

present arguing with referees and editors to try to get our papers into places where we hope they will be read. Eventually, this shouldn't be necessary. The problem is getting from here to there — it is not at all clear to me how and when this should happen most effectively.

**What do you think are the biggest challenges to the scientific community in the short/medium/long term?** I think we need to get out more. Science has become ghettoised. The pressures of the grant-publication-grant cycle are keeping people in their labs, talking to a very narrow range of people. Science is increasingly a disconnected and segregated activity. This situation has a lot of very negative consequences. Among them, the public becomes suspicious of science and innovation, delaying or preventing the adoption of science-driven solutions to societal problems; interesting synergies between unlikely partners are missed; and research careers look unattractive to the next generation.

There has been a lot of complaint in the community about the UK Research Council Impact Agenda, and the requirement to explain 'pathways to impact' in grant applications. People think it is about making us predict how our research might be applied in the future and/or making us do research that is immediately applicable. I disagree with this interpretation. I think it is about highlighting the imperative that science and scientists engage with a much wider range of people than is currently usually the case. This includes wider engagement with academia; the public, private and charitable sectors; and a range of general audiences. The current isolationism is giving the impression that science is some kind of special activity accessible only to the chosen few who think they are infallible. Science is a very creative and inclusive human thing, with tremendous power to improve life for everyone. If we can't reintegrate it with everything else, then its potential will be lost. So I think we should stop complaining and get out more.

Sainsbury Laboratory, University of Cambridge, Bateman Street, Cambridge, CB2 1LR UK.  
E-mail: [OL235@cam.ac.uk](mailto:OL235@cam.ac.uk)

## Quick guide

# Antiparasite behavior

Brian Gray, Anne C. Jacobs, Adrienne B. Mora, and Marlene Zuk

### What is antiparasite behavior?

Parasites are ubiquitous, and organisms have evolved a number of ways for dealing with parasitism. However, the traditional view of antiparasite defense is one steeped in host physiological responses, such as mounting an immune response. In contrast, antiparasite behavior is relatively understudied, despite being a particularly robust way for organisms to resist parasitism.

Antiparasite behavior is used to evade, kill, or otherwise avoid parasites. It is analogous to antipredator behavior, but unlike those behaviors, antiparasite behavior includes a variety of post-infective behaviors — actions animals can take to rid themselves of parasites, or mitigate the effects of parasitism — which take place only *after* an animal is infested by a parasite, rather than behaviors aimed at avoiding infection in the first place.

### Can you give me some examples?

Many animals display antiparasite behavior. Cattle avoid areas that are potentially infected with parasites, such as areas littered with feces that may contain worm larvae, and several species of birds counter the activities of brood parasites by rejecting parasitic eggs or deserting nests containing such eggs.

However, much of the available literature on antiparasite behavior is restricted to a small number of taxa. Such behavior has been best described in birds affected by brood parasites, and in mammals, especially primates and ungulates. Only recently have researchers turned their attention to describing similar behaviors in other taxa, and much remains to be discovered. For example, honeybees remove larvae infected with mites and bacteria from their hives to prevent the spread of the infection to the rest of the colony. European starlings line their nests with specific types of green

plant material to kill ectoparasites, a form of fumigation. Sticklebacks take advantage of the dilution effect by shoaling to reduce an individual's likelihood of being infected with ectoparasites, and a species of North American field cricket grooms extensively when exposed to the larvae of a lethal parasitoid fly, dramatically reducing the risk of death associated with infestation. Expanding studies to include a broader range of taxa is likely to yield exciting new insights into antiparasite behavior.

**How is this different from antipredator behavior?** Antiparasite behavior can be similar to the behaviors employed in avoiding predators — using camouflage, spending time in groups to take advantage of the dilution and selfish herd effects, and avoiding areas frequented by the predators/parasites. However, antiparasite behaviors may also differ substantially from antipredator behaviors; the two may even trade-off against one another, with particular behaviors that protect against predators increasing the likelihood of parasitism and *vice versa*. For example, when cattle congregate in groups, they often turn their heads in towards the center of the group. This helps protect their faces from biting flies, but reduces their ability to watch for predators.

Also, unlike predators, which kill their prey, many parasites depend on the continued survival of hosts. As such, hosts can utilize a number of post-infective behaviors, which may differ substantially from antipredator behaviors.

### What do you mean by post-infective behavior?

Post-infective behavior refers to anything an animal might do to reduce parasite load *after* being infected by a parasite. This might include grooming to remove attached ectoparasites, such as lice or ticks, ejecting parasitic eggs (in the case of brood parasitism), or moving to a warm place (for ectotherms) to generate behavioral fever and combat pathogens. In some cases, animals may self-medicate with plants or other antiparasitic compounds, which may be particularly effective against endoparasites. These behaviors are used by hosts to either reduce the number of parasites or somehow



Figure 1. Fur rubbing in capuchin monkeys. Capuchins use foliage and other plant material to anoint themselves with insect-repelling compounds. Image credit: Mary Baker.

compensate for the effect those parasites have on host fitness.

