This is the peer reviewed version of the following article: *Ruxton, GD, Humphries, S,* ***Morrell, LJ*** *& Wilkinson, DM. (2014) Why is eusociality an almost exclusively terrestrial phenomenon? Journal of Animal Ecology 83: 1248-1255*, which has been published in final form at dx.doi.org/10.1111/1365-2656.12251. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

JAE: forum

Why is eusociality an almost exclusively terrestrial phenomenon?

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Summary

1. Eusociality has evolved multiple times across diverse terrestrial taxa, and eusocial species fundamentally shape many terrestrial ecosystems. However, eusocial species are far less common, and have much less ecological impact, in aquatic than terrestrial environments.
2. Here we offer a potential explanation for these observations. It appears that a precondition for the evolution of eusociality is the defence and repeated feeding of offspring in a nest or

other protected cavity, and so eusocial species must be able to exploit a predator-safe, long-lasting (multigenerational) expandable nest. We argue that a range of factors mean that opportunities for such nests are much more widespread and the advantages more compelling in terrestrial than aquatic ecosystems.

Keywords: sociality, social insects, ants, termites, shrimp

Introduction

Ants dominate many terrestrial ecosystems: for example, it is estimated that in the Brazilian Amazon there is approximately four times more ant- than vertebrate-biomass (Hölldobler and Wilson, 1994). In many systems other social insects, such as termites, can be just as dominant. Given the key role ants and other social insects play in terrestrial systems, the absence of eusociality from almost all aquatic habitats is at first glance surprising. Also surprising is the observation that this key difference between terrestrial and aquatic ecosystems has received very little discussion in the scientific literature. Here we begin to rectify this omission by speculating on why eusocial species are so rare in aquatic systems.

Defining eusociality and describing its prevalence and importance in terrestrial environments

Eusociality, broadly defined, is characterised by cooperative brood care, overlapping adult generations and division of labour by reproductive and (sometimes partially) non-reproductive individuals (Andersson 1984). Eusocial insects in particular have been conspicuously successful across diverse terrestrial habitats since at least the late Mesozoic (Hölldobler and Wilson, 2009).

For example ants are found on all continents except Antarctica; and only a few large islands such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species (Lach et al. 2010). Ants occupy a wide range of ecological niches, and are able to exploit a great diversity of food resources: either as direct or indirect herbivores, predators, or scavengers. Their ecological dominance can be measured by their biomass, and estimates suggest that they contribute 15–20% (on average and nearly 25% in the tropics) of the total terrestrial animal biomass, which exceeds that of all the vertebrates (Lach et al 2010). Given that Grime (1998) and others have argued that species that dominate a community's biomass control the main fluxes of matter and energy through that system – such insects are likely of great importance in many terrestrial ecological processes. More than 12,000 species of ant are currently known (with upper estimates of the potential existence of about 22,000); all these species are eusocial (Hölldobller and Wilson 1990).

All the termites (Isoptera) are also eusocial (Andersson 1984). Ten per cent of the estimated 4,000 species (about 2,600 taxonomically known) are economically significant as pests that can cause substantial damage to buildings, crops or plantation forests (Pearce 1997). Globally, termites are found roughly between 50 degrees north and south, with the greatest biomass in the tropics and the greatest diversity in tropical forests and Mediterranean shrublands. They are major detritivores, particularly in subtropical and tropical regions, and their recycling of wood and other plant matter – aided by microbial symbionts - is of considerable ecological importance (Turner, 2004). As detritivores, termites clear away leaf and woody litter and so reduce the severity of the annual bush fires in African savannas; which are not as destructive as those in Australia where termite densities are lower (Milewski et al. 1994). Termites are also considered to be a major source (11%) of atmospheric methane, a key 'greenhouse gas' (Rasmussen & Khalil 1983); and their biomasses in many tropical regions are comparable to those of ants (Milewski et al. 1994).

