tone and state that “the study of manipulation is far from being weak”. This serves as a timely antidote to Poulin’s sobering message of a Kuhnian type weakening paradigm (Poulin, 2000). This is not to say that the authors find fault with Poulin’s analyses, but rather they find reasons for optimism through their emphasis on multiple approaches, such as detailing proximate mechanisms of control (e.g. proteomics), insights through comparisons with broader behavioural ecological theories (Mafia Hypothesis), understanding the role of habitat on manipulating parasites (e.g. other parasites within the host and the host’s metapopulation), and intraspecific genotypic variation in the ability of parasites to control the hosts’ phenotype. Perhaps implicit in their interdisciplinary approach is the need for the parasite manipulator community to judiciously choose host–parasite systems which have the greatest potential pay-off in determining the factors underlying the expression and evolution of parasitic manipulators. There are a large number of candidate parasite taxa which manipulate the host behaviour (Moore, 2002) and in many cases substantial progress has been made in understanding the proximate mechanisms of control (e.g. Thomas et al., 2003). However, some hosts groups, which may have potential benefits, have been underexploited. With this in mind I would like to draw the reader’s attention to the potential of social insects (wasps, bees, ants and termites) as model systems in which to study parasitic manipulation of host behaviour.

The social insects can be seen as victims of their own success! Insect societies have long fascinated man as evidenced by their mention in the Bible “Go to the ant, thou sluggard; consider her ways, and be wise” (Proverbs 6:6). E.O. Wilson called them “among the great achievements of organic evolution” (1971:1). The occurrence of sterile workers presented Darwin with his “one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory” (Darwin, 1859). This difficulty was resolved by Hamilton (1964a,b), which led to a voluminous literature of diverse aspects of kin selection. Unfortunately this had been at the expense of understanding the behaviour of social insects in an ecological context, particularly with respect to parasites. In recent years there has been a change in direction and the role of parasites has received more attention (Boomsma et al., in press; Schmid-Hempel, 1998, 2001). However, the perspective has mainly been host centred and has largely ignored parasitic manipulation of host phenotype. This is somewhat ironic considering one of the most famous examples of manipulation is the change in ant behaviour by following infection by

---

[*] Tel.: +358 8 5531791; fax: +358 8 5531061.
E-mail address: david.hughes@oulu.fi.

doi:10.1016/j.beproc.2004.09.006

the ‘brainworm’ *Dicrocoelium dendtriticum* (Carney, 1969). Here ants infected by trematodes leave the colony and ascend blades of grass to which they attach themselves with their mandibles: this promotes trophic transmission to grazing definitive hosts (e.g. sheep). Despite being a very visible phenomenon with infected ants being common around ant nests (Manga-Gonzalez et al., 2001) it suffers from a lack of attention. It appears to me that while there are many examples of the manipulation of social insect behaviour by parasites they are largely anecdotal and have not been examined thoroughly. Or, where there is detailed work it is often by parasitologists or ecologists who have little dialogue with the social insect community. This is disturbing considering the model organism status of some social insects and the huge information available regarding their behaviour, physiology, morphology, population genetics and genomics which certainly facilitates Thomas et al.’s multidisciplinarian approach. Here I highlight the utility of social insects systems to examine parasite mediated changes in behaviour, as well as two recent examples.

Since the appearance of insect societies over 100 million years ago they have become the dominant animal members of almost all terrestrial habitats (Agosti et al., 2000; Tobin, 1991; Wilson, 1992). All social insect groups (technically eusocial) share three common features: (1) cooperative care of young; (2) reproductive division of labour with some more or less sterile individuals working on behalf of fecund individuals; (3) at least two overlapping generations (Wilson, 1971: 4). Because of their ecological dominance, the obvious parallels with our own society, and importance for kin selection theory, a great deal is known about the behaviour of social insects (Abe et al., 2001; Hölldobler and Wilson, 1990; Ross and Matthews, 1991; Seeley, 1995). For example: interactions between dominants and subordinates in the colony, between different castes, between adults and immatures, as well as behaviour away from the nest, particularly foraging behaviour and navigation. In many cases behaviour has been studied in the context of proximate cues such as glandular pheromones or cuticular chemistry of the individual (Vander Meer et al., 1998). Such a strong understanding of the behavioural repertoire and roles of colony members gives researchers of parasite manipulation a solid background against which to examine aberrant behaviour which may be result of parasitic manipulation. With some model systems such as the honeybee, *Apis mellifera*, active research avenues include understanding the neural, neuroendocrine and molecular basis of social behaviour (see Gene Robinson’s site http://www.life.uiuc.edu/robinson/index.html). Besides the molecular basis of social behaviour (Whitfield et al., 2002) the whole genome of the honeybee is currently being sequenced by the Human Genome Sequencing Centre (http://www.hgsc.bcm.tmc.edu/projects/honeybee). This gives researchers interested in studying proximate mechanisms of parasite manipulation in other social insects a very strong base from which to begin.