**There are ‘natural’ pharmacists out there? (And I thought I could only find those in hippie communes and on college campuses!)** Nature is full of surprises. For example, capuchin monkeys perform ‘fur rubbing’ with various items to prevent and treat parasitism (Figure 1). Plants rubbed through the fur are thought to ward off ectoparasites such as lice, mites, and ticks. Evidence suggests that millipedes are used for their defensive secretions, which have potent insect-repelling properties. These little critters are especially sought after during the rainy season, when mosquito vectors are most abundant. Some animals ingest materials to combat parasites. Chimpanzees swallow folded leaves whole, presumably to flush out intestinal worms; they also chew on plant stems, releasing a number of potentially antiparasitic compounds in the process.

Self-medication is not limited to charismatic megafauna. Wood ants often supplement their nests with conifer resin. The resin contains various antimicrobial compounds that protect conifers from pathogenic bacteria and fungi. The addition of resin has been shown to decrease the density of harmful bacteria and fungi in ant nests. Furthermore, wood ants infected with these pathogens exhibited higher survival rates when their nests were enhanced with conifer resins. And as recently reported in this journal by Tom Schlenke and colleagues, *Drosophila melanogaster* larvae self-medicate with ethanol when infested by parasitoid wasp larvae. Ethanol is typically toxic to insects, including parasitoids, but

*Drosophila* larvae have evolved resistance to lower concentrations of ethanol, enabling them to utilize alcohol as an effective antiparasitic compound.

**Is this like those videos of monkeys and apes picking fleas off of one another?** That’s one form of antiparasite behavior — in this case, allogrooming. Allogrooming — grooming between conspecifics — is a common form of parasite removal, used by everything from impala and penguins to ants and bees. However, it is important to note that grooming in at least some animals may also serve other functions, such as facilitating social interactions.

#### **So why does this matter?**

Antiparasite behavior is important in ecology and evolution for a number of reasons. The presence of parasites can alter host population size, structure, and geographical distribution. The use of behavior to resist and mitigate the effects of parasitism comes at a cost to animals, leading to potential trade-offs against other host behaviors that are crucial for survival and reproductive success, such as foraging, mate choice, and predator avoidance.

As a result, antiparasite behaviors may also be important for conservation because they can help susceptible animals survive even in the face of new and deadly infections. For example, Hawaiian birds are particularly vulnerable to avian malaria. Since the arrival of malaria, these birds have changed some of their behaviors in ways that may help them avoid being bitten by mosquitoes and infected with the disease. They have changed their posture when they sleep, keeping their heads tucked under their wings and one leg pulled up under the feathers to protect bare, featherless patches of the body. They also spend nights at higher elevations, where there are fewer mosquitoes, and travel down slope during the day when mosquitoes are less active. These behavioral changes may help these endangered birds survive in the face of this new threat.

Studying antiparasite behaviors can better inform conservation efforts in other ways, too. For example, habitat loss and

fragmentation can prevent animals from accessing medicinal plants used to prevent and treat parasitism. In knowing which plants are crucial for wildlife health, reserve managers can restore areas with these pharmaceutical species. Moreover, some animals migrate, seek refuges, or shift habitat use in response to parasites, and managers need to consider such movements when setting aside habitat for conservation. Finally, some researchers have suggested that plasticity in antiparasite behavior may provide invasive species with a foothold in their introduced ranges by enabling such species to avoid paying the costs of antiparasite behavior when released from parasitism.

#### **Can behavior play a role in coevolutionary arms races?**

Certainly. In coevolutionary arms races, hosts evolve to minimize the impact of parasitism, and parasites evolve new ways to get around host defenses. Given the growing number of examples of antiparasite behavior utilized by hosts, we expect to find an increasing number of documented cases of coevolution of parasites to avoid host behavioral defenses.

Surprisingly, only a few cases of this have been reported. One example is the nose botfly, which deposits its larvae in the noses of deer and has to carefully stalk its prospective hosts. Deer confronted with the flies will protect their noses, and so the fly remains concealed until the last possible moment so as not to elicit a host defensive response.

Another example involves larval worms, which use various strategies to transport themselves away from piles of feces. Potential hosts frequently avoid foraging in fecally contaminated areas to steer clear of parasites. In one notable case, lungworm larvae launch themselves away from dung piles atop fungal spores, a strategy that may help the larvae reach locations where they are more likely to encounter new hosts.

Despite the examples mentioned above, surprisingly little work has been done on this topic, and the literature contains very few described examples of parasite counter-strategies. One place we particularly expect to see parasite counter-strategies is in the use of medications. Human medicine has

struggled for years with parasites that evolve resistance to commonly used drugs. Why should it be any different in animals? Yet as far as we know, no study has ever looked at whether parasites become resistant to the chemicals in the plants that hosts use for protection, though in the *Drosophila* example referenced above, ethanol did not negatively affect larvae of specialist wasps as strongly as larvae of generalist wasps. Exploring how parasites do or do not gain such resistance would be useful, both for people interested in animal behavior and in human medicine.