The 250 species of bumblebee (*Bombus* spp) and approximately 500 species of stingless bees (tribe Meliponini) are all eusocial, as well as the 7 species of honeybees (*Apis* spp; Roubik 1989). Together these species are considered fundamental to pollination networks in many diverse natural ecosystems, as well as providing essential pollination services to 20-30% of all global human agriculture (Abrol 2012). Among the wasps, eusocial species include the 1100 species of the paper-wasp subfamily *Polistinae*, the 24 hornet species of the genus *Vespa*, and the "yellow-jackets" (23 species of the genus *Vespula* and 20 species of the genus *Dolichovespula*; Hoell et al. 1998). Their ecological importance is less obvious than those of bees, termites and ants; but they can certainly exist at sufficient local densities to be agricultural pests, especially to soft fruit production (Edwards & Archer 1980); and may also be ecologically important predators of some other invertebrate insect pests. This distribution of eusociality across the bees and wasps suggests at least 11 separate evolutionary origins of eusociality in this group (Crozier & Pamilo 1996).

As well as these ecologically important insect groups, eusocially has evolved independently several other times in terrestrial environments. Amongst mammals, the burrow-living naked mole rat *Heterocephalus glaber* and Damaraland mole rat *Fukomys damarensis* are eusocial; these two species are generally considered to involve independent evolutionary adoptions of eusociality (Jarvis & Bennett 1993). Two species of Australian gall-making thrips have also be demonstrated to be eusocial (Crespi 1992), as have some gall-making aphids (Tanka & Ito 1994). Colonies of the Australian weevil beetle *Austroplatypus incompertus* excavate and live in tunnels in living wood and have recently also been demonstrated to be eusocial (Kent & Simpson 1992). Finally, the spider *Anelosimus eximis* lives in colonies of several thousand individuals within a silken nest and shows strong evidence of eusociality (Vollrath 1986).

Hence, eusociality has evolved multiple times across diverse terrestrial taxa, and eusocial species have also powerfully shaped many terrestrial ecosystems.

The prevalence and importance of eusocial species in aquatic environments

The overwhelming majority of the aquatic realm is marine, and marine insects are conspicuously uncommon: there are over one million living insect species, but only about 1400 live in marine habitats. Within this group, only 46 species (all gerrid skaters) inhabit the surface of the seas that cover the majority of the surface area of the earth and of these, no more than five are completely oceanic (Andersen & Cheng 2005). Since the overwhelming majority of eusocial terrestrial species are insects, the scarcity of fully aquatic insects is one potential explanation for the lack of eusociality in aquatic ecosystems. However, this scarcity of aquatic insects need not lead to rarity of eusociality. Eusociality occurs in other groups (as discussed above) including aquatic crustaceans (as we discuss directly below). There are thought to be over 50,000 species of crustacean (Margulis and Chapman, 2009), of which most are aquatic but very few (three species, all belonging to the "gambarelloides group" within the same *Synalpheus* genus) have become eusocial.

In 1993, Spanier et al. published a paper entitled "Why are there no reports of eusocial marine crustaceans?" In fact, at that time there were no records of eusocial organisms of any kind in any type of aquatic habitat. We should point out that there are a great many colonial aquatic animals (such as the sponges, ascidians, cnidarians and bryozoans) but these all lack the cooperative brood care that is characteristic of eusocial species. Such coloniality provides the potential for kin selection to be important in marine environments (Kamel and Grosberg, 2013), making it even more noteworthy that eusociality is so rare in the seas. Spanier et al. argued that it was plausible that at least some marine crustaceans might be eusocial, and urged marine biologists to explore this possibility. Soon afterwards, their suggestion was confirmed in obligate sponge-living shrimps of the genus *Synalpheus* (Duffy 1996). Eusociality seems to have evolved at least three times in the *Synalpheus* genus of around 100 described species (Duffy et al. 2000). Specifically, the three species known to be eusocial (*S. regalis*; *S. filidogitus*, and *S. chacei*) are not closely related, and phlogenetic reconstructions of life history strategies in this genus suggest that all three evolved eusociality independently (Duffy et al. 2000). The genus *Synalpheus* is one of the most species rich genera of tropical crustaceans and is present across coral reef faunas worldwide (Chace 1989). Most of the described species form specific and obligate associations with sessile invertebrates (mostly sponges and crinoids) and feed either on host tissue or microalgae and detritus (Duffy 1998). Since the 'nest' of most *Synalpheus* colonies is a living sponge, the size of the colony must be limited by the dimensions of the host. The shrimps must only harm the host in a limited way, since the colony requires host survival over several shrimp generations; so the ecological impact of the shrimp colony must be less than that of the host. These factors impose severe constraints upon the ecological impact of the crustacean compared with any eusocial species that can build its own nest. Hence the three known aquatic eusocial species have modest ecological impact compared with many of the terrestrial eusocial groups discussed in the last section.