Additionally, social insects are, on the whole, amenable to laboratory study. This, in conjunction with the very large number of individuals in the colony and high relatedness among colony members facilitates repeated sampling of numerous individuals with a similar genetic background. In line with Thomas et al. (2005) attention to determining the cost of intraspecific variation in the manipulative process the ability to examine hosts with an almost identical genetic background would assist in determining how variable parasites of the same species are in their effect on host phenotype. Because of the interest in determining relatedness values among social insects there are a large number of genetic markers and within some groups the population genetics is well understood (Pamilo et al., 1997; Ross, 2001) which assists with the examination of parasitic manipulators within the context of the host’s metapopulation (Thomas et al., 2005).

There are drawbacks to social insects however (despite the obvious and painful one!). They are generally difficult to mate under laboratory conditions and have long generational times which means they are not suitable for selection experiments. Though, in some groups mating and even artificial insemination is possible (Baer and Schmid-Hempel, 1999, 2000).

In their review the authors state that “host–parasite systems in which the host exhibits a completely novel behaviour the causal connection between a parasitic effect and host behavioural change may be easier to establish”. Without wishing to be tautological, by their very definition social insects are social! Thus, aberrant behaviours whereby infected individuals (particularly workers) desert the colony are easier to see. There are a number of prominent examples of parasitized individuals leaving the colony and in most cases is believed to facilitate parasite life cycle completion: trematodes, cestodes, mermithid nematodes, *Cordyceps* fungi, conopid parasitoids and Strepsiptera. The last example, Strepsiptera, deserve special mention because they highlight the advances which can be made using social insects.

Strepsiptera (Insecta) are parasitic castrators which infect larval social insects and complete development in adult hosts (besides Hymenoptera they infect six other insect orders). Their presence in adult workers causes a distinct behavioural change where infected individuals do not work and actually desert the colony early in adult life which facilitates parasite life cycle completion (Hughes et al., 2004). Because their hosts (*Polistes* wasps) are so well studied the aberrant behaviour of parasitized individuals in the field was easily seen (wasps form extra-nidal aggregations where 98% of occupants are infected: first observed by W.D. Hamilton). It is cautionary to note that despite the huge amount of research into *Polistes* behaviour over the last 50 years (Turillazzi and West-Eberhard, 1996) this aberrant behaviour was not observed until 1998; and then not by someone researching studying *Polistes* behaviour! The ability to move from documenting the existence of aggregations and observing the behaviour of parasitized wasps in the field to a laboratory based study where larval wasps were infected owes much to the biology of Strepsiptera, in which the first instar is the host seeking stage. However, the background knowledge on *Polistes* and wealth of laboratory studies certainly assisted in examining this host–parasite system under controlled conditions. Indeed, before my own work Strambi and Strambi (1973) infected wasps and showed how the presence of the parasite resulted in neuroanatomical changes.

In contrast to the desertion behaviour which is relatively common, another striking example of behavioural change associated with parasitism deserves special mention. Honeybees following infection with the picorna-like virus, *Kakugo* become more aggressive (Fujiyuki et al., 2004). The name *Kakugo* is Japanese for ‘ready to attack’ and, using reverse transcriptase-real time PCR, these researchers found that the virus was only expressed within the mushroom bodies of infected bees and individuals which would attack a colony predator (a social wasp) were more likely to be infected. The adaptive value, to either party, of this change in behaviour is speculative but it is noteworthy that the rabies virus mentioned by Thomas et al. (2005) is also a picorna virus. Currently attempts are continuing to artificially infect bees, as well as screen wasps for the presence of this virus (T. Fujiyuki and T. Kubo, personal communication).

Whilst not all parasitic manipulators of social insects are so amenable to artificial infection as Strepsiptera there are good candidate taxa with which to proceed to elucidate the ontogeny, mechanisms and costs of parasitic manipulators. So why have parasitic manipulators of social insects not been the subject of more scrutiny? One probable reason is the attention placed on social behaviour in the context of kin selection. As I mentioned at the outset this is thankfully changing and there is an increasing focus on parasitism within the colony. Thus the time is ripe for members of the parasitic manipulation community to benefit from the advances made by students of social insect research. This of course would be reciprocal. Currently there is an attempt to construct a framework to examine how social insect life history affects the transmission and type of disease experienced by colonies (Boomsma et al., in press). Since colonies are generally heavily defended fortresses that are widely distributed (think of islands!), then parasite manipulation of individuals may facilitate horizontal transmission. For example an infected ant containing a gravid parasite may not only leave its colony but, by overcoming kin recognition cues, may be motivated by the parasite to gain ingress into another colony and like the ‘parasitized’ wooden horse of Troy, have serious consequences for its new home. This is of course highly speculative but does, I think, highlight the need for communication between social insect researchers and the parasitic manipulator community. Indeed, as the authors optimistically conclude, one of the advantages of studying parasitic manipulators is that “these little worms, tiny protozoa and viruses are . . . promoting communication among [disparate] groups”.