Finally, humans depend on both the ability to defend against parasites, especially in terms of human and agricultural health, as well as the *lack of current ability* to defend against parasites. The latter is critical in the use of biological control — the use of natural enemies to control pests, especially in agriculture. Many of these natural enemies are parasites or parasitoids. Biological control can be an effective and safe method of pest management, and may reduce or eliminate the need for chemical pesticides. However, understanding how pest species may evolve to resist parasitism is critical for successful implementation of biological control.

#### Where can I find out more?

- Castella, G., Chapuisat, M., and Christe, P. (2008). Prophylaxis with resin in wood ants. *Anim. Behav.* 75, 1591–1596.
- Clayton, D.H., and Wolfe N.D. (1993). The adaptive significance of self-medication. *Trends Ecol. Evol.* 8, 60–63.
- Daly, E.W. and Johnson, P.T.J. (2011). Beyond immunity: quantifying the effects of host antiparasite behavior on parasite transmission. *Oecologia* 165, 1043–1050.
- DeJoseph, M., Taylor, R.S.L., Baker, M., and Aregullin, M. (2002). Fur-rubbing behavior of capuchin monkeys. *J. Am. Acad. Dermatol.* 46, 924–925.
- Hart, B.L. (1990). Behavioral adaptations to pathogens and parasites: five strategies. *Neurosci. Biobehav. Rev.* 14, 273–294.
- Hughes, D.P., and Cremer, S. (2007). Plasticity in antiparasite behaviours and its suggested role in invasion biology. *Anim. Behav.* 74, 1593–1599.
- Milan, N.F, Kacsoh, B.Z., and Schlenke, T.A. (2012). Alcohol consumption as self-medication against blood-borne parasites in the fruit fly. *Curr. Biol.* 22, 488–493.
- Moore, J. (2002). *Parasites and the Behavior of Animals*, (Oxford: Oxford University Press).
- Schmid-Hempel, P. (2011). The natural history of defences. In *Evolutionary Parasitology*, P. Schmid-Hempel, ed. (Oxford: Oxford University Press), pp. 52–97.

Department of Biology, University of California, Riverside, 900 University Ave, Riverside, CA 92521, USA.  
E-mail: [briang@ucr.edu](mailto:briang@ucr.edu)

## Primer

### Sex determination

Tony Gamble and David Zarkower

Multicellular animals are a diverse lot, with widely varied body plans and lifestyles. One feature they share, however, is a nearly universal reliance on sexual reproduction for species propagation. Humans have long been fascinated by human sex differences and formal theories on how human sex is determined date at least to Aristotle (in *De Generatione Animalium*, ca. 335 BCE). However, it is only in the past couple of decades that the genetic and molecular programs responsible for generating the two sexes have been understood in any detail. Sex, it turns out, can be established by many very different and fast-evolving mechanisms, but often these involve a conserved class of transcriptional regulators, the DM domain proteins.

#### Making sexes: determination and differentiation

Sexual reproduction in multicellular animals requires, at a minimum, male and female gametes. Indeed, these specialized haploid cells are how we define the sexes: in a given species individuals with big gametes are females and those with small gametes are males. Individuals that can make both kinds are hermaphrodites, and may be self-fertile or cross-fertile with other individuals. Gametes in most animal species are made in a specialized organ, the gonad. Before sexual reproduction can take place, sexual development must occur. That is, a mechanism is needed to decide which sex a given embryo will adopt — sex determination — as well as mechanisms to control subsequent development of those parts of the embryo that differ between sexes — sexual differentiation. The final result is individuals that can differ remarkably not just in their gametes and gonads but in many aspects of their anatomy, physiology, and behavior — think of the tail of the male peacock, milk production in female mammals, or the courtship rituals of the male bowerbird. Even though these sexual

dimorphisms are essential to the propagation of the species, they can be so extreme that in some cases it is difficult to recognize that their bearers are in fact members of the same species. Some sexually dimorphic traits are essential for reproduction or have obvious benefits to reproductive fitness. However, many sexually dimorphic characters seem antithetical to natural selection, which greatly troubled Darwin (“The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!”). The prevalence of these seemingly disadvantageous traits led to Darwin’s second great insight, the theory of sexual selection based on “the advantage which certain individuals have over other individuals of the same sex and species solely in respect of reproduction,” proposing that these traits provide a competitive advantage in mating. In thinking about the molecular basis of sexually dimorphic traits and how they evolve it helps to be mindful of the distinctive selection mechanisms shaping them.

#### Many paths lead to sexual dimorphism

Despite its near universality, sex determination is controlled by quite different mechanisms in different species. Broadly speaking, sex can be determined two ways: genetically (genotypic sex determination or GSD), where the chromosomal composition determines an individual’s sex at fertilization; or environmentally (environmental sex determination or ESD), where conditions encountered during development determine an individual’s sex. These two categories can be further subdivided based on the precise mechanisms involved. In some GSD species, for example, the male is the heterogametic sex, that is, the gender with two different sex chromosomes. This includes the familiar XX/XY sex-determining mechanism in humans and other mammals where the presence of a Y chromosome initiates male development. Alternatively, as in birds, snakes and butterflies, the female can be the heterogametic sex; this is termed a ZZ/ZW system.

Just as GSD is composed of several distinct mechanisms, ESD can involve a variety of