Since the discovery of sponge-dwelling eusocial shrimps, no further reports of eusociality in any other aquatic species have emerged. It seems likely that eusocial species are less common in aquatic environments than in terrestrial environments (that is, very few aquatic species are eusocial), and even more likely that eusocial species have much less ecological impact on aquatic environments than terrestrial environments due to small biomass densities. Below we offer a potential explanation for these observations.

Can the paucity of eusocial species in aquatic environments be explained by physical factors?

Many previous studies (Andersson 1984, Alexander et al. 1991 Spanier et al. 1993, Crespi 1994, Wilson 2008; Nowak et al. 2010; Wilson, 2012) have argued that a critical (necessary but not sufficient) precondition for the evolution of eusociality is the defence and repeated feeding of offspring in a nest or other protected cavity, and so a eusocial species must be able to exploit a predator-safe, long-lasting (multigenerational) expandable nest. Such nest sites are a consistent feature of all the terrestrial examples of eusociality discussed earlier and are also used by the eusocial shrimp discussed in the previous section. All three eusocial shrimp species have an obligate association with a host sponge in which they live.

In this section, we suggest that physical differences between air and water (and thus between terrestrial and marine environments) are likely drivers of the relative lack of eusociality in water. One key difference is that the much greater density of water gives in much greater inertia and momentum than air. Another difference relates to the generally reduced oxygen availability in water. The high heat capacity of water means that temperature fluctuations are much less rapid and much less extreme than in terrestrial ecosystems. Finally, water absorbs light much more readily than air and so sunlight penetrates only into shallow and surface waters. Each of these issues will be picked up and developed in this section.

We suggest that these issues combined mean that availability of suitable nest sites for eusocial organisms is much more constrained in aquatic than terrestrial environments. Some evidence consistent with this comes from the *Synalpheus* eusocial shrimps where “virtually all suitable host sponges are occupied in the field” (Duffy et al. 2000), suggesting an extreme shortage of suitable nest sites for these species.

We first consider the consequences of the greater density of water. One general consequence of this is that a given volume of water has greater inertia and momentum than air, and so moving water can apply greater forces to objects such as nests. Secondly, objects are much more buoyant in water; and one consequence of this is the greater mobility of aquatic sediments, which can impact on nest building.

The two eusocial mammals, together with many termites and ants make large and complex nest structures in the substrate that last over multi-generational timescales. This is more difficult in aquatic substrates than terrestrial substrates for two reasons. Firstly, aquatic substrates that are soft enough to burrow in are less cohesive and more prone to collapse, particularly in the absence of investment in animal–derived coatings – generally silk or mucous - to the walls of tunnels (Hansell 1984; 2005; Wildish & Kristmanson 1997). Secondly, at larger scales marine and lotic freshwater sediments are more mobile than terrestrial ones, and thus a burrow in such aquatic environments is more vulnerable to either being destroyed by bulk movement of substrate or buried too deep by the same (Wildish & Kristmanson 1997; Little 2000; Herring 2002).

