

that one sees with comment sections in the social media. There is no clear definition of who a peer is or should be. It could be a well-trained colleague or it could be a proponent of intelligent design. Papers do get discussed and critiqued in journal clubs and over coffee conversations after they are published — that may not be a formal process, but it is livelier.

Any strong views on social media and science? For the most part, I find social media a distraction and waste of time. It is full of opinions rather than facts, and a lot of bogus leads. There are of course exceptions, but finding good blogs is like looking for needles in a haystack. Of course, blogs can be powerful because they sometimes expose problems that peer reviews might miss. I do worry that the profusion of journals and blogs is serving to elevate the ‘noise’ and making it harder to find papers of substance. This makes even scientists prone to the ‘post-truth’ era.

Which aspect of science would you wish the general public knew more about? I wish the general public knew just how much fun science is, and how wrong is the general view that science is the domain of a few eggheads who have learned a lot of facts. My specific field, in my own (biased) opinion, is fun because it allows me to operate seamlessly between my lab and the outdoors. It makes science that much more exciting to be able to see organisms in their natural context — in my case, insects flying to find food or mates, or guarding territories, or just going about their daily business. I crafted my entire research program around locally observed fauna for that very reason. I also wish that the general public recognised that science is imperfect — but that is what makes it so powerful. Wisdom, as Socrates recognised, is to know that you don’t know. Being a scientist has taught me that the more you find out, the more you discover about what you did not know. I love that process of generating new questions!

Insect Flight Laboratory, National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore 560065, India.

E-mail: sane@ncbs.res.in



Quick guide Staphylinids

Joseph Parker

Staphyli-what? Staphylinids! If more palatable, you can call them ‘rove beetles’.

Thanks! So, what are rove beetles? Rove beetles are the most species-rich and ecologically diverse beetle family. They can generally be distinguished by their short elytra (hardened wing cases) and exposed dorsal abdomen, but their morphology varies dramatically between taxonomic groups (Figure 1). Their body size spans two orders of magnitude (0.5–50 mm; most are between 2–8 mm). A familiar example is the Devil’s Coach Horse beetle (*Ocypus olens*), a large, conspicuous European species that has made its way to the US (Figure 1A).

How many species are there? At a first approximation, rove beetles are life on earth: over 61,000 described species makes the Staphylinidae the largest family of the largest order (Coleoptera) of the largest class (Insecta) of the largest phylum (Arthropoda) of the largest kingdom (Animalia). Far more species no doubt await discovery. When biologists try to predict the total number of species on earth, staphylinids, along with groups like weevils, parasitoid wasps and nematodes are one of the great unknowns. Sift some rainforest litter, or visit a museum collection and browse the unidentified beetles. You will find new staphylinids. Their species richness and abundance in the tropics is staggering, and they remain diverse and ecologically predominant beetles throughout temperate regions.

Impressive, but why have they been so successful? Their innovative body plan probably helped catalyze their diversification. The staphylinid abdomen is usually elongate with flexible, telescoping segments — a snake-like morphology that allows efficient movement through litter and soil. Crucially, the flight wings fit underneath the short elytra via a remarkable space-saving pattern of

folds, so staphylinids retain the capacity to disperse on the wing, increasing the chances of speciation. Down in the dirt, the family has diversified explosively, living mostly as predators that hunt invertebrates. Today, staphylinids dominate the forest floor, but their body plan has conferred an adaptive flexibility to gain footholds in a huge number of other niches, further enhancing diversification. Apart from litter, habitats include fungi, vertebrate nests and dung (in the case of *Amblyopinus*, rodent and marsupial fur, where they live as mutualists preying on ectoparasitic arthropods), waterside and intertidal areas (*Brachypronomaea esakii* is known from temporally submerged coral reefs, while *Liparocephalus* can survive immersed in seawater for more than two weeks), under bark, in and on plants and trees (the first truly phytophagous species, *Himalusa thailandensis*, was recently discovered), in deep soil (*Leptotyphlus* and *Mayetia* are minute, slender, eyeless and depigmented for subterranean life), and in caves (including blind, long-legged troglomorphic species like *Texamaurops reddelli*, one of only a handful of beetles on the US Endangered Species List). Some, such as *Aleochara*, are ectoparasitoids of other insects, and numerous groups thrive as symbionts inside colonies of ants, termites and even hornets. Two staphylinid species occur on South Georgia, a subantarctic island that marks Earth’s southernmost limit of beetle life.

