

cairostris (Cuvier's beaked whale) and *Mesoplodon densirostris* (Blainville's beaked whale).

The authors find that both of these species undertake long, deep dives to capture deep-water prey. Diving is highly regular with most deep foraging dives being followed by an extended period of shallow dives and slow travel and resting near the surface. All foraging dives of both species are considerably longer than the estimated aerobic dive limits, suggesting that the whales return to the surface with an oxygen debt.

"We propose that the shallow dives and the long periods in between foraging dives are needed to repay the oxygen debt before the next deep dive", the authors report.

Another consistent feature of the dive profiles, the authors find, is the slow ascent from the deep foraging dives, which remains a puzzle. The long ascents, which are acoustically inactive but involve active

swimming, appear to divert substantial time away from foraging, suggesting that the animals are constrained by some physiological requirement or behavioural need that prevents them from optimizing foraging performance.

The depths now found at which these whales forage may also throw light on the effects of naval sonar activities. Mass strandings of whales associated with sonar activity have revealed animals with gas and fat emboli in their bodies.

The researchers consider whether sonar may disrupt the ascent after deep dives and that "the observed pathologies may follow from a behavioural response that has adverse physiological consequences".

They argue that regardless of the precise reason for whale strandings, "it is a pressing issue to develop effective mitigation protocols to reduce the accidental exposure to sonar".

Quick guide

Social-insect fungus farming

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Which social insects rear their own food? Growing fungi for food has evolved twice in social insects: once in new-world ants about 50 million years ago; and once in old-world termites between 24 and 34 million years ago [1,2]. The termites domesticated a single fungal lineage — the extant basidiomycete genus *Termitomyces* — whereas the ants are associated with a larger diversity of fungal lineages (all basidiomycetes). The ants and termites forage for plant material to provision their fungus gardens. Their crops convert this carbon-rich plant material into nitrogen-rich fungal biomass to provide the farming insects with most of their food (Figure 1). No secondary reversals to the ancestral life style are known in either group, which suggests that the transitions to farming were as drastically innovative and irreversible as when humans made this step about 10,000 years ago.

Why is insect fungus farming interesting? The two independently evolved agricultural systems are impressive examples of mutualistic symbiosis — reciprocally beneficial relationships between different species. Some of the insect societies that evolved fungus farming are pinnacles of social evolution. Cooperation and social evolution within families is now fairly well understood from kin selection theory [3], but we are only beginning to understand the direct and indirect evolutionary benefits of cooperation between unrelated individuals of different species [4].

What factors stop such cooperative efforts from being corrupted by cheating mutants



Mysteries: Tagging experiments have revealed the extreme depths and durations of dives by two little-known species of small-beaked whales but many questions remain. (Photo: courtesy of Nick Tregenza.)

that reap the benefits without paying the costs? Active partner choice, conditional partner fidelity and host sanctions towards non-cooperative symbionts have been suggested to be crucial factors that help defend against such cheats, and there is at least some evidence from other mutualisms to support these suggestions [5]. All these traits vary in fungus-growing social insects, making them good model systems for studying cooperation and conflict. Also, we now know that the ant–fungus symbiosis includes at least two further parties: a genus of specialized fungal parasites that attack fungus gardens; and specialized cultures of mutualistic bacteria that the ants rear on their own bodies to produce antibiotics against this disease [6]. Recent studies have provided evidence for varying degrees of coevolution between these mutualistic and parasitic lineages [7,8].

Starting a fungus farm: collecting spores from the wild or inheriting your parent’s crop? A young queen of a fungus-growing ant species takes a small clonal fungus fragment from her natal nest along on her mating flight, and uses this to start her own fungus garden in the newly founded colony. Some evolutionarily derived fungus-growing termites have a similar system of vertical symbiont transmission by a single parent, but in most species the first fungus garden is established from environmental spores on the first substrate structure in the centre of the nest. This horizontal mode of symbiont transmission should make it much easier to exchange crops between termite lineages, but for some reason these ‘hop-overs’ rarely happen between genera [2]. In fact, the genus-level symbiont specificity in fungus-growing ants and termites is rather similar, because sexual reproduction (symbiont fruiting) and horizontal exchange also happen within genera of fungus-growing ants [9,10].

Figure 1. Two clades of eusocial insects have evolved fungi farming for food: the old-world macrotermite termites (top, *Macrotermes bellicosus*; photo courtesy of Jacques Renoux) and the new-world attine ants (bottom, *Atta cephalotes*; photo courtesy of David Nash).