An alternative to a substrate-burrowed nest is the use of a self-created nest such as those of many eusocial wasp species. Again, there are several challenges to these in aquatic environments. In deepwater environments, the biomass of potential food for the eusocial species is concentrated in the upper sunlit layer (except in unusual situations like hydrothermal vent communities), where there will be no solid substrates to attach a self-created nest to (Herring 2002). Some deepwater marine species do construct structures larger than themselves: most famously the houses of larvaceans. However, these mucous houses are fragile and short-lived (Hansell 1984). There is no naturally-secreted or easily-collected substance that would allow a notional open-water species to construct a nest that was simultaneously strong enough to deter predatory attacks and close enough to the density of water to allow it to maintain its depth in the water column over timescales relevant to juvenile development (Hansell 2005).

Nest construction by fish is an uncommon but taxonomically widespread phenomenon whose occurrence is not confined to particular ecological niches (see Barber 2013 for a review). But here, nests only survive for a short duration: unlike many avian nests, previous nests are not reused for subsequent breeding attempts. Further, active maintenance to avoid physical damage or burial of the nest is often a very substantial cost to nesting in fish, and likely explains its uncommonness (Jones & Reynolds 1999; Olsson et al. 2009).

In tube-living polychaete worms, the tube is made of calcareous crystals set in an organic matrix; and (in contrast to fishes' nests) this provides a durable structure that can survive long after the death of its builder. However, this type of construction can only be expanded relatively slowly and at considerable energetic costs by adding additional material to the end, rather than by remodelling. Specifically, Dixon (1980) argued that a need to move up the tube during ontogenic growth means that the tube can often end up being four times the length of the worm inside. Dixon (1980) also estimated that the worm devotes 68% of its energy production over its lifetime to tube construction, compared to 20% to somatic growth and 12% of gamete production; and so tube worms have a very slow life history strategy. This argues that such rigid structures would not be effective homes for eusocial species that benefit from the ability of colonies to grow rapidly to take advantage of temporal variation in food availability, but require a home that can expand to accommodate such rapid growth.

In shallow-water environments, it might be theoretically possible to site a self-created nest on a rigid structure in the substrate. However, construction of a self-created structure like a paper wasps' nest would be difficult because of the much greater likelihood of rigid structures buckling due to lateral pressure from bulk movement of water than air (because water is a factor of a 800 times denser; Denny 1993). Clearly, breaking waves in shallow marine waters and bulk transport of water in lotic systems would be a huge challenge to the structural integrity of any such nest (Denny 1988). Based on these physical arguments, "stand alone" self-constructed nests seem practical nowhere except perhaps shallow water margins of still-water lakes. But here except in very unusual circumstances, winds can produce strong turbulence causing substantial sediment movement (Denny 1988). Also such shallow waters can experience very strong seasonal variation in physical factors (compared to larger, deeper bodies of water), making them a more challenging environment in which to make a permanent home in (Williams 2006). Finally, these areas are often characterised by soft, unstable silt-like substrates that are difficult to build on because times of low water movement allows the settling of fine particles.

A large constructed nest has great potential to attract predators and may be difficult to conceal. It can be protected by being inaccessible, structurally impregnable and/or by behaviour defence by the inhabitants. Wasps' nests, for example, may be protected by all three of these. Hanging the wasps' nest from a tree renders access difficult for ground predators; but the enhanced buoyancy of water around a nest may rule out this kind of protection. As previously discussed, an outer protective cover through a tough carton-like material may not be possible in water. As for a standing army of inhabitants, many crustacea (for example shrimp, crabs and lobsters) are certainly able to defend themselves at an individual level, so that does not appear to impose an obvious evolutionary constraint. Hence the greatest evolutionary impediment to self-made structures for a putative marine social species is likely to come from risk of mechanical damage rather than predation.