References

Abe, T., Bignell, D.E., Higashi, M. (Eds.), 2001. Termites: Evolution, Sociality, Symbiosis, Ecology. Kluwer Academic Publishers.

Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.E., 2000. Ants: Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institute Press.

Baer, B., Schmid-Hempel, P., 1999. Experimental variation in polyandry affects parasite loads and fitness in a bumble-bee. Nature 397, 151–154.

Baer, B., Schmid-Hempel, P., 2000. The artificial insemination of bumblebee queens. Insect. Soc. 47, 183–187.

Boomsma, J., Schmid-Hempel, P., Hughes, W.O.H., in press. Life histories and parasite pressure across major groups of social insects. In: Fellowes, M., Holloway, G., Rolff, J. (Eds.), Insect Evolutionary Ecology. CAB International.

Carney, W.P., 1969. Behavioral and morphological changes in carpenter ants harbouring dicrocoeliid metacercariae. Am. Midl. Nat. 82, 605–611.

Darwin, C., 1859. On the Origin of Species. John Murray, London (Chapter 7).

Fujiyuki, T., Takeuchi, H., Ono, M., Ohka, S., Sasaki, T., Nomoto, A., Kubo, T., 2004. Novel insect picorna-like virus identified in the brains of aggressive worker honeybees. J. Virol. 78, 1093–1100.

Hamilton, W.D., 1964a. The genetical evolution of social behaviour. I. J. Theor. Biol. 7, 1–16.

Hamilton, W.D., 1964b. The genetical evolution of social behaviour. II. J. Theor. Biol. 7, 17–52.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Harvard University Press.

Hughes, D.P., Kathirithamby, J., Turillazzi, S., Beani, L., 2004. Social wasps desert the colony and aggregate outside if parasitized: parasite manipulation? Behav. Ecol. 15, 1037–1043.

Manga-Gonzalez, M.Y., Gonzalez-Lanza, C., Cabanas, E., Campo, R., 2001. Contributions to and review of dicrocoeliosis, with special reference to the intermediate hosts of *Dicrocoelium dendriticum*. Parasitology 123, S91–S114.

Moore, J., 2002. Parasites and the Behavior of Animals. Oxford University Press.

Pamilo, P., Gertsch, P., Thoren, P., Seppa, P., 1997. Molecular population genetics of social insects. Annu. Rev. Ecol. Syst. 28, 1–25.

Poulin, R., 2000. Manipulation of host behaviour by parasites: a weakening paradigm? Proc. Roy. Soc. Lond. B 267, 787–792.

Ross, K.G., 2001. Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. Mol. Ecol. 10, 265–284.

Ross, K.G., Matthews, R.W., 1991. The Social Biology of Wasps.

Schmid-Hempel, P., 1998. Parasites in Social Insects. Princeton University Press.

Schmid-Hempel, P., 2001. On the evolutionary ecology of host–parasite interactions: addressing the question with regard to bumblebees and their parasites. Naturwissenschaften 88, 147–158.

Seeley, T.D., 1995. The Wisdom of the Hive. Harvard University Press.

Strambi, A., Strambi, C., 1973. Influence du développement du paraiste Xenos vesparum Rossi (Insecte, Strepsitere) sur le systéme neuroendocrinien des femelles de Polistes (Hyménoptère Vepside) au debut de leur vie imaginable. Archives D’Anatomie Microscopique et de Morphologie Expérimentale 62, 39–54.

Thomas, F., Adamo, S., Moore, J., 2005. Parasitic manipulation: where we are and where should we go? Behav. Process. 68, 185–199.

Thomas, F., Ulitsky, P., Augier, R., Dusticier, N., Samuel, D., Strambi, C., Biron, D.G., Cayre, M., 2003. Biochemical and histological changes in the brain of the cricket *Nemobius sylvestris* infected by the manipulative parasite *Paragordius tricuspidatus* (Nematomorpha). Int. J. Parasitol. 33, 435–443.

Tobin, J.E., 1991. A neotropical rain forest canopy ant community: some ecological considerations. In: Huxley, C.R., Cutler, D.F. (Eds.), Ant–Plant Interactions. Oxford University Press.

Turillazzi, S., West-Eberhard, M.J., 1996. Natural History and Evolution of Paper-wasps. Oxford University Press.

Vander Meer, R.K., Breed, M., Winston, M., Espelie, K.E. (Eds.), 1998. Pheromone Communication in Social Insects: Ants, Wasps, Bees, and Termites. Westview Press.

Whitfield, C.W., Band, M.R., Bonaldo, M.F., Kumar, C.G., Liu, L., Pardinas, J.R., Robertson, H.M., Soares, M.B., Robinson, G.E., 2002. Annotated expressed sequence tags and cDNA microarrays for studies of brain and behavior in the honey bee. Genome Res. 12, 555–566.

Wilson, E.O., 1971. The Insect Societies. Harvard University Press.

Wilson, E.O., 1992. Social insects as dominant organisms. In: Billen, J. (Ed.), Biology and Evolution of Social Insects. Leuven University Press, pp. 1–7.