So, a global beetle superpower then — do they use chemical weapons? Yes. Evolution of the soft, exposed abdomen may have been an Achilles’ heel for staphylinids, leaving them vulnerable to attack, so many lineages have evolved abdominal defensive glands. Irritants such as iridoids, quinones and acids may be sprayed or smeared on potential predators, but the arsenal of synthesized compounds is vast and largely uncharacterized, with complex chemistry tailored to the ecology of each species. Members of *Stenus* (Figure 1K) have a unique chemical defence: some can walk on water, and glands at the abdominal tip exude stenusine, a molecule that disrupts the surface tension, propelling the beetle



Figure 1. Rove beetle diversity.

(A) *Ocyopus olens* (Staphylininae, UK; credit: Warren Photographic). (B) *Paederus* sp. (Paederinae, Singapore; credit: M. Yeo). (C) *Phanolinus pretiosus* (Staphylininae, Venezuela; credit: N. Rahmé). (D) *Lomechusa sinuata* (Aleocharinae) licked by the ant *Formica lemni* (Japan; credit: T. Shimada/Antroom). (E) *Aenictocupidus jacobsonorum* (Aleocharinae, Malaysia; credit: T. Shimada/Antroom). (F) *Aenictus aratus* ants with how many *Aenictocupidus* beetles? (credit: T. Shimada/Antroom). (G) *Micropeplus hiromasai* (Micropeplinae, Russia; credit: K.V. Makarov, zin.ru). (H) *Syndicus jaloszynskii* (Scydmaeninae, China; credit: Z-w Yin/Zootaxa). (I) *Ogmocerodes navigator* (Pselaphinae, Cameroon; credit: Z-w Yin/G. Cuccodoro). (J) *Lordithon bicolor*, head extended beyond prothorax (Tachyporinae, Russia; credit: ME Smirnov, zin.ru). (K) *Stenus comma* (Steninae, Germany; credit U. Schmidt).

across the water surface away from predators at up to 70 cm/s (*Stenus* also have adhesive, protrusible mouthparts that are fired at prey). Groups less reliant on chemical defence often have

physical protection, such as a thick, armoured cuticle, compaction/fusion of abdominal segments, evolutionary re-gain of long elytra, or an enlarged prothorax that protects the head

(Figure 1G–J). The latter is exaggerated into a large shield to withstand host aggression in many rove beetles that live as symbionts with social insects.

Tell me more about these social insect symbionts! Ants and termites are the usual targets: this lifestyle – myrmecophily or termitophily – manifests itself as social parasitism, where the rove beetle profits from colony resources without providing much, if anything, in return. This way of life has led to the evolution of intricate and intimate symbioses. The best studied example is the myrmecophile *Lomechusa*, a sophisticated nest intruder with multiple abdominal glands that secrete compounds that worker ants lick, duping them into feeding the beetle (Figure 1D). *Lomechusa*'s eggs are laid in brood chambers where larvae are raised by the workers, and preferentially fed over the ants' own offspring. The genera *Claviger* and *Adranes* are so dependent on ants that their eyes and wings have evolutionarily degenerated; they are fed by workers, gaining their hosts' acceptance again by employing chemical trickery. Striking anatomical mimicry has also evolved numerous times: some termitophiles have a grotesquely swollen 'physogastric' abdomen that appears termite-like; 'myrmecoid' ant mimics, with narrow-waisted (petiolate) abdomina and long legs, live with army ants, marching with them over the tropical forest floor. Look at *Aenictocupidus* (Figure 1F) and see how many of these beetles you can spot among the *Aenictus* army ants in Figure 1E. Such close resemblance may confer tactile mimicry, so the beetles can socially interact with hosts. Relationships with social insects are so widespread that staphylinids provide a paradigm for exploring the evolution of complex interspecies symbioses, and the repeated evolution of this lifestyle again probably stems in part from the staphylinid body plan. The exposed abdomen has fostered the evolution of various kinds of glands, and can evolve into mimetic shapes.