Another alternative for nesting is to use already-existing cavities; again this is likely to be more difficult in aquatic systems. Bumblebees generally use burrows made and subsequently abandoned by rodents; however as argued above, such burrows would quickly collapse in aquatic sediments without constant investment. For example, many marine organisms (such as the variety of species collectively known as mud-shrimp) construct sometimes elaborate burrows in soft sediment. However, burrow maintenance involves substantial time and energy costs (Stamhuis et al. 1997) that are only sustainable for such creatures because maintenance can be combined with foraging activity (Stamhuis et al. 1996); this would not hold for structures created primarily for protection of the young in a eusocial species. Mud shrimp burrows quickly collapse in the absence of regular maintenance, allowing burrow openings to be a reliable means of population estimation. Living and dead woody plants also offer cavities to (for example) honeybees. However, whereas terrestrial vegetation commonly invests in lignin to give structural strength to resist wind, aquatic 'plants' (both true plants and other groups such as brown algae) generally are flexible; and so living or dead aquatic 'plants' do not offer woody material that is suitable for extensive burrowing (Niklas 1988). At a smaller scale, the tendency of aquatic plants to be compliant in the face of currents and waves may even make small structural cavities within plants such as the galls found in many terrestrial plants less attractive homes in aquatic than in terrestrial environments. Although such structures might structurally survive the plant being whipped around by breaking waves, any animals inside the cavities would be subject to extreme accelerations and decelerations, and damage through being thrown into each other and the walls of their nest seems likely (Denny 1988) . The only wood that might offer tunnelling opportunities in aquatic systems will be dead wood from terrestrial origins that has fallen into water bodies and come to rest on substrates with the correct properties to avoid the wood sinking so deeply into the substrate that it becomes inaccessible to potential burrowers. Cracks in rocks offer effective homes to many ants, and the same might be true for a notional aquatic eusocial species. However, again the higher movement of soft sediments in aquatic environments acts against this, and many otherwise suitable crevices in rocks will fill more readily with soft sediments in aquatic environments than terrestrial cavities, animal-excavated ones would be in constant danger of refilling or even being entirely buried in bulk transport events. Solid rough surfaces are readily available at least in the intertidal and immediately subtidal zones, provided by shelled creatures such as oysters and barnacles, whether these are living or just their remaining shells; but these niches are prone to periodic loss in storm events.

Another relevant physical aspect of aquatic ecosystems driven by the higher density of water than air may be buoyancy. Firstly, this may reduce the need for nest building generally in aquatic ecosystems because it makes it much less expensive for adults to carry their offspring on their body even to advanced stages of development. Secondly, buoyancy may reduce the likelihood of evolution of eusociality specifically, since the buoyancy of water makes broadcast dispersal of very early stage organisms much more prevalent in aquatic than terrestrial systems, this life history strategy of broadcasting very early stages is at odds with the retention and long-term care of offspring that is central to eusociality.

In addition to the mainly structural challenges described so far, large underwater nests may be difficult to maintain because of the challenges of delivering fresh oxygen at a sufficient rate to the nest. Oxygen diffuses much more slowly through water than air (Denny 1993), and free convection is less powerful. Free convection, the tendency for which is defined by the Grashof number, depends on density gradients, most often resulting from temperature differences. Water has a very much lower thermal expansion coefficient than air, so ventilation driven by free convention is much less of a feature of aquatic than terrestrial systems (Denny 1993). Further the costs of ventilation by active pumping are orders of magnitude higher in water than in air (Vogel 1994). One way round this may be to position the nest to take advantage of natural water currents for ventilation, as some burrow-living fish do (Hansell 1984); but (for small organisms especially) the greater potential for structural damage through water than air currents may argue against this solution. Another simple solution is to be tolerant of hypoxia. However, there is strong evidence from a range of burrowing aquatic species that although they can survive periods of hypoxia, such conditions curtail the levels of activity required for burrow construction and maintenance (Weissberger et al. 2009). Before leaving the subject of temperature, we mentioned at the start of this section that temperature fluctuations are less rapid and less extreme in aquatic habitats. This may be very relevant for the relative uncommonness of nesting in aquatic ecosystems: the lack of need in the aquatic environment for the types of nest structures that protect terrestrial species from temperature fluctuations may largely eliminate an important selection pressure that might otherwise promote nest building.