Fungus-growing termites eat unripe mushroom-like structures (the white nodules on the picture) that contain asexual spores. These spores mix with the consumed plant substrate in the termite gut and are deposited with the feces on top of the fungus garden. Gardens thus consist mostly of solid ‘fungus comb’ constructed from primary feces, which later gets consumed entirely. In fungus-growing ants all fruiting and spore production is suppressed. Here the symbiont is propagated vegetatively from the older bottom to the newer top of a fungus garden. During this process, small fragments of substrate are added to the mycelial ridges together with fecal droplets that stimulate mycelial growth of the resident symbiont. The same droplets react antagonistically towards genetically different fungal symbionts from neighboring colonies that foraging workers might bring in.



Why is it important and interesting to know these symbiont transmission modes? Although the fungus-farming symbioses are clear examples of advanced obligate mutualism — reciprocal cooperation for direct fitness benefits to each of the parties — the reproductive interests of the insects and their fungi are not the same. The insect farmers have no interest in their symbiont allocating resources to growing mushrooms for horizontal spore transmission. Similarly, the fungal symbionts have no interest in farmers producing sexual offspring rather than workers that can provide them with more substrate [11,12]. Furthermore, an established fungus garden has no interest in a competing strain becoming established, even though the insect farmers would possibly benefit from a genetically more variable crop. These reproductive conflicts play a role in the daily life of social insect farmers: leaf-cutting ants are known to actively suppress symbiont fruiting in lab colonies

[13], and resident fungal clones express mycelial incompatibility reactions to eliminate introduced fungal strains [14].

These conflicts can be understood from levels of selection theory. Both parties gain fitness by cooperating for the common good, but they are also individually selected to express selfish traits when the fitness benefits to be gained exceed the ensuing losses in group-level fitness [15]. A major unanswered question is why termites with horizontal symbiont transmission do not suppress fungal fruiting in the same way as ants and termites with vertical symbiont transmission do. Such a parasitic trait would have an immediate colony-level advantage, whereas there would hardly be any colony-level cost since neighboring colonies would produce the fungal spores that the offspring of these cheating farmers need [12].

Do reproductive conflicts threaten the evolutionary stability of fungus farming

or are they resolved? Both the ants and the termites cultivate their fungal crops in monocultures. This is remarkable, because there is ample genetic variation of fungal strains across colonies so that horizontal transmission should at least occasionally (in the ants) or regularly (in most termites) establish genetically variable fungus gardens. In the ants, monocultures are actively enforced because fungal incompatibility compounds hitchhike through the ant guts to be expressed in the feces that fertilize new implants of somatic fungal fragments [14]. The termites, however, propagate their symbionts within colonies by asexual spores that they embed in newly deposited fecal substrate. This system is therefore expected to produce symbiont monocultures by a combination of genetic drift and selection for rapid spore formation, rather than by active competition via incompatibility compounds [11,12].

Can we learn something from the sustainable farming practices of insect societies?

The farming insect societies had tens of millions of years of natural selection to solve many of the challenges that are also well known to human farmers. They have conveyor belt substrate processing, produce their own pesticides and antibiotics, and practice active waste management [1]. Neither the ants, nor the termites, however, have been able to overcome the fundamental laws of host-symbiont conflicts, which imply that only monoculture farming is evolutionarily stable. Our own farming practices evolved culturally by frequent exchange of crops, learning and copying innovative practices. The problem is that, on the larger scale that we apply today, many of these practices are unlikely to be sustainable, even on an ecological time scale. It may be, therefore, that further research on the long-term evolutionary stable farming systems of the ants and termites may provide useful

lessons for our own future food production.

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The difference between organelles and endosymbionts

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Three recent contributions in *Current Biology* [1–3] have addressed new findings on the classical cyanobacterial endosymbiont of *Paulinella chromatophora*, but refer to the endosymbiont as a ‘plastid’. Yoon *et al.* [2] even opine that *Paulinella* “has the honor of being the only known case of an independent primary (cyanobacterial) plastid acquisition.” Others have called the *Paulinella* endosymbiont a “photosynthetic organelle” [4] instead.

Endosymbionts are organisms that live within other organisms. Many endosymbionts are obligate — they cannot live outside their hosts [5] — as also reported for *Paulinella chromatophora* [2]. And many obligate endosymbionts are essential for their hosts as well [5], for example *Buchnera aphidicola*, which supplies amino acids for its aphid host [6].

Plastids, such as mitochondria, are not endosymbionts; they are organelles. They once were endosymbionts, but they now are double membrane-bounded organelles, compartments of eukaryotic cells.

All of the functional proteins in the cytosol of an endosymbiont are encoded by its own genome. By contrast, only a very small fraction of the proteins that function in organelles are encoded by organellar DNA. The majority of organellar proteins are encoded by the nuclear DNA, translated on cytosolic ribosomes and imported into the organelle with the help of a protein import apparatus [7,8].