Are staphylinids of economic or biomedical importance? Several species, such as the Greenhouse Rove Beetle (*Dalotia coriaria*), are effective biological control agents of

crop pests. More generally, staphylinid predominance in many habitats implies an important functional role in contributing to ecosystem services. Their high diversity in intact habitats, and the capacity of many species to colonize new areas and withstand disturbance means the family is increasingly used as an indicator taxon of ecosystem health. The unexplored chemical cache of staphylinids also makes the beetles a prospective source for novel biomedical compounds. A promising candidate has come from the aposematically-coloured *Paederus* (Figure 1B), a genus harbouring haemolymph bacteriocytes that synthesize Pederin, a dermatitis-causing polyketide that also has potent antitumor properties. *Stenus*-derived stenusine exerts antimicrobial effects, a further role of staphylinid glandular secretions that may be widespread, and warrants exploration.

Where can I find out more?

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Department of Genetics and Development, Columbia University, New York, NY 10032, USA, and Division of Invertebrate Zoology, American Museum of Natural History, New York, NY 10024, USA.
E-mail: jp2488@columbia.edu

Correspondence

Current desires of conspecific observers affect cache-protection strategies in California scrub-jays and Eurasian jays

Ljerka Ostojčić^{1,*}, Edward W. Legg¹, Katharina F. Brecht^{2,5}, Florian Lange^{3,6}, Chantal Deininger³, Michael Mendl⁴, and Nicola S. Clayton¹

Many corvid species accurately remember the locations where they have seen others cache food, allowing them to pilfer these caches efficiently once the cachers have left the scene [1]. To protect their caches, corvids employ a suite of different cache-protection strategies that limit the observers' visual or acoustic access to the cache site [2,3]. In cases where an observer's sensory access cannot be reduced it has been suggested that cachers might be able to minimise the risk of pilfering if they avoid caching food the observer is most motivated to pilfer [4]. In the wild, corvids have been reported to pilfer others' caches as soon as possible after the caching event [5], such that the cacher might benefit from adjusting its caching behaviour according to the observer's current desire. In the current study, observers pilfered according to their current desire: they preferentially pilfered food that they were not sated on. Cachers adjusted their caching behaviour accordingly: they protected their caches by selectively caching food that observers were not motivated to pilfer. The same cache-protection behaviour was found when cachers could not see on which food the observers were sated. Thus, the cachers' ability to respond to the observer's desire might have been driven by the observer's behaviour at the time of caching.

California scrub-jays (*Aphelocoma californica*) and Eurasian jays (*Garrulus*

glandarius) served as model species for the current study. Both species are known to engage in a variety of cache-protection strategies [1–4,6,7] and both have previously been shown to be able to disengage from their current desire in order to cache food they will desire at the time they will retrieve their caches [8,9]. Thus, both species would appear to have the pre-requisites necessary to employ a cache-protection strategy that is sensitive to another's desire.

A cache-protection strategy sensitive to an observer's desire is only beneficial if the observer's current desire influences its pilfering behaviour. Thus, in a pilfering experiment we manipulated the jays' desire by pre-feeding them a particular food to induce a decreased desire for the pre-fed food (specific satiety). After pre-feeding, jays could observe a human hiding food in a caching tray before being able to access that tray. The jays participated in three trials, each on a separate day. A baseline trial in which jays were pre-fed a maintenance diet (MD) revealed an average preference for pilfering food A over food B (see raw data in Table S1 in the Supplemental Information). A direct comparison between the two test trials (jays pre-fed food A or food B) showed that this preference was influenced by the observers' specific satiety: the preference for pilfering food A over food B relative to the baseline was smaller after jays had been pre-fed food A than after they had been pre-fed food B ($n = 16$, permutation test, $Z = -2.61$, $p < 0.001$, Cohen's $d = 0.833$, Figure 1A). Thus, observers pilfer according to their current desire such that it would be beneficial for cachers to cache less of the food that an observer is most motivated to pilfer.

In the caching experiment, cachers and observers were tested in adjacent compartments. In the seen condition, cachers first witnessed observers being pre-fed a particular food and could subsequently cache both test foods in a caching tray. A baseline trial (observer pre-fed MD) revealed an average preference for caching food A over food B (Table S2). A direct comparison between the two test trials (observer pre-fed food A or food B) showed that this preference