Another key difference between air and water mentioned at the start of this section was light penetration. Huge volumes of the marine and even freshwater habitats experience insufficient sunlight for photosynthesis and therefore, with minor local exceptions like hydrothermal vents, have no primary productivity. Consequently fixed aquatic plants are limited to shallow water areas. However, water is not just a supportive medium but a nutritive one, so primary productivity can occur in the upper, light penetrating waters across whole oceans. These features have two important habitat consequences. Firstly, many aquatic habitats are structurally simpler than many heavily vegetated terrestrial ones. There may be a shortage of 'tangled bank' habitats compared with terrestrial habitats to promote species diversity and provide opportunities for the evolution of eusocial lifestyles. Secondly, vast areas of open water provide not simply a medium for dispersal or migration but also, unlike air, a feeding ground. As a result, open water is a medium for the development of immature or larval stages (e.g. many crustaceans) or of whole life cycles (e.g. pelagic fish). In other words it offers an evolutionary incentive for offspring to leave home or for organisms not to have a home at all, both rendering the evolution of eusociality less likely.

From our previous arguments, the most suitable environment for a notional eusocial aquatic organism will be within a relatively stiff living organism with a complex structure offering crevices to act as a nesting site for our focal species. Living examples of the host organism will be more attractive than dead examples, because they likely have some ability to combat sediment build-up in crevices, and mechanisms promoting relative water movement potentially providing increased local oxygen availability. The host-organisms should also be long-lived relative to the focal eusocial one (since a single nest site must survive long enough to support several generations of the eusocial species). We see all these criteria met in the sponges utilised by the only known aquatic eusocial species already discussed. Shrimps of the genus *Synalpheus* form colonies in sponges, and each shrimp species inhabits a different sponge species, making *Synalpheus* one of the most diverse crustacean genera. Eusociality has evolved several times within this group, which is the main group of organisms with a strong association with sponges. The living host will generally require substantial water movement around and through it, in order to feed on suspended material; and this may benefit eusocial lodgers in terms of oxygen (and potentially food) delivery, and avoiding sediment built up in cavities. However, we may also find tension with the living host: significant water movement may make water-borne chemical communication by the eusocial species much more difficult by flushing water-borne signals before they are detected by nest-mates, and may even potentially be powerful enough to expel members of the eusocial species. Chemical communication is extensively used within social insect nests and is also the most common form of communication among the crustaceans (Breithaupt & Thiel 2011). Sponges can produce currents of the order of 0.2 ms^{-1}, often pumping their own volume of water every five seconds (Nickel 2004).

Discussion

In the preceding section we have argued that the apparent extreme scarcity of eusocial aquatic organisms arises because differences in the physical properties of air and water make finding, or making, suitable nesting sites for a eusocial colony more challenging in aquatic environments; and reduce some incentives for investing in nest construction. However, we should also acknowledge that other factors may also be important. The overwhelming majority of eusocial species are arthropods, and (even considering that terrestrial species have been more extensively studied) there is greater species diversity of arthropods in terrestrial than aquatic environments (Brusca & Brusca 2003). Hence, phylogeny may be an important factor, although the two eusocial mole rat species demonstrate that eusociality is not restricted only to the arthropods. Food supply may also be a factor, eusociality clearly requires spatial aggregation of individuals that will need a substantial local food supply, and it may be that as a generality that the nature of food availability in many aquatic habitats (generally characterised by more spatially defuse primary productivity than terrestrial systems) discourages aggregation. However against this argument colonial organisms thrive in aquatic environments (as previously discussed) and aggregations of organisms is not uncommon (consider the shoaling tendencies of many fish). Clearly vast expanses of macro algae or sea grass *Zostera* spp beds also provide high biomasses of potential food for aquatic species with a leaf cutter ant like lifestyle.

Our argument above that physical aspects of water make nest building more challenging and less advantageous for eusocial species should also apply to non-eusocial species – and indeed nest building does seem more prevalent amongst terrestrial species (see survey in Chapter 1 on Hansell 1984). We argue that this might be for two separate but non-exclusive reasons – relative shortage of suitable nest sites and relative shortage of nest materials. The relative importance of these two factors is unclear. Lower levels of vegetation in aquatic systems likely contribute to both these factors, but their relative importance will likely vary between different aquatic habitats. We note that *Synalpheus* species, which contain the only eusocial aquatic organisms, do not appear to use materials to build anything, but depend entirely upon microhabitats provided by the structure of another organism for nesting.

We should be clear that we consider the ability to exploit a protected nest site appears to be a necessary pre-condition for the evolution of eusociality. In this we have reached a similar conclusion about the key role of the nest to recent – controversial – ideas on the evolution of eusociality (Nowak et al, 2010; Wilson, 2012), albeit by rather different arguments. However, a large nest is certainly not a sufficient condition. For example, many social mammals have large and complex nesting burrows that survive over multi-generational timescales, but only two burrowing mammalian species are eusocial.

We should also consider the plausibility of a notional amphibious eusocial species that builds its nest in a terrestrial environment but forages in an aquatic environment. This might seem plausible in (for example) mangrove habitats, and ants can be common in such habitats; however this life-history tactic is not known for any mangrove species, and only seen in one known species with a very specialist foraging niche. The unusual foraging mode of that species is insightful as to the rarity of amphibious ants. The ant *Camponotus schmitizi* lives in symbiosis with the Bornean pitcher plant *Neptnthus bicarata*. Ants regularly dive and swim in the pitcher's digestive fluid to forage for food, on their foraging trips they repeatedly enter and leave the fluid apparently unrestricted by surface tension forces. However, Bohn et al. (2012) showed that ants become stuck on the surface of pure water, and their behaviour in the fluid of pitchers is only possible because that fluid contains plant-produced detergents that lower surface tension. As a generality, eusocial species appear relatively small-bodied, and surface tension makes breaking through the surface of water a greater challenge for smaller organisms (that have a proportionally greater surface area in comparison to their weight and the propulsive power they can generate) (Denny 1993). Small body size in eusocial animals might well be related to the need to fit multiple adult individuals into the protective nest, thus the limitation imposed by surface tension may be important generally in explaining the extreme rarity of amphibious eusocial insects. Many insect species have an aquatic juvenile stage and an aerial adult stage, and thus must overcome surface tension once in their lifetime when they emerge from that water. However, if such emergence is costly in energy and/or time, then these costs can be more easily borne once in a life-time than repeatedly as they would have to be by a notional amphibious eusocial species.

While the two eusocial mammals show that eusociality is possible at body-sizes that would make overcoming surface tension a trivial challenge, other factors may argue against an amphibious eusocial lifestyle. One such factor may be that eusociality requires the production of cheap workers and the unit cost of workers is much greater if they have a physiology that can deal with the two very different environments in air and water (e.g. in terms of respiration, water balance, communication mechanisms and sensory systems). In fact, many ant species exploit terrestrial ecosystems like mangroves where their nests are periodically engulfed by rising water levels. Such species survive by nest design and/or behaviours that limit water penetration into the nest, sometimes combined with the ability of foraging ants to return safely to the nest by swimming across the water surface (reviewed in Nielsen 1977). However these should be considered as aspects of flooding tolerance, rather than exploitation of the aquatic zone; since there are no reported cases where such ants collect food from the water. The fire ant *Solenopsis invicta* can make rafts out of their own bodies that allow migration events across the water's surface that can last many months (Mlot et al. 2011); however again this adaptation to flooding should be seen as a lifeboat mechanism, and the ants do not feed until they return to the terrestrial substrate. More generally the ability to cope with the different physical regimes of air and water likely explains why amphibious lifestyles are relatively uncommon across the animal kingdom, and in this context there being only one example of an amphibious eusocial species is unsurprising.

Conclusion

The near absence of eusociality in aquatic systems is a striking but often-overlooked ecological difference between terrestrial and aquatic habitats. We feel that it can be explained through a combination of physical properties of water than are markedly different from those of air. In addition, asking why there are no aquatic 'ants' provides a useful thought experiment; the results of which might usefully inform our understanding of the evolution and diversity of terrestrial eusociality, and the evolution of building behaviours in aquatic environments.

Acknowledgement

We thank Mike Hansell and another anonymous referee for very helpful comments